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Temporal variation of species distribution and species morphological traits along altitude in the Alps

Ph.D. Dissertation

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Introduction

Mountain habitats support some of the world's most rare and fragile ecosystems (Diaz et al. 2003, Pauchard et al. 2009) and they are very sensitive to environmental changes and global warming (Beniston 2003, 2006, Huber et al. 2005).

In particular, the Alps exhibit an impressive variety of habitat and climatic conditions often along reduced spatial scales, originated by a complex of physical and biological interactions, as well as forged by a long history of human presence and exploitation (Chemini and Rizzoli 2003). This extraordinary variability results in high species diversity with heterogeneous communities adapted to various environmental and climatic factors that gradually change from foothills to the high alpine areas (Viterbi et al. 2013, Fernandes et al. 2016). Thus, the Alps are considered a biodiversity hot-spot (Villemant et al. 2015) that contain high level of endemic and specialized species that live close to the limits of their physiological tolerances (Dirnbock et al. 2011, Viterbi et al. 2013).

Alpine ecosystems are mainly determined by low temperatures and are therefore considered to react sensitively to climate warming (Gottfried et al. 2012, Pauli et al. 2012). Furthermore, higher mountain areas are threatened by land abandonment (Hinojosa et al. 2016) with the consequential loss of open habitats caused by forest regrowth and tree line upward shift (Gehrig-Fasel et al. 2007, Tasser et al. 2007, Pellissier et al. 2013). The pure or combined action of these factors might have negative direct effects on the distribution of animal and plants (Parmesan and Yohe 2003, Mantyka-pringle et al. 2012). Habitat alteration and climate warming might generate other adverse processes, like higher predation rate (Melendez and Laiolo 2014, Prop et al. 2015), higher competitive pressure (Gifford and Kozak 2012), increase of physiological stress (Barbosa et al. 2007), reduction in food supply (García-González et al. 2016) and phenological changes (Møller et al. 2008, Thackeray et al. 2016), exacerbating the already known negative scenario (Nogués-Bravo et al. 2007, Sekercioglu et al. 2008).

As a response, species changed and are still changing their distributional ranges in elevation (Maggini et al. 2011, Reif and Flousek 2012, Baur and Baur 2013).

Ranges size is a fundamental criterion for determining when a species faces a heightened risk of extinction (Sekercioglu et al. 2008) and estimates of changes in range distribution are used regularly to predict extinctions due to habitat loss or climate change (Thomas et al. 2006).

Population size and range size are typically strongly linked (Brommer 2008), suggesting that a shrinking range is likely a proxy of the population decline.

Even basic, but nonetheless essential, information on species distributions along altitudinal gradients is scarce (Chamberlain et al. 2016). In the last decades some studies pointed out the shift in species' altitudinal ranges (Lenoir et al., 2010; Lenoir & Svenning, 2015) but less researches focused on high-altitude habitats (Chamberlain et al. 2012) despite their fragile and vulnerable conditions (Dirnbock et al. 2011, Chamberlain et al. 2013).

The main reason is the undoubtedly logistical constraints of carrying out rigorous monitoring schemes in such challenging environments (Chamberlain et al. 2012). However, the altitudinal transect approach is an important and useful tool for understanding potential climatic effects on species distribution. Altitudinal gradient, compared to latitudinal gradient, allow for investigating the relationships between species distribution and abiotic/biotic parameters on a reduced spatial scale, where complications involving broader-scale biogeographic processes, evident in geographic distribution studies, are largely avoided (Rahbek 2005). Moreover, altitudinal gradients are particularly appropriate to investigate species distributions because they allow for covering different belts along the vertical zonation of the vegetation patterns.

To gain a comprehensive understanding of biodiversity distributional patterns, the comparison of elevation trends between taxa and between different mountain contexts is crucial (Lomolino 2001). Furthermore, studies at different time resolutions are essential for forecasting future changes on species distributions (Dornelas et al. 2012). There is therefore a need to quantify the distribution of species groups along altitudinal gradients (Roth et al. 2014, Chamberlain et al. 2016) at different temporal scales (Etterson et al. 2007, Dornelas et al. 2012) and in different geographic contexts (Magurran and Henderson 2010, Chamberlain et al. 2016) in order to act as a fundamental basis for future studies on environmental and climatic change impacts. It is necessary to know the extent to which temporal trends in species altitudinal distributions change among different taxa and across geographically separated areas, to determine the relative contributions of the processes affecting species altitudinal distributions and thus apply the results obtained for making reliable predictions viable for other areas (Whittingham et al. 2007, Schaub et al. 2011). Moreover, information deriving from researches focused on multi-species or multi-taxa comparisons can be used as a primary tool to recognise areas of high natural value, to address management actions and to develop a more effective measure to counteract biodiversity loss (Hannah and Midgley 2002, Thomassen et al. 2011).

Climate condition could affect not only species distributions but also morphological traits and their clines along altitude. Thus the measure and description of how body size varies along altitude could be a good basis to monitor the potential effects of climate change (Gardner et al. 2011).

Body size directly affects energy and water requirements for thermoregulation (Porter & Kearney 2009; McKechnie & Wolf, 2010), mass acquisition, metabolic rates (Koijman, 2010) and life-history characteristics (Roff 2002). Therefore, understanding the mechanistic relationships between body size and environmental heterogeneity allows identifying key traits that shape the potential of a species to respond to climate change and provides insights into thermal tolerances, information that is currently lacking for most species (Kearney et al., 2009).

Nevertheless, few researches focused on the link between body size, altitude and temperature (Gardner et al. 2011) and how these relationships vary among different geographic areas and species. Since the relevance of body size variation in indicating climate variability (Gardner et al. 2011, Eweleit and Reinhold 2014) and since the alarming temperature raise in mountain areas (Beniston 2006, Brunetti et al. 2009) there is a need to gain more insights into the distribution of body size along altitudinal gradients.

Research goals

The aim of the PhD research consisted in evaluating the effects of altitude and the related environmental and climatic factors in shaping species distributions and species morphological traits over time and in different mountain areas.

We explored this topic following three different approaches at three different levels of biological organization: multi-species, multi-taxa and individual levels.

Chapters 1 and 2 focused on the temporal variations in altitudinal distributions of mountain breeding birds in two alpine areas. The first part analysed the birds altitudinal pattern of changes on two temporal scales (medium-term and long-term changes) and between two alpine contexts (western Alps and central Alps). The second part is based on the potential factors affecting bird altitudinal distribution changes during 34 years in central Alps. In particular, we aimed to detect which factor between temperature warming and forest expansion had a major role in shaping altitudinal ranges variations of mountain breeding birds.

In Chapter 3 we described how different taxa (ground beetles, butterflies and birds) changed their altitudinal distributions on a short-time scale. For each taxon we analysed altitudinal variations at ecological group level and how communities' composition changed over time along altitude.

In Chapter 4 we analysed the individual morphometric variation along altitude of five ground beetles species. The aim of the research consisted in detecting a potential cline of body size along elevation and understanding if this relationship was consistent or different among species and geographic contexts.

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Chapter 1 - Long- and medium-term changes in the altitudinal distribution of breeding birds in the Italian Alps

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1.1 Introduction

Several studies have demonstrated that species ranges have changed in recent decades (Parmesan et al. 1999, Hickling et al. 2006, Zuckerberg et al. 2009, Gillings et al. 2015). In many cases, the ranges have shifted upwards or polewards, and it was documented that they were probably driven by the recent raise of temperatures (Thomas and Lennon 1999, Parmesan and Yohe 2003, Hitch and Leberg 2007, Chen et al. 2011). Generally, changes on biota are more evident with increasing latitude or elevation (Loarie et al. 2009). Nevertheless, species inhabiting medium-latitude mountains, such as the Alps, have been shown to suffer not only the effects of global warming, but also changes in agro-forestry and pastoral practices, which have played an important role in shaping their distribution in those areas for a long time (Ausden 2007). Indeed, even though species are theoretically expected to move upwards with the increase of temperatures, both physical (Sun et al. 2013) and ecological limiting factors (Newton 1998, 2013) can prevent the establishment of suitable habitats at high elevations. This process may lead to the extinction of a species at the lower boundary of its distributional range, but not necessarily to a colonization at the upper parts. This can result in a range restriction instead of a range shift. However, not all species respond in the same way to the drivers of altitudinal range change (Maggini et al. 2011, Reif and Flousek 2012), probably because of differences in ecological traits (Reif and Flousek 2012; Auer et al. 2014, Hovick et al. 2016). Moreover, species responses may vary within different geographic contexts due to the local specificity and variability in climatic and ecological features (Archaux 2004; Popy et al. 2010, Chamberlain et al. 2013, Flousek et al. 2015). For this reason, in order to obtain a more comprehensive picture of the heterogeneity in altitudinal changes, it is fundamental to compare different species in different geographic areas. Moreover, long-term series of data on distribution are needed in order to depict and quantify the actual changes in a species' range. This requirement is also crucial to counteract the intrinsic and often wide sources of noise contained in biological data, which could make it difficult to detect significant and strong long-term trends (Hovick et al. 2016).

In our study, we explored the changes occurred in the altitudinal ranges of breeding birds in two areas located in the central and western Italian Alps. Birds are a conspicuous taxon for which long-time series of data are often available, and are particularly sensitive to climate and land-use changes (Laiolo et al. 2004, Lemoine et al. 2007, Lehikoinen et al. 2014). They are also relatively easy to study (Hovick et al. 2016). Indeed, several recent studies on climate change impact have focused on the range shift of bird species (Auer et al. 2014, Massimino et al. 2015, Tayleur et al. 2015).

In our study areas, long-term series of breeding bird data have been available since 1982 and 2006 in the central and western Alps, respectively. This gave us the opportunity to investigate changes occurred in the altitudinal ranges of 44 species in the central Alps, and of 27 species in the western Alps. In order to detect any possible pattern of change, we analysed the whole distribution of the species within the altitudinal range considered instead of its average or centroid, according to the conceptual framework first proposed by Maggini et al. (2011), which allows assessing range changes along altitudinal gradients and classifying the patterns of change. Different authors successfully applied this concept to bird species to detect upward and northward shifts (Massimino et al. 2015, Tayleur et al. 2015).

We compared the altitudinal shift patterns of species between the two mountain areas (central and western Alps), considering the overlapping period of 10 years (2006-2015) within the two time series, in order to identify differences or similarities in changes of bird ranges between different alpine contexts.

Finally, assuming that ecological traits could play a crucial role in shaping the pattern of range shifts in birds, we classified species based on their breeding habitat and migration strategy, and we searched for differences in ecological group responses.

The aim of this study can be summarized by three main questions:

(1) Has the altitudinal range of mountain breeding birds shifted during the last 34 years?

(2) Are the shifting patterns consistent in the western and central Alps? (3) Are there any differences in changes of elevation distribution between ecological groups?

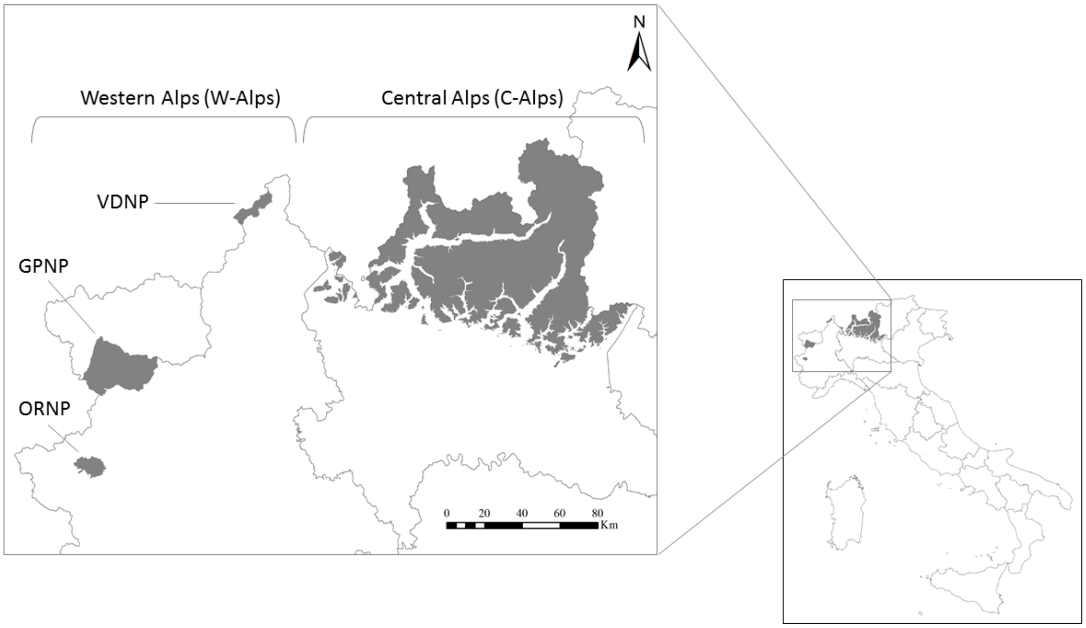

Figure 1. Location of the study areas: Central Alps (C-Alps), in grey the zones above 600 m; Western Alps (W-Alps) with the protected areas (Gran Paradiso National Park – GPNP; Orsiera Rocciavrè Natural Park – ORNP; Veglia Devero Natural Park – VDNP).

1.2 Study areas

Central Alps (C-Alps)

The study area located in the central Italian Alps (C-Alps*)* encloses the whole mountain area of the Lombardy region (northern Italy, 45°N, 9°E) (Fig. 1). Northern Lombardy is a mainly mountainous area, which covers almost half of the whole region, whereas lowland areas prevail in the South. A small portion of the northern Apennines is also present in the south-western corner of the Region (not investigated in the present study).

Lombardy mountains can be divided into two main sub-regions: the Prealps in the South, and the Alps. The Prealps have a mean altitude of 840 m and cover 27% of the Lombardy territory, while the Alps covers 17% of the regional surface and has a mean altitude of 1860 m.

The two mountainous sub-regions show some differences in land cover patterns. About one half (52%) of the prealpine area is covered by forests, mainly composed of deciduous species. Grasslands cover 15% of this sub-region, waterbodies 8%, and both rocks and shrubs 6%.

By contrast, the Alps are mostly occupied by rocks (35%) and forests (35%), with a large amount of coniferous species, while both grasslands and shrubs percentages are similar to those of the Prealps.

The two sub-regions are subjected to a different degree of continentality, which leads to a variation in climate regimes. Indeed, climatic conditions gradually change from the Prealps to the inner Alps, ranging from a suboceanic regime to a strictly continental one (Caccianiga et al. 2008).

Western Alps (W-Alps)

The study area in the western Italian Alps (W-Alps) was split into three sampling sites located in different protected areas: the Gran Paradiso National Park (GPNP; 44°25’N - 7°34’E), the Orsiera Rocciavrè Natural Park (ORNP; 44°75’N - 6°90’E) and the Veglia Devero Natural Park (VDNP; 46°18' N - 8°13' E) (Fig. 1).

The GPNP covers an area of 720 km^2 and has a mean altitude of 2400 m. ORNP has a surface of 110 km^2 and is the site with the lowest mean altitude, equal to 1970 m , while the VDNP has an area of 86 km^2 and a mean altitude of 2230 m.

The GPNP is dominated by rocks and grasslands, which cover 31% and 27% of the protected area, respectively, while forests and shrubs cover 24% and 6%, respectively. The ORNP is mainly characterized by grasslands (39%) and forests (35%), and, secondly, by rocks (18%) and shrubs (7%). Grasslands and rocks are the predominant land cover classes in the VDNP, showing the same cover percentages as in the GPNP. Forests cover 22% of this study site, while shrubs occupy 6% of the area.

All protected areas are characterized by a continental climate showing modest differences in terms of climatic regimes (highest monthly precipitation and lowest annual mean temperature in the VDNP). The overall environmental variability of the three parks can be considered a representative sub-sample of the western Italian Alps (Viterbi et al. 2013).

1.3 Sampling design and bird data

Central Alps

Bird data for the C-Alps were taken from the long-term series (1992-2015) of the monitoring program of breeding birds in Lombardy (Bani et al. 2009). The project started in 1992 with the aim of monitoring the population status of breeding birds in the whole region. Due to the discontinuity in the availability of resources, data are not available for the years 1993, 1994, 1997 and 1998.

Data collection followed a stratified sampling design, according to the landscape and habitat variability of the study area (for details see Massimino et al. 2008, Bani et al. 2009).

Bird data were collected using the unlimited distance point count technique, performed during the breeding season (10 May-20 June) from sunrise to 11.00 am, only in good weather conditions (sunny to cloudy, without rain or strong winds) (Blondel et al. 1981, Fornasari et al. 1998, Bibby et al. 2000, Massimino et al. 2008). From the regional database, we selected the 4680 point counts performed above 600 m in order to compare them with historical data collected only above this threshold.

Indeed, the time series was extended backwards with data covering a timespan of 7 years (1982-1988), collected and published by Realini (1988). These data were georeferenced and collected using a comparable sampling technique adopted for the monitoring program of breeding birds in Lombardy. Because the author performed yearly sampling activities even outside the breeding season, we only considered the data collected from the last week of April until the second week of July.

The two sources of data were joined, and a 34-year bird data time series (1982-2015) was obtained, which included 6617 sampling points distributed across the whole mountain areas of Lombardy.

Western Alps

For the W-Alps, we used bird data collected during the Alpine Biodiversity Monitoring program, a multi-taxa project started in 2006 (Viterbi et al. 2013). The 69 sampling units were located between 1150 m and 2700 m at 200 m intervals (for details see Viterbi et al. 2013).

As in the C-Alps, birds were recorded by means of point counts with the unlimited distance method (Blondel et al. 1981, Bibby et al. 2000), performed twice during the breeding season (from the last week of April to the first week of July). Because of logistical constraints, the number of performed points differed between years and study areas.

For this study, we focused on a time series of 451 point counts performed in the three protected areas from 2006 to 2015.

1.4 Data analysis

We investigated the altitudinal species' range changes calibrating separate models for three distinct periods of assessment (t_0=1982-1986, t_1=2006-2010 and t_2=2011-2015). Data analysis was performed in two main steps. The first step focused on C-Alps study area, where we aimed to detect changes in altitudinal distribution over the longest time interval (t_0 vs t_2, long-term changes), considering the widest altitudinal range (from 600 m to 2700 m). In the second step of the analysis, in order to compare range shift patterns in the two mountain areas, we selected a C-Alps bird data subset according to the lower altitudinal range (from 1150 m to 2700 m) and the shorter time interval (t_1 vs t_2, medium-term changes) covered by W-Alps bird data. We considered bird data collected up to 2700 m because few bird occurrence data were available for higher altitudes in our study areas.

The sampling units showed some differences between years in terms of quantity and altitudinal distribution. The use of 5-years time-windows allowed us to obtain a more balanced and robust sample to model species altitudinal distribution in each period of assessment (t_0, t_1 and t_2) and for both study areas (Supplementary material, Appendix 1, Table A1, A2, A3). Furthermore, by combining data sampled over several years in one single period we were able to counteract the possible environmental and demographic yearly stochasticity (Maggini et al. 2011). Because W-Alps point counts were performed twice a year, we considered a species as present when it was detected at least in one of the two sampling sessions.

In order to assess bird altitudinal ranges, we modelled the presence of each species as a smooth function (thin plate regression spline; Wood 2006) of the elevation and of the interaction between northing and easting, using generalized additive models (Wood 2006, Maggini et al. 2011). We set the maximum degrees of freedom to 15 for the space smooth (geographic coordinates) and to three for elevation. The latter setting allowed us to avoid overfitting and obtain unimodal curves, which are more easily comparable between periods of assessment (Maggini et al. 2011, Massimino et al. 2015).

The response curve that defines the species' elevation distribution was calculated keeping the spatial coordinates at their average over the whole sample (Massimino et al. 2015). Three types of curves can describe the altitudinal distribution of birds. Bell-shaped curves represented the entire altitudinal distribution of species, while truncated curves at lower or upper ends were typical of partially captured distributions (Supplementary material, Appendix 1, Fig. A1). Indeed, working within a predefined altitudinal range could lead to truncated distributions, thus preventing the detection of changes at the non assessable boundary and the unequivocal identification of the change pattern. The curves were described using up to five reference points: OBL (outer border left); CBL (central border left); OPT (optimum); CBR (central border right); OBR (outer border right) (Heegaard 2002, Maggini et al. 2011, Massimino et al. 2015, Tayleur et al. 2015). The optimum represents the maximum occurrence probability, while the central and the outer borders result from a fraction of the maximum response (Heegaard 2002). The outer border points were defined as the OPT * exp(-2), while the central border points were defined as the OPT* exp(-0.5).

Bird occurrence data were bootstrapped (n=200) and one curve for each bootstrapped sample was fitted in order to assess the estimates variability within each period of assessment.

For each species, the difference between reference point values of two periods of assessment was tested using the Mann-Whitney *U* test in order to detect the statistical significance of changes in altitudinal distribution. When the number of bootstrapped reference point values for each period of assessment was lower than or equal to 20, the Mann-Whitney *U* test was considered unreliable and the changes non-significant. The change of each reference point within each time interval (e.g. t_0 vs t_2) was coded according to Maggini et al. (2011): + for a significant upward shift; – for a significant downward shift; 0 for a non-significant shift; n meaning "no data available", usually for truncated curves or for models not fitting the data.

By combining the codes of the five reference points, we classified the changes in altitudinal distribution between two periods of assessment according to the theoretical framework proposed by Maggini et al. (2011) (Supplementary material Appendix 1, Table A4). We integrated the classification method reported by the authors with patterns of change that included their directionality. Thus, we defined 12 theoretical patterns of change: trailing edge retraction, trailing edge expansion, optimum downward shift, optimum upward shift, downward shift, upward shift, leading edge retraction, leading edge expansion, retraction, expansion, range expansion, range retraction. When the combination of codes of the reference points was not interpretable, we classified it as an unclear pattern. In the case of truncated curves, changes in altitudinal distribution can be classified according to one or two potential patterns. We observed these conditions for some species and we reported both patterns in the results. To summarize the results, we also classified the patterns into three general categories: retraction, expansion and shift (Supplementary material, Appendix 1, Table A4).

In order to detect differences in altitudinal range changes between ecological groups, we classified each bird species according to its breeding habitat and migration strategy. We defined three habitat groups (woodland, edge, and grassland species) and three migration groups (long-distance migrant, short-distance migrant, and resident species). Since habitat and migration features were defined according to the mountainous geographical context where birds were surveyed, the ecological traits of some species may differ from the traditional classification of European birds (Pan-European Common Bird Monitoring Scheme, http://www.ebcc.info/index.php?ID=592#Explantions, accessed on August 16, 2016). We considered bird seasonal movements occurring between mountains and plains as narrow-area displacements, and we thus classified altitudinal migrants as resident species. We defined the bird species that complete the migration within the Mediterranean area as short-distance migrants, whereas bird species moving beyond the Sahara desert were considered as long-distance migrants.

We assessed long-term (t_0 vs t_2) changes in the altitudinal distribution range of 44 bird species in the C-Alps, and we also compared the medium-term (t_1 vs t_2) changes for 39 and 27 species in the C-Alps and in the W-Alps, respectively. In this study, we analysed species belonging to *Passeriformes* and *Piciformes* only, as they are typically more linked to the site where they were surveyed.

All analyses were performed using R (R Core Team 2015), with the package *mgcv* (Wood 2006).

1.5 Results

C-Alps (long-term changes)

In the C-Alps, in the t_0-t_2 time period, six of the 44 species (14%) shifted upwards. Eleven bird species (25%) showed an expansion pattern, while 17 species (39%) experienced a retraction of their altitudinal distribution (Table 1). For bird species classified according to two patterns of change, we observed a shift or expansion pattern in eight species (seven with an upward shift and one with an optimum upward shift), while one species showed a downward shift or retraction. Only one species did not show any clear pattern.

Considering the 24 species for which the reference points moved upwards, with a significant variation in the long-term, we observed conspicuous mean altitudinal shifts: 309±67 m for OBL, 255±56 m for CBL, 176±39 m for OPT, 256±28 m for CBR, 195±36 m for OBR.

Among the woodland species, expansion was the predominant pattern of change. Nine of the 25 species showed an expansion pattern, whereas three species shifted upwards. Eight species showed a truncated distribution and were classified according to two potential patterns of change (seven with an upward shift or expansion, one with an optimum upward shift or expansion; Table 1, Fig. 2a).

The state of the edge species appeared less clear. Six of the 12 edge species (50%) experienced a retraction, three showed an upward, two expanded their altitudinal range, and one displayed a downward shift or retraction pattern (Table 1, Fig. 2b).

For grassland species, in case of curves truncated at the upper end, we considered retraction as the only potential pattern because of the physical limitations of their upper altitudinal distribution. Consequently, species living at the highest altitudes highlighted a dramatically noticeable framework, as they suffered a remarkable retraction of the lower altitudinal boundary (six out of 7 species; 86%; Table 1, Fig. 2c).

Considering the migration group, we detected a clear predominant pattern of change for long-distance migrants. Indeed, four of the seven trans-Saharan migrants (57%) retracted their altitudinal distribution. Conversely, most short-distance migrants (74%) colonized high altitudes with an expansion or an upward shift. Resident species did not show any clear altitudinal pattern of change (Table 1).

C-Alps vs W-Alps (medium-term changes)

Considering all species together, we did not observe any reliable variation between the two alpine areas for the altitudinal patterns of change in the medium-term period.

In the C-Alps, 10 species (26%) expanded their range, 11 species (28%) showed a retraction, whilst three species (8%) displayed a shift (one completely upwards, one completely downwards and one shifted its optimum downward) in the medium-term period (t_1-t_2). Considering the bird species classified according to two patterns of change, we observed four species (10%) shifting downwards or retracting, and four (10%) shifting upwards or expanding their altitudinal range. Seven species showed an unclear pattern (Table 2).

During the medium-term period, in the W-Alps, two the 27 bird species (7%) showed a shift (one shifted its optimum upwards while the other shifted downwards), 12 (44%) expanded their altitudinal range, and 10 (37%) suffered a retraction pattern. Two of the 27 species (7%) displayed a downward shift or a retraction pattern. Only one species did not show a clear pattern (Table 3).

Overall, the analysis of the medium-term period surprisingly showed that some species had moved towards lower altitudes. Indeed, for 14 species out of the 39 (36%) in the C-Alps, and for six species out of the 27 (22%) in the W-Alps, all the significant reference points had negative values (Table 2, Table 3). For instance, in the C-Alps we found a noticeable average shift at all the five reference points for these species: -54±23 m for the OBL, -106±32 m for the CBL, -103±37 m for the OPT, -113±28 m for the CBR, -81±18 m for the OBR.

Conversely, focusing on ecological groups, the differences between the two alpine areas became more evident. In the C-Alps, the most represented pattern of change for woodland species was expansion, but with a smaller number of species than in the W-Alps. Indeed, in the C-Alps, 7 of the 23 species (30%) expanded their altitudinal range and three species (13%) showed either an upward shift or an expansion pattern, while in the W-Alps almost all woodland species (83%) expanded their altitudinal range (Table 2, Table 3, Fig. 3a).

The edge species group revealed some slight similarities between the central and western Alps. Retraction was the predominant pattern in both areas (50% of the species in the C-Alps; 38% in the W-Alps). In the C-Alps, both expansion and downward shift patterns were observed in one species out of 10, while one species showed a downward shift or retraction. In the W-Alps, two out of the 8 species showed an expansion, one species displayed a downward shift, and one species exhibited either a downward shift or a retraction pattern (Table 2, Table 3, Fig. 3b).

Almost all grassland species (86%) showed a remarkable retraction at the trailing edge of their altitudinal range in the W-Alps. In the C-Alps we observed a more heterogeneous framework. Two of the six species suffered a retraction of their altitudinal range, two species expanded their distribution towards lower altitudes in clear contrast with the W-Alps, one showed a downward shift or retraction, while the last one showed an unclear pattern (Table 2, Table 3, Fig. 3c).

As regards the migration group, long-distance migrants in the C-Alps showed a clear pattern of overall retraction. In particular, three of the 8 species suffered an altitudinal range retraction, whereas three species showed a retraction or downward shift. On the contrary, most resident species experienced clear expansion patterns (69%).

We did not find any clear predominant pattern for the other migration group (Table 2, Table 3).

Twenty-two bird species occurred in both study areas during the medium-term period (t_1 vs t_2). Of these, only six species showed the same general patterns of change, while 11 species displayed different altitudinal range changes. Six of the 11 species were even characterized by opposite patterns. Five species were not comparable because they showed an unclear pattern in at least one area (Supplementary material, Appendix 1, Table A5).

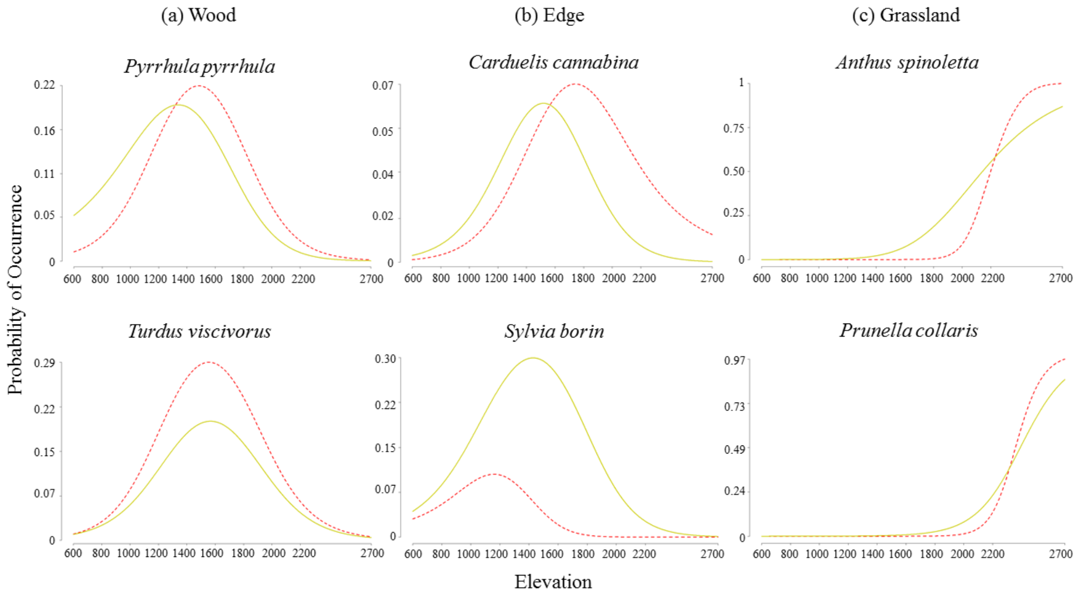

Figure 2. Response curves of six bird species in the central Alps for the period t_0=1982-1986 (solid line) and t_2=2011-2015 (dashed line). We reported two examples per habitat group. From left to right, we represented (2a) two predominant patterns of change for woodland species (upward shift, expansion), (2b) the contrasting patterns showed by edge species (upward shift, range retraction), and (2c) the retraction pattern of grassland species.

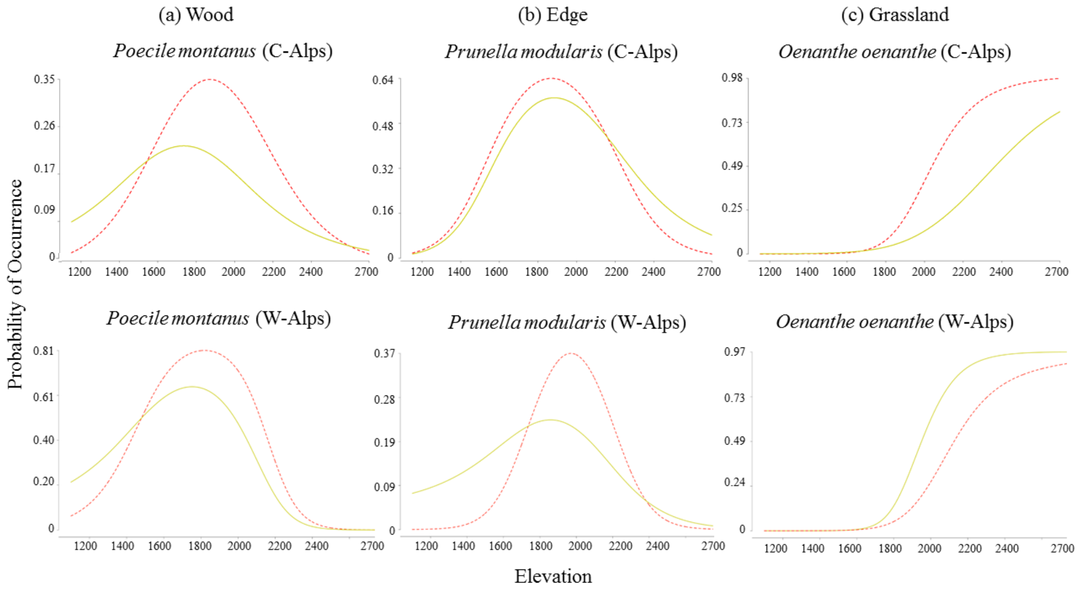

Figure 3. Comparison between the response curves of three bird species occurring both in the central and the western Alps for the period t_1=2006-2010 (solid line) and t_2=2011-2015 (dashed line). We reported one example per habitat group in order to highlight analogies and differences between the two areas. (3a) For the woodland group the predominant pattern is consistent in both areas (e.g. *Poeciloe montanus*, expansion), while edge and grassland species showed some differences in change patterns, i.e. (3b) *Prunella modularis* experienced a range retraction in the W-Alps and a downward shift in the C-Alps, while *Oenanthe oenanthe* suffered a range retraction in the W-Alps and a trailing edge expansion in the C-Alps (3c).

1.6 Discussion

Central Alps (long-term changes)

All 44 studied breeding bird species exhibited long-term changes (1982-2015) in their altitudinal distribution in the C-Alps. To our knowledge, no previous researches on bird altitudinal shifts reported similar results. For instance, in two areas of French Alps, Archaux (2004) observed significant altitudinal changes for 33% and 8% of the bird species, respectively, over a 30-years study period (1973-2002). In Switzerland, 64% of the bird species experienced altitudinal changes during 9 years (1999-2007; Maggini et al. 2011). For the Italian Alps (Val Sessera, Piedmont), Popy et al. (2010) did not find any significant shift at the community level, although most species showed an increment in altitude between 1992 and 2005. More recent studies, carried out in other geographic contexts, demonstrated that bird altitudinal ranges had changed over time, but to a much lower extent compared to our findings (Auer et al. 2014, Massimino et al. 2015).

Overall, bird altitudinal ranges have changed over the last 34 years in the C-Alps, following different patterns. Considering only the species with unequivocal patterns of change, we observed that 14% of the bird species have shifted upwards, 25% have expanded their altitudinal distribution, and 39% have experienced a retraction pattern. Even though the study performed by Maggini et al. (2011) covered a shorter period of time, the authors reported percentage values per category similar to our findings. On the other hand, we found a much more evident altitudinal displacement for our bird species compared to those studied by Maggini et al. (2011). This difference between mean reference points values may be due to the different time period considered. During our long-term study period (34 years), several drivers, such as habitat modifications (Lemoine et al. 2007), competition (Lenoir et al. 2010) and climate change (Reif and Flousek 2012, Tayleur et al. 2015) may have affected bird distribution on a long time scale, thus causing much clearer altitudinal changes. Indeed, if we compare our results with the study carried out by Archaux (2004) during 30 years, the variation in altitudinal shift for some species is highly consistent (e.g. *Erithacus rubecula,* upward shift of 114 m and 112 in the French Alps and in the central Italian Alps, respectively).

Some recent studies have demonstrated the important role of species ecological traits in shaping the altitudinal changes of birds (Reif and Flousek 2012, Auer et al. 2014, Hovick et al. 2016), and our results confirm the relevance of this aspect, as demonstrated by the different responses between ecological groups. For the woodland species group, we observed that 80% of the species have extended their range to either higher or lower altitudinal areas during the last 34 years. One of the possible drivers enhancing this trend is forest expansion, which may act together with warming. Indeed, there is a growing evidence that the abandonment of traditional agricultural practices has favoured forest regrowth, thus reducing the availability of open areas (Gehrig-Fasel et al. 2007, Gellrich et al. 2007, Pellissier et al. 2013). This phenomenon has been occurring across all Europe (Hatna and Bakker 2011), in the European mountains (Beguería 2006, Gehrig-Fasel et al. 2007) and particularly in the Alpine regions (Hunziker 1995, Tasser et al. 2007, Pellissier et al. 2013). Moreover, the altitude of the treeline has been increasing, probably enhanced by the documented increase of temperature, which may have spurred the development of forest vegetation at higher altitudes (Dirnböck et al. 2003, Gehrig-Fasel et al. 2007, Švajda 2008). In the Alps of Lombardy, huge portions of pastures and meadows have been abandoned, leading to forest regrowth (ERSAF 2012, Supplementary material, Appendix 1, Table A6). Our findings suggest that woodland birds have likely expanded and shifted their altitudinal ranges upwards following forest recolonization at lower and higher altitudes. Tree encroachment resulting from the abandonment of open areas has made the invasion by woodland bird species easier (Laiolo et al. 2004, Rolando et al. 2006), and this trend might continue in the future (Chamberlain et al. 2013). In contrast with our results, Reif and Flousek (2012) and Popy et al. (2011) did not find any altitudinal changes for woodland bird species, which showed that the upper limit of forests was probably acting as a barrier against their shifts. However, the two above-mentioned researches focused on shorter time periods than those analysed in our study, and forest cover changes were thus less detectable. Moreover, the study sites were located in different mountain contexts, which were likely subjected to different local land use dynamics. A methodological perspective might explain the different reactions of woodland birds, too. The response curve technique is sensitive to changes at different portions of the altitudinal distribution, which allows to detect even an initial shifting process, and thus more detailed patterns of change (Maggini et al. 2011). By using only the central part of the distribution (optimum), we would have not probably detected the altitudinal shift of woodland birds, because most changes occurred at the trailing and/or the leading edge of the species distribution. It should be acknowledged that climate warming might have acted as an important driver of upward expansion, too. It is widely known that the Alps have suffered a temperature increase in the last century (Beniston 2003, 2006, Brunetti et al. 2009, Acquaotta et al. 2014). Even if wide-scale, fixed-station and long-term instrumental meteorological measures are not available, there are many robust clues indicating that temperatures have increased in the Alps of Lombardy, too, during the 34-years study period. Milder climatic conditions may have favoured the upward colonization of woodland bird species inhabiting lower altitude forest areas.

We did not identify a common pattern of change for the edge species group, probably due to the structural and climatic complexity of the treeline habitat (MacDonald et al. 1998, Alftine and Malanson 2004, Rai et al. 2012) or lower altitude edge habitats, where each bird species may react differently.

Conversely, almost all grassland species retracted their altitudinal range. Because of logistical constraints, the trends and distribution of this ecological group are poorly known (EEA 2010, Chamberlain et al. 2012), and only few researches have focused on alpine birds altitudinal changes. In the Alps, high altitude birds did not show any significant altitudinal range shifts

(Archaux 2004, Popy et al. 2010, Maggini et al. 2011), whilst some evidence was reported for the Giant Mountains in the Czech Republic (Reif and Flousek 2012). High altitude birds are among the most threatened species (Chamberlain et al. 2016), but the lack of knowledge complicates the assessment of the main threats (habitat loss or climate change) affecting them (EEA 2010; Chamberlain et al. 2013). The upward shift of the treeline, with the consequent loss of open habitats, is one of the main threats for alpine birds (Chamberlain et al. 2013, 2016). Our results suggest that grassland species have retracted the trailing edge of their altitudinal range, thus losing the lower altitude open habitats, because of the considerable forest cover expansion at lower altitudes (ERSAF 2012, Supplementary material, Appendix 1, Table A6) and the upward shift of the treeline that has occurred in Lombardy. This habitat loss has led to the concentration of alpine species at higher altitudes, where the availability of suitable habitat is increasingly limited. The scenario could be exacerbated by the impossibility of the grassland habitats to colonize new upper areas. The reduction of the snow cover at high altitudes causes inadequate soil insulation and colder soils temperatures, which prevent the formation of grassland habitats (Edwards et al. 2007, Freppaz et al. 2010). Simultaneously, at lower altitudes, a further adverse factor like the edge effect may negatively affect high altitude birds (Chamberlain et al. 2012). Besides physically limiting the occurrence of grassland bird species, treeline habitats may act as a functional barrier. As reported by Donald (2010) for lowland areas, the proximity of the forest negatively affects the nesting behaviour of *Alauda arvensis*. Similar results were recently obtained by Masoero et al. (2016), who demonstrated that nesting close to the treeline in alpine environment increases predation pressure. Thus, a potential edge effect may amplify the treeline advancement impact on high altitude species, further reducing the availability of suitable areas. Habitat loss is likely the major threat for alpine birds, but climate change may play an additional negative role (Sekercioglu et al. 2008), interacting with the habitat loss process (Mantyka-Pringle et al. 2012, Oliver and Morecroft 2014) and favouring other adverse factors such as a decreasing food supply (Pearce-Higgins et al. 2010), increasing competition (Jankowski et al. 2010), predation rate (Prop et al. 2015, Masoero et al. 2016) or physiological stress (Barbosa et al. 2007, Gifford and Kozak 2012).

As for migratory birds, we observed that most long-distance migrants (about 60%) contracted their altitudinal distribution. Several studies have demonstrated that long-distance migrant birds are particularly vulnerable and show noticeable populations declines (Møller et al. 2008, Bani et al. 2009, Both et al. 2010, Vickery et al. 2014). On the contrary, few researches have focused on the range contraction or shift of migratory birds (Auer et al., 2014; Hovick et al., 2016), and, to our knowledge, no specific studies have ever reported altitudinal range changes for this ecological group. It is quite hard to identify the main cause of the retraction pattern showed by our results, because long-distance migrants could be affected by processes acting at breeding sites, like the phenological mismatch (Jenni and Kéry 2003, Both and te Marvelde 2007), or by threats acting on the often unknown wintering areas (Vickery et al. 2014). Anyway, our findings confirmed a negative assessment for this group of birds, which, due to its globally threatened status, should be better investigated in mountain areas, too. We also observed an expansion for most short-distance migrants, but almost all these species breed in forests, and their patterns are thus probably linked to the expansion of this habitat.

Central Alps vs Western Alps (medium-term changes)

In both areas, during the medium-term period, the number of bird species showing downward movements was remarkable. This trend is in contrast with the expectations and results of several studies showing and predicting upward shifts as a response of mountain birds to climate warming (Maggini et al. 2011, Reif and Flousek, 2012, Auer et al. 2014) and habitat loss (Chamberlain et al. 2013). However, downward shifts are not so unusual. A review made by Lenoir et al. (2010) reported that, in a warming climate, many species pertaining to different taxa, had moved downwards, while other species had moved upwards. About 25% of the species involved had moved their mid-range positions towards lower altitudes. Among the studies involved, the one considering mountain bird species (Archaux 2004) outlined that five out of 8 species had shifted downwards. In a more recent study, Maggini et al. (2011) reported that 30% (28 out of 95) of birds had shifted downwards.

According to our findings, 36% and 22% of the species have shifted downwards in the C-Alps and the W-Alps respectively, which confirms that downward displacements are important patterns of altitudinal change.

Stochastic population fluctuations, associated with measurement errors, may potentially lead to this unexpected pattern (Lenoir et al. 2010). By using 5-years time windows, we tried to avoid the effect of yearly random population fluctuations (Maggini et al. 2011), and to obtain a more reliable altitudinal range assessment. Indeed, the unexpected downward shifts reported by our findings were likely caused by other factors. Lenoir et al. (2010) pointed out that climate warming alone, or in concert with habitat alterations, might reduce interspecific competition at lower altitudes. As the lower boundaries of the altitudinal range are mainly controlled by biotic interactions (MacArthur 1972, Connell 1978, Brown and Lomolino 1998), when environmental stressors, such as warming and habitat modifications, become more severe, some species are forced to move upwards, with a consequent decrease of competitive pressure that likely allows other species to move towards lower altitudes. Actually, the downward movements of birds might be affected only by habitat alterations, without any biotic influence, as reported for the French Alps, where some forest species shifted downwards probably thanks to coniferous regrowth at lower altitudes (Archaux 2004). However, analysing the available digital cartography, DUSAF 1.1 (ERSAF, 2000) and DUSAF 4.0 (ERSAF, 2014), it appears that no significant forest expansion occurred in the C-Alps between 1999 and 2012 along the whole altitudinal range considered (Supplementary material, Appendix 1, Table A6). This suggests that changes in species interactions may have played an important role in driving bird species downwards during the short-term period. However, further *ad hoc* studies on bird interspecific competition in mountain habitats are required to confirm this hypothesis.

The comparison between the C-Alps and the W-Alps confirmed that the altitudinal range changes of mountain birds are not universal, as reported by several studies (Archaux 2004, Popy et al. 2010, Maggini et al. 2011, Reif and Flousek 2012). The two alpine areas showed important dissimilarities both at the species and at the ecological group level. For all ecological groups, the birds of W-Alps revealed change patterns more similar to those found for the C-Alps long-term period, rather than for the medium-term period.

As mentioned above, the Alps of Lombardy experienced forest recolonization in the past, but no significant forest changes during the recent period (1999-2012). Consequently, woodland birds of the C-Alps have expanded their altitudinal ranges in the long-term period, but not evident patterns were detected during the more recent medium-term period. By contrast, in the W-Alps, most woodland birds showed an expansion pattern as in the C-Alps during the long-term period. Taking into account this relationship, we might suppose that during the medium-term interval, the C-Alps and W-Alps may have experienced different land use dynamics. Even though all Europe has undergone a well documented and widespread dynamic of land abandonment (Pellissier et al. 2013, Lasanta et al. 2016), this process may have occurred at different times and with a different intensity across the continent. Thus, land abandonment was probably delayed and slower in the W-Alps compared to the C-Alps, which instead has suffered a faster depopulation of the mountain rural areas due to the huge urban development in the southern urban district of the Greater Milan area and in the Po Valley during the last 50 years (ERSAF 2012). Hinojosa et al. (2016) reported different patterns of land abandonment across mountain areas, depending on the attractive power of urban centres and on the land use regulation of national or regional Parks. In the W-Alps, all bird data were collected in protected areas. Therefore, a protected area effect may be present, which may have mitigated the land abandonment process. Indeed, in the W-Alps protected areas, forest expansion is probably still occurring, while in the C-Alps this process is now more stationary.

As showed by the C-Alps long-term analysis, even in the W-Alps almost all grassland species lost the lower portion of their altitudinal range, likely as a consequence of the advancement of forest cover (Chamberlain et al. 2012, 2013) and warming (Reif and Flousek 2012, Flousek et al. 2015), or due to the interaction of the two factors (Lenoir et al. 2010, Mantyka-Pringle et al. 2012, Oliver and Morecroft, 2014).

In the medium-term comparison, the C-Alps showed unexpected patterns, providing evidence of the downward expansion of two grassland birds, while one species retracted its distribution and moved towards lower altitudes.

Several processes and factors, like changes in population size (Lehikoinen et al. 2014, Flousek et al. 2015), biotic interactions (Melendez and Laiolo 2014), new habitats availability (Archaux 2004) or the degree of plasticity (Lenoir et al. 2010), may have acted simultaneously leading to contrasting responses by alpine birds in different areas. Furthermore, species responses might change between areas due to sensitivity to the local environmental (Randin et al. 2009) and climatic variability (Lenoir and Svenning 2015). Species traits and local-scale processes and factors might explain the results provided by the comparison between the species occurring in both areas, too. Most of the 22 bird species occurring in both study areas showed different or even opposite altitudinal changes, likely because they were affected by environmental and climatic pressures at different spatial and time scales.

Conclusions

We observed that *all* the investigated mountain bird species have changed at least a part of their altitudinal distribution during the last decades. However, the patterns of change differ between species, both in entity and directionality. This variability can be partially due to processes acting at a local-scale (e.g. habitat transformations or biotic interactions), as suggested by the observed differences in altitudinal ranges between the two investigated geographic areas. However, when grouping species according to homogeneous ecological traits (breeding habitat or migratory strategy), we observed consistent responses. This suggests that the general patterns of change may be shaped mainly by the effect of two processes acting at a wide scale, climate change and forest expansion. Therefore, in order to obtain a more detailed picture on the drivers affecting the entity and directionality of range changes, it is crucial to isolate the effects of these two wide-scale processes.

Table 1

			Reference points mean shifts					Reference points codes						
Species	Habitat	Migration	OBL	CBL	OPT	CBR	OBR	OBL	CBL	OPT	CBR	OBR	Patterns of change	General pattern
Aegithalos caudatus	w	r			-3	-58	-105	n	n	0	-	-	leading edge retraction - range retraction	retraction
Alauda arvensis	g	sd	1027	1084	930			+	+	+	n	n	retraction*	retraction
Anthus spinoletta	g	sd	395	102	0			+	+	0	n	n	trailing edge retraction*	retraction
Anthus trivialis	e	ld	355	238	221	257	280	+	+	+	+	+	upward shift	shift
Carduelis cannabina	e	sd	208	189	241	367	324	+	+	+	+	+	upward shift	shift
Carduelis carduelis	e	sd			-358	-469	-300	n	n	-	-	-	downward shift - retraction	-
Carduelis flammea	e	r	250	173	118	75	1	+	+	+	+	0	retraction	retraction
Carduelis spinus	w	sd	420	402	257	155	78	+	+	+	+	+	upward shift	shift
Certhia familiaris	w	r	-203	-173	-86	2	91	-	-	-	0	+	range expansion	expansion
Chloris chloris	e	sd			-2	-205	-401	n	n	0	-	-	leading edge retraction - range retraction	retraction
Cyanistes caeruleus	w	r			35	267	213	n	n	+	+	+	upward shift - expansion	-
Dendrocopos major	w	r			-2	-35	-67	n	n	0	0	-	leading edge retraction - range retraction	retraction
Emberiza citrinella	e	r	0	508	371	289	265	0	+	+	+	+	expansion	expansion
Erithacus rubecula	w	sd		107	112	158	170	n	+	+	+	+	upward shift - expansion	-
Fringilla coelebs	w	sd			21	224	176	n	n	+	+	+	upward shift - expansion	-
Garrulus glandarius	w	r			174	293	29	n	n	+	+	+	upward shift - expansion	-
Lophophanes cristatus	w	r	-54	-41	-22	4	18	-	-	-	0	+	range expansion	expansion
Loxia curvirostra	w	r	178	180	229	315	384	+	+	+	+	+	upward shift	shift

Montifringilla nivalis	g	r	344	69	-17			+	+	-	n	n	trailing edge retraction - range retraction	retraction
Nucifraga caryocatactes	w	r	151	165	224	351	0	+	+	+	+	0	retraction	retraction
Oenanthe oenanthe	g	ld	319	-30	4			+	-	0	n	n	trailing edge retraction - range retraction	retraction
Parus major	w	r			0	250	269	n	n	0	+	+	leading edge expansion - range expansion	expansion
Periparus ater	w	r		56	61	114	65	n	+	+	+	+	upward shift - expansion	-
Phoenicurus ochruros	g	sd	223	151	0			+	+	0	n	n	trailing edge retraction*	retraction
Phoenicurus phoenicurus	w	ld			134	640	581	n	n	+	+	+	upward shift - expansion	-
Phylloscopus bonelli	e	ld		0	329	29	-148	n	0	+	+	-	range retraction	retraction
Phylloscopus collybita	w	sd		229	222	326	441	n	+	+	+	+	upward shift - expansion	-
Picus viridis	w	r			1	-13	-83	n	n	0	-	-	leading edge retraction - range retraction	retraction
Poecile montanus	w	r	440	320	280	294	298	+	+	+	+	+	upward shift	shift
Prunella collaris	g	r	116	-55	-41			+	-	-	n	n	trailing edge retraction - range retraction	retraction
Prunella modularis	e	sd	385	242	176	145	70	+	+	+	+	+	upward shift	shift
Pyrrhula pyrrhula	w	sd	0	233	149	121	119	0	+	+	+	+	expansion	expansion
Regulus ignicapillus	w	sd	-33	-43	-8	32	56	-	-	-	+	+	range expansion	expansion
Regulus regulus	w	sd	-34	-46	-20	13	13	-	-	-	+	+	range expansion	expansion
Saxicola rubetra	g	ld	56	-49	-22	20	50	+	-	-	0	+	unclear pattern	-
Sylvia atricapilla	w	sd			-13	272	225	n	n	-	+	+	range expansion	expansion
Sylvia borin	e	ld	62	-152	-268	-378	-490	+	-	-	-	-	range retraction	retraction
Sylvia curruca	e	ld	294	197	129	68	-3	+	+	+	+	0	retraction	retraction
Troglodytes troglodytes	w	sd		15	147	393		n	0	+	+	n	optimum upward shift -	-

													expansion	
Turdus merula	w	sd			0	274	136	n	n	0	+	+	leading edge expansion - range expansion	expansion
Turdus philomelos	w	sd		-295	-129	118	296	n	-	-	+	+	range expansion	expansion
Turdus pilaris	e	sd	-159	-123	-75	-20	49	-	-	-	-	+	range expansion	expansion
Turdus torquatus	e	r	283	51	-263	-370		+	+	-	-	n	range retraction	retraction
Turdus viscivorus	w	r	34	-7	-12	-8	-16	+	0	-	0	-	range retraction	retraction
Parus major	w	r			0	250	269	n	n	0	+	+	leading edge expansion - range expansion	expansion

Table 1. Changes of the altitudinal distribution for 44 species in the central Alps during the long-term period (t_0, 1982-1986 and t_2, 2011-2015). We calculated the mean shift (m) between the periods of assessment (t_0 vs t_2) and the significance of the change with a code (+ for significant upward shift; – for significant downward shift; 0 for non-significant shift; n for no data available) for each reference point (OBL: outer border left; CBL: central border left; OPT: optimum; CBR: central border right; OBR: outer border right) that described distribution. Code combinations were classified according to the patterns of change (* unique pattern defined for grassland species due to the physical limitations of their upper altitudinal distribution) and to a general pattern. Each species was assigned to an ecological group according to its breeding habitat (w: wood; e: edge; g: grassland) and migration strategy (r: resident, sd: short-distance, ld: long-distance).

Table 2

			Reference points mean shifts					Reference points codes						
Species	Habitat	Migration	OBL	CBL	OPT	CBR	OBR	OBL	CBL	OPT	CBR	OBR	Patterns of change	General pattern
Alauda arvensis	g	sd	672	683	482			+	+	+	n	n	retraction*	retraction
Anthus spinoletta	g	r	142	143	0			+	+	0	n	n	trailing edge retraction*	retraction
Anthus trivialis	e	ld	77	86	75	62	9	+	+	+	+	0	retraction	retraction
Carduelis carduelis	e	sd		-209	-24	70	148	n	0	0	+	+	leading edge expansion - range expansion	expansion
Carduelis flammea	e	r	70	7	-81	-86	-16	+	+	-	-	0	range retraction	retraction
Carduelis spinus	w	sd	-70	-192	-238	-65	30	-	-	-	-	0	expansion	expansion
Certhia familiaris	w	r		1	185	278	135	n	n	+	+	+	upward shift - expansion	-
Cyanistes caeruleus	w	r	0	53	40	31	54	0	+	+	+	+	expansion	expansion
Dendrocopos major	w	r			-318	-203	-58	n	n	-	-	0	unclear pattern	-
Erithacus rubecula	w	sd			11	-21	20	n	n	+	-	+	unclear pattern	-
Fringilla coelebs	w	sd			-41	-7	22	n	n	-	0	+	range expansion	expansion
Garrulus glandarius	w	r		0	-154	-78	8	n	0	-	-	+	range expansion	expansion
Lophophanes cristatus	w	r			-264	-284	-104	n	n	-	-	-	downward shift - retraction	-
Loxia curvirostra	w	r	0	-332	-162	247	397	0	-	-	+	+	range expansion	expansion
Monticola saxatilis	g	ld	-61	31	-29			0	+	-	n	n	unclear pattern	-
Muscicapa striata	e	ld		-32	41	31	-115	n	0	+	0	-	range retraction	retraction
Nucifraga caryocatactes	w	r	56	167	141	108	83	+	+	+	+	+	upward shift	shift
Oenanthe oenanthe	g	ld	-138	-275	0			-	-	0	n	n	trailing edge expansion*	expansion
Parus major	w	r			-9	46	-11	n	n	0	+	0	unclear pattern	-
Periparus ater	w	r			12	-105	-125	n	n	0	-	-	leading edge retraction -	retraction

													range retraction	
Phoenicurus ochruros	g	sd	-36	-34	-4			-	-	0	n	n	trailing edge expansion*	expansion
Phoenicurus phoenicurus	w	ld			-35	-96	-157	n	n	-	-	-	downward shift - retraction	-
Phylloscopus bonelli	e	ld		-24	11	-12	-107	n	-	0	-	-	downward shift - retraction	-
Phylloscopus collybita	w	sd		59	52	36	19	n	+	+	+	+	upward shift - expansion	-
Poecile montanus	w	r	0	187	140	66	52	0	+	+	+	+	expansion	expansion
Prunella modularis	e	sd	-14	-17	-19	-71	-114	-	-	-	-	-	downward shift	shift
Pyrrhula pyrrhula	w	sd		0	-118	-13	114	n	0	-	0	+	range expansion	expansion
Regulus ignicapillus	w	sd		17	58	28	-19	n	+	+	+	-	range retraction	retraction
Regulus regulus	w	sd		-4	-10	-76	-88	n	n	0	-	-	leading edge retraction - range retraction	retraction
Saxicola rubetra	g	ld		-191	-393	-298	-181	n	-	-	-	-	downward shift - retraction	-
Serinus serinus	e	sd			74	160	150	n	n	+	+	+	upward shift - expansion	-
Sylvia atricapilla	w	sd			44	37	-73	n	n	+	+	-	unclear pattern	-
Sylvia curruca	e	ld	16	-2	-39	-102	-82	+	0	-	-	-	range retraction	retraction
Troglodytes troglodytes	w	sd		38	53	-103	-33	n	+	+	-	-	range retraction	retraction
Turdus merula	w	r			0	-38	0	n	n	0	-	0	unclear pattern	-
Turdus philomelos	w	sd			88	251	53	n	n	+	+	+	upward shift - expansion	-
Turdus pilaris	e	sd	-12	-89	-127	-95	-57	0	-	-	-	0	optimum downward shift	shift
Turdus torquatus	e	r	127	-62	-258	-214	-218	+	0	-	-	-	range retraction	retraction
Turdus viscivorus	w	r		-130	-53	-8	-13	n	-	-	0	0	unclear pattern	-

Table 2 Changes of the altitudinal distribution for 39 species in the central Alps during the medium-term period (t_1, 2006-2010 and t_2, 2011-2015). We calculated the mean shift (m) between the periods of assessment (t_0 vs t_2) and the significance of the change with a code (+ for significant upward shift; – for significant downward shift; 0 for non-significant shift; n for no data available) for each reference point (OBL: outer border left; CBL: central border left; OPT: optimum; CBR: central border right; OBR: outer border right) that described distribution. Code combinations were classified according to the patterns of change (* unique pattern defined for grassland species due to the

physical limitations of their upper altitudinal distribution) and to a general pattern. Each species was assigned to an ecological group according to its breeding habitat (w: wood; e: edge; g: grassland) and migration strategy (r: resident, sd: short-distance, ld: long-distance).

Table 3

			Reference points mean shifts					Reference points codes						
Species	Habitat	Migration	OBL	CBL	OPT	CBR	OBR	OBL	CBL	OPT	CBR	OBR	Patterns of change	General pattern
Alauda arvensis	g	sd	251	376	342	15	119	+	+	+	0	0	retraction	retraction
Anthus spinoletta	g	sd	82	136	113			+	+	+	n	n	retraction*	retraction
Anthus trivialis	e	ld	24	-22	-58	-41	-70	0	0	-	-	-	retraction	retraction
Carduelis cannabina	e	r	-19	-141	-219	-123	-14	-	-	-	-	0	expansion	expansion
Emberiza cia	e	sd	-132	18	138	-71	-179	0	0	+	-	-	range retraction	retraction
Erithacus rubecula	w	sd			0	32	32	n	n	0	+	+	leading edge expansion - range expansion	expansion
Fringilla coelebs	w	r			-42	122	85	n	n	0	+	+	leading edge expansion - range expansion	expansion
Garrulus glandarius	w	r			-5	147	213	n	n	0	+	+	leading edge expansion - range expansion	expansion
Lophophanes cristatus	w	r	-175	-129	-73	-10	39	-	-	-	0	+	range expansion	expansion
Loxia curvirostra	w	r	111	80	45	-62	-15	+	+	+	-	0	range retraction	retraction
Montifringilla nivalis	g	r	70	74	-42			+	+	-	n	n	trailing edge retraction - range retraction	retraction
Nucifraga caryocatactes	w	r	-335	-346	-266	-130	16	-	-	-	-	0	expansion	expansion
Oenanthe oenanthe	g	ld	87	186	78			+	+	+	0	n	retraction*	retraction
Parus major	w	r			-158	-158	-98	n	n	-	-	-	downward shift - retraction	-

Periparus ater	w	r		47	48	115	121	n	0	+	+	+	expansion - range expansion	expansion
Phoenicurus ochruros	g	sd	98	46	-15			0	+	-	n	n	unclear pattern	-
Phylloscopus bonelli	e	ld	-42	-62	-100	-4	98	0	-	-	0	+	range expansion	expansion
Phylloscopus collybita	e	sd		-76	-214	-148	-70	n	-	-	-	-	downward shift - retraction	-
Poecile montanus	w	r	11	70	88	85	66	0	+	+	+	+	expansion	expansion
Prunella collaris	g	r	60	61	6			+	+	0	n	n	trailing edge retraction	retraction
Prunella modularis	e	sd	267	248	176	41	-89	+	+	+	+	-	range retraction	retraction
Saxicola rubetra	g	ld	55	28	137	103	50	+	+	+	+	0	retraction	retraction
Sylvia borin	e	ld	63	37	82	23	1	0	0	+	+	0	optimum upward shift	shift
Sylvia curruca	e	ld	-256	-131	-140	-178	-170	-	-	-	-	-	downward shift	shift
Turdus merula	w	r			-3	49	77	n	n	0	+	+	leading edge expansion - range expansion	expansion
Turdus philomelos	w	sd			-10	215	189	n	n	0	+	+	leading edge expansion - range expansion	expansion
Turdus viscivorus	w	r	-67	-174	-37	102	101	0	-	-	+	+	range expansion	expansion

Table 3. Changes of the altitudinal distribution for 27 species in the western Alps during the medium-term period (t_1, 2006-2010 and t_2, 2011-2015). We calculated the mean shift (m) between the periods of assessment (t_0 vs t_2) and the significance of the change with a code (+ for significant upward shift; − for significant downward shift; 0 for non-significant shift; n for no data available) for each reference point (OBL: outer border left; CBL: central border left; OPT: optimum; CBR: central border right; OBR: outer border right) that described distribution. Code combinations were classified according to the patterns of change (* unique pattern defined for grassland species due to the physical limitations of their upper altitudinal distribution) and to a general pattern. Each species was assigned to an ecological group according to its breeding habitat (w: wood; e: edge; g: grassland) and migration strategy (r: resident, sd: short-distance, ld: long-distance).

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1.8 Supplementary material

Appendix 1

Tab A1. Numbers of sampling points per 300-m altitudinal belt for the long-term comparison (t_0: 1982-1986, t_2: 2011-2015) in the central Alps.

C-Alps	600-900	900-1200	1200-1500	1500-1800	1800-2100	2100-2400	2400-2700	Total
1982-1986	215	349	407	388	288	143	60	1850
2011-2015	220	230	143	172	316	68	27	1176
Total	435	579	550	560	604	211	87	3026

Tab A2. Numbers of sampling points per altitudinal belt for the medium-term comparison (t_1: 2006-2010, t_2: 2011-2015) in the central and western Alps.

	1150-1400	1400-1600	1600-1800	1800-2000	2000-2200	2200-2400	2400-2700	Total
C-Alps								
2006-2010	132	97	83	188	108	18	10	636
2011-2015	135	106	112	242	113	29	27	764
Total	267	203	195	430	221	47	37	1400
W-Alps								
2006-2010	11	22	42	33	42	34	43	227
2011-2015	14	23	40	33	41	33	40	224
Total	25	45	82	66	83	67	83	451

Tab A3. Numbers of sampling points per protected area (Gran Paradiso National Park – GPNP; Orsiera Rocciavrè Natural Park – ORNP; Veglia Devero Natural Park – VDNP) for the medium-term comparison (T_1: 2006-2010, T_2: 2011-2015) in the central and western Alps.

W-Alps	GPNP	ORNP	VDNP	Total
2006-2010	150	46	31	227
2011-2015	144	32	48	224
Total	294	78	79	451

Table A4. Combination of the reference point codes obtained from our analysis and their pattern classifications. The unique pattern defined for grassland species due to the physical limitations of upper altitudinal distribution is reported in brackets.

Patterns of change	General pattern	Reference points codes						
retraction	retraction	(+++nn)	++++0	+++00	(+++0n)	00---		
expansion	expansion	0++++	----0					
leading edge expansion	expansion							
leading edge retraction	retraction							
trailing edge expansion	expansion	(--0nn)						
trailing edge retraction	retraction	(++0nn)						
range expansion	expansion	nn-++	----+	---0+	---++	n--++	n0-0+	0--++
		nn-0+	n0--+	0--0+	0--++			
range retraction	retraction	+----	n0++-	++--n	+0-0-	+0---	n+++-	+0---
		++--0	n0+0-	n++--	+++-0	++++-	00+--	
optimum upward shift	shift	00++0						
optimum downward shift	shift	0---0						
downward shift	shift	-----						
upward shift	shift	+++++						
leading edge retraction - range retraction	retraction	nn0--	nn0--	nn00-				
trailing edge retraction - range retraction	retraction	+-0nn	++-nn	+--nn				
upward shift - expansion	-	n++++	nn+++					
leading edge expansion - range expansion	expansion	nn0++	n00++					
downward shift - retraction	-	nn---	n-0--	n----				
expansion - range expansion	expansion	n0+++						
unclear pattern	-	nn0-0	nn--0	n--00	n0++n			

	Western Alps							Central Alps					
Species	General pattern	Patterns of change	OBL	CBL	OPT	CBR	OBR	General pattern	Patterns of change	OBL	CBL	OPT	CBR
Alauda arvensis	retraction	retraction	+	+	+	0	0	retraction	retraction*	+	+	+	n
Anthus spinoletta	retraction	retraction*	+	+	+	n	n	retraction	trailing edge retraction*	+	+	0	n
Anthus trivialis	retraction	retraction	0	0	-	-	-	retraction	retraction	+	+	+	+
Erithacus rubecula	expansion	leading edge expansion - range expansion	n	n	0	+	+	-	unclear pattern	n	n	+	-
Fringilla coelebs	expansion	leading edge expansion - range expansion	n	n	0	+	+	expansion	range expansion	n	n	-	0
Garrulus glandarius	expansion	leading edge expansion - range expansion	n	n	0	+	+	expansion	range expansion	n	0	-	-
Lophophanes cristatus	expansion	range expansion	-	-	-	0	+	-	downward shift - retraction	n	n	-	-
Loxia curvirostra	retraction	range retraction	+	+	+	-	0	expansion	range expansion	0	-	-	+
Nucifraga caryocatactes	expansion	expansion	-	-	-	-	0	shift	upward shift	+	+	+	+
Oenanthe oenanthe	retraction	retraction*	+	+	+	0	n	expansion	trailing edge expansion*	-	-	0	n
Parus major	-	downward shift - retraction	n	n	-	-	-	-	unclear pattern	n	n	0	+
Periparus ater	expansion	expansion - range expansion	n	0	+	+	+	retraction	leading edge retraction - range retraction	n	n	0	-
Phoenicurus ochruros	-	unclear pattern	0	+	-	n	n	expansion	trailing edge expansion*	-	-	0	n
Phylloscopus bonelli	expansion	range expansion	0	-	-	0	+	downward shift - retraction	downward shift - retraction	n	-	0	-
Phylloscopus collybita	-	downward shift - retraction	n	-	-	-	-	upward shift - expansion	upward shift - expansion	n	+	+	+
Poecile montanus	expansion	expansion	0	+	+	+	+	expansion	expansion	0	+	+	+
Prunella modularis	retraction	range retraction	+	+	+	+	-	downward shift	shift	-	-	-	-
Saxicola rubetra	retraction	retraction	+	+	+	+	0	downward shift - retraction	-	n	-	-	-
Sylvia curruca	shift	downward shift	-	-	-	-	-	range retraction	retraction	+	0	-	-
Turdus merula	expansion	leading edge expansion - range expansion	n	n	0	+	+	unclear pattern	-	n	n	0	-
Turdus philomelos	expansion	leading edge expansion - range expansion	n	n	0	+	+	upward shift - expansion	-	n	n	+	+
Turdus viscivorus	expansion	range expansion	0	-	-	+	+	unclear pattern	-	n	-	-	0

Table A5. Comparison between the 22 species occurring both in the central and the western Alps during the medium-term period (t_1:2006-2010 and t_2: 2011-2015). We reported the significance of change with a code (+ for significant upward shift; – for significant downward shift; 0 for, non-significant shift; n for no data available) for each reference point (OBL: outer border left; CBL: central border left; OPT: optimum; CBR: central border right; OBR: outer border right). Code combinations defined a pattern of changes (* unique pattern defined for grassland species due to the physical limitations of their upper altitudinal distribution) and a general pattern.

Table A6. Changes in woodland cover between altitudinal belts for the central Alps area from 600 m to 2700 m during two time periods (1980-2012, 1999-2012). We considered as woodland the combination of three different land cover classes (coniferous, mixed and deciduous forests). Sources: digital cartography, Land Use Map 1980 (ERSAF 2011), DUSAF 1.1 (ERSAF, 2000) and DUSAF 4.0 (ERSAF, 2014).

		Altitudinal belts								
		600-800	800-1000	1000-1200	1200-1400	1400-1600	1600-1800	1800-2000	2000-2200	2200-2700
Woodland increase 1980-2012	(%)	5.9	7.1	8.9	6.2	4.2	2.3	1.7	2.5	0
	(ha)	5704	6744	7576	4584	2676	1456	1148	1528	16
Woodland increase 1999-2012	(%)	0.5	0.8	1.0	0.6	0.4	-0.1	0	-0.1	0
	(ha)	492	776	828	404	280	-84	-20	-56	-16

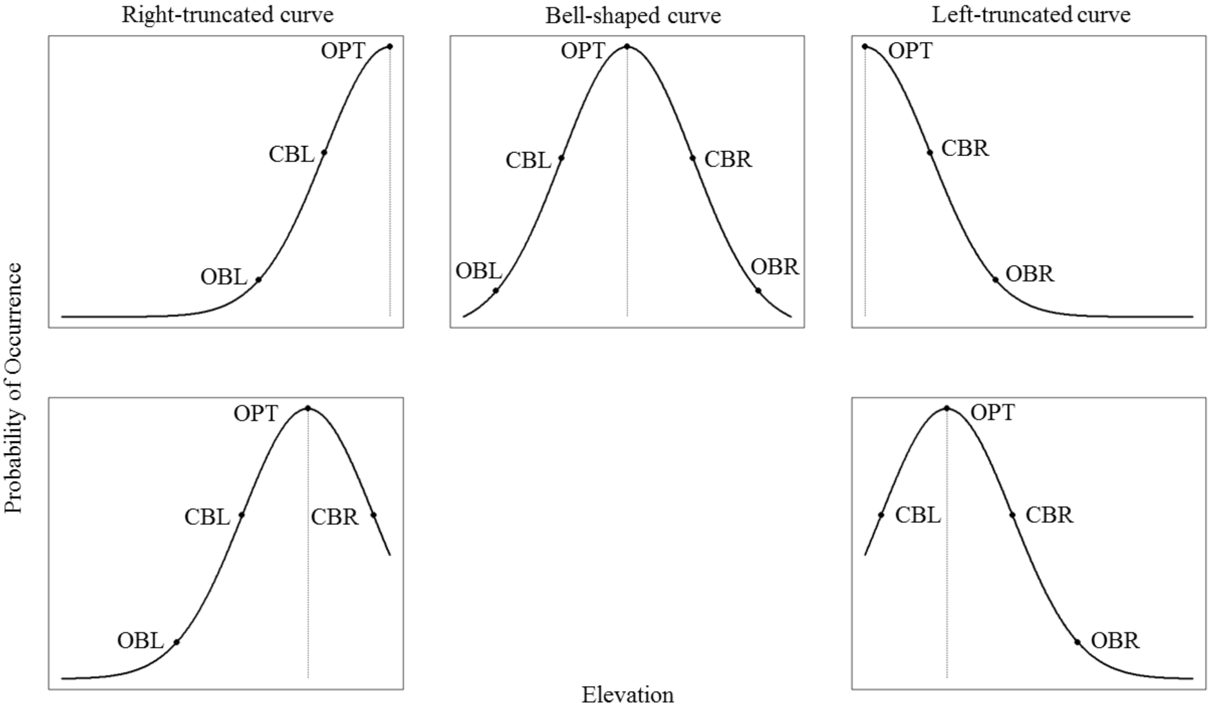

Fig. A1. Three types of curves describe the altitudinal distribution of birds and the reference points (OBL: outer border left; CBL: central border left; OPT: optimum; CBR: central border right; OBR: outer border right). Bell-shaped curves represent the entire altitudinal distribution of a species, while truncated curves are typical of partially captured distributions.

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Chapter 2 - Long-term change (1982-2012) in breeding bird ranges in the Italian central Alps: the effects of climate and habitat drivers.

2.1 Introduction

Although the human-induced habitat transformation is still recognized as one of the major drivers of species distribution alteration at global scale (Foley et al. 2005), in the last decades a rising attention has been also addressed to the effects produced on biota by the climate change (Walther et al. 2002; Parmesan & Yohe, 2003; Thuiller, 2007). In fact, if climatic conditions change, habitats change consequently, forcing species to adjust their distribution according to their ecological niches (Thomas, 2004; Thuiller et al. 2005). Among the changes in climate features, those involving the raise of temperatures (referred as global warming) are certainly the best known and probably the most studied. The magnitude of temperature change appears to be different respect to the geographic areas, and becomes more severe with increasing latitude or elevation (Loarie, 2009). In addition, many other co-occurring processes (e.g. land-use changes, pollution, harvesting, and species interactions) may affect species ecology, having conflicting, additive or even synergic effects with climate processes. This is particularly noticeable in those areas where different relevant environmental changes are still acting simultaneously. Indeed, species inhabit medium latitude mountains, as the Alps are, have been documented to suffer not only the effects of rising temperatures, but also those due to changes in agro-forestry and pastoral practices, which played an important role in shaping species' distribution since long time (Ausden 2007). In fact, until few decades ago, herds grazing restrained the Woodland cover upward, but after the abandonment of pastures, the tree line tended to raise in elevation, probably as consequence of a synergic action of climate change and land abandonment (Gehrig-Fasel et al., 2007; Parolo & Rossi, 2008; Leonelli et al., 2010). This phenomenon was probably enhanced by the increase of temperature that, limiting the period of the snow cover, led to the development of forest vegetation at higher elevations (Peterson 2005, Gehrig-Fasel et al. 2007). However, this phenomenon appears more complex, since the pastures abandonment does not involve only the rangeland areas, as it also promote the forest expansion at the expense of open areas even at medium elevations.

As birds are particularly mobile, they could arguably be among the firsts taxa modifying their distribution as a response to both climatic and other environmental changes (Both & Visser 2001; Both et al. 2004; Visser et al. 2004; Ambrosini et al., 2011). In the Italian Alps, 44 breeding bird species have significantly modified their altitudinal range, between 1982 and

2015 (Rocchia et al. *submitted*). However, in this geographic area, while the temperature has shown a clear increase during the considered period, not all species moved upward. Indeed, some species simply expanded or shrank their altitudinal range, or even shifted downward. For this reason, in this context, birds are a particular intriguing taxon to disentangling the effects produced by both climatic changes and human-induced habitat transformations, such as that of pastures abandonment.

Nevertheless, to quantify objectively the effects induced on biodiversity by climate change, and by gradual changes in habitat, as forest recolonization, long time series of information are essential. This requirement derives from the need to counteract the intrinsic, often wide, sources of variability, as well as the measurement and sampling noises contained both in biological and in environmental data, which could make it difficult to find significant and strong relationships between them. Of course, the data noise due to the stochastic errors of measurement of biological and environmental information can be difficulty managed without a long time series of data. On the other hand, the actual variability of biological data is due to multiple and often interacting environmental factors of which is not always possible to take into account. Moreover, to better infer relationships between species distribution and climate or habitat data, all information should be detailed and temporally and spatially explicit.

The main purpose of this study was to investigate the drivers of the altitudinal range changes of breeding birds trying to disentangling between the effect produced by climatic and habitat drivers. To this aim, we considered a long time series of breeding bird data, from 1982 to 2012, the longest available in Italy. Moreover, as the pattern of species altitudinal shifts and change are not universal (e.g. Chamberlain et al. 2012), we decided to perform the study in a large portion of the Italian Alpine chain, as wide as 160 km, laying in the Central Alps, covering the groups of Lepontine and Rhaetian, and the Prealps of Lombardy. To our knowledge, this is the first study, that explicitly investigate the statistical relationship between the change of species altitudinal range with those of climatic and habitat covariates.

2.2 Materials and methods

Study area

The study was carried out in the Alps and Prealps of Lombardy (Italy), over 600 m asl, in an area of approximately 7,600 km^2, 45% of which (3400 km^2) is covered by Woodlands, manly located (97%) below 2000 m asl (Fig. 1). The highest peak (Punta Perrucchetti of the Bernina Massif) reaches 4000 m asl and, overall, about the 30% of the area (2200 km^2) lays above 2000 m asl. The Alps of Lombardy are characterized by a high seasonal temperature variation. While in winter the mean temperatures fall well below freezing at 2000 m asl, during summer they can reach values of 10-12°C. In the hills and mountains, the climate is humid continental, and during winter it can be severely cold above 1500 m. Precipitations are more intense in the Prealps, where annually can reach up to 1500 to 2000 mm, but they are abundant even in the Alps, with an annual average of 600 to 850 mm (RSY 2015).

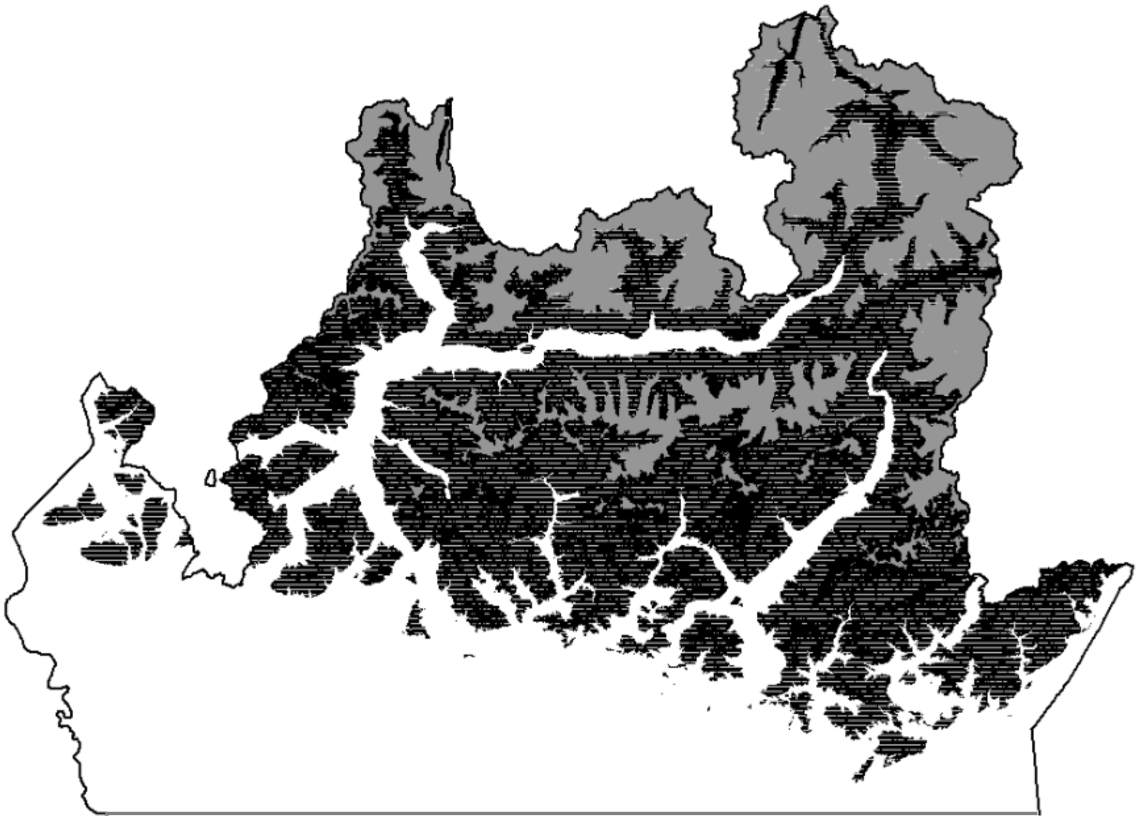

Figure 1. Study area (northern Lombardy). In black: area between 600 and 2000 m asl; in grey: area above 2000 m asl; dashed area: Woodland cover (source DUSAF 1980; ERSAF 2010).

Breeding bird data

Bird data from 1982 to 1988 were obtained from a dataset published by Realini (1988). This is the first and the only big dataset available concerning the historic data on breeding bird in the Alps and Prealps of Lombardy. All data were georeferenced, and collected in the field using a methodology absolutely comparable with that used for the long-term monitoring programme of breeding birds in Lombardy started in 1992 (see further on for the description of point counts survey technique), and collected in the field from the last week of April to the second week of July. The historic data are overall evenly distributed, both geographically and along the altitudinal gradient. For this period, the point counts amount to 1937, but unfortunately, for the analyses we had to discharge data gathered on 1988 because of too scarce, with a number of point counts of 10 only. Thus, between 1982 and 1987, the mean number point counts performed yearly is 322 (range 67 – 782). No data are available from 1988 and 1991, as the Realini research ended and the long-term monitoring programme of breeding birds in Lombardy had not yet started.

Bird data from 1992 to 2012 were obtained from the long-term monitoring programme of breeding birds in Lombardy (Bani et al., 2009). Data were collected using a standardized method based on the 10-minute, unlimited-distance point count technique (Blondel et al., 1981; Fornasari et al., 1998) with a minimum distance of at least 500 m between sampling locations. To limit the effects of the within-species detection probability, bird surveys were performed each year during the breeding season (10th May – 20th June), from sunrise to 11.00 am and only in good weather conditions (sunny to cloudy, without rain or strong winds). The point count technique allows the detection of bird species pertaining to *Columbiformes*, *Cuculiformes*, *Apodiformes*, *Coraciiformes*, *Piciformes* and *Passeriformes* (Bani et al., 2009). Overall, in this period, the collected point counts are 3966, with a yearly mean of 233 (range 82 – 482), but no data are available for 1993, 1994, 1997 and 1998, when the long-term monitoring programme of breeding birds in Lombardy was interrupted due to the lack of funding.

Both large-scale projects provided us a large amount of data collected over wide areas, with point counts (sampling units) randomly chosen each year. Nevertheless, as they did not rely on fixed sites and did not even include multiple surveys in the same season, it was impossible to account for species detection probability. Anyway, the large dataset used for this research might limit this potential bias, reducing the noise produced by stochasticity in species detection (Dondina et al. 2016).

As in the long-term monitoring programme of breeding birds in Lombardy were collected bird abundance data, while in the Realini survey relied on different kind of bird data (presence/absence, semi-quantitative and abundance data), we were forced to merge the two data sets considering presence/absence data only.

Overall, from the 23 surveyed years between 1982 and 2012 we had a total of 5893 point counts, while the number of species analysed, having a substantial part of their range in mountain and/or alpine area of Lombardy, is 40.

Habitat data

As one of our aims is evaluating the effects produced by habitat changes on bird distribution over time, it is crucial to obtain information about the habitats related to species presence. The working protocol of the long-term monitoring programme of breeding birds in Lombardy provides for the collection of all the information concerning the habitats present in a radius of 200 m from the observation point (Bani et al., 2009). We evaluated the Woodland cover at sight, as fractional cover, with an accuracy of the 5%. Besides knowing the habitat changes occurred in the species presence points, it is also crucial understanding the changes occurred in the overall habitat distribution, as they may drive the variations in bird species distribution. In this case, the large number of point counts collected along the whole time series may give a realistic idea of the habitat transformations throughout the study area. Unfortunately, during the 1982-1988 survey, Realini (1988) did not collect any detailed habitat information associated to each point count. However, the same author, georeferencing each point count, has made it possible to associate with them the habitat types obtained from the digital cartography DUSAF 1980 (ERSAF 2010), the only available for this historic period.

The Woodland cover trend along the time series was investigated considering the Woodland cover associated to each point count, within altitudinal belts 300-m wide, starting from 600 m to up to 2100 m asl.

Temperature data

Temperature data were obtained from a downscaled version of E-OBS (Haylock et al., 2008), at 1 per 1 km resolution, produced by Moreno & Hasenauer (2016), containing information on daily temperatures. The data are freely and publically available at ftp://palantir.bYESu.ac.at/Public/ClimateData.

To each georeferenced point count, besides the habitat data, we associated its relative temperature data, considering the mean of the minimum and the mean of the maximum temperature registered in the main local breeding season (May-June; see Bani et al., 2009). As the two temperatures are strongly correlated (R=0.907), all the analyses were performed considering the mean of the maximum temperature only.

Thus, the temperature trend along the time series was investigated considering the mean of the maximum temperature associated to each point count, within altitudinal belts 300-m wide, starting from 600 m to 2400 m asl.

2.3 Data analyses

Balanced sample

As one of the aim of this research was to depict changes in elevation range of breeding birds, we explored the variation over time in the 10th, 50th and 90th percentile of the species altitudinal distribution. This requires the availability of a sample without bias in sampling effort along altitude. Unfortunately, although the sampling design adopted from 1992 aimed to avoid this bias, the field data collection did not guarantee its absence, especially for logistical reasons (e.g. inaccessibility of the scheduled sampling unit). Moreover, the data of Realini (1988) being not specifically collected for monitoring purposes did not have an among-year balanced sample along altitude. To obtain an unbiased sample, we assessed the number of sampling units needed to keep constant their ratio among 300 m wide elevation bands, for all years. This guaranteed that, among years, each elevation band resulted explored with the same sampling effort, respect to all the other bands. Thus, the altitudinal data resulted unbiased among surveyed years. To this aim, we adopted an under vs over-sampling procedure (Chawla, 2010), with a balanced trade-off between the discharged and added sampling units, respectively, in each elevation band. The procedure was performed by means of a resampling method, producing 200 replicates of the unbiased sample. Based on these replicates, for each year, we calculated the mean elevational values of the 10th, 50th and 90th percentile of the species altitudinal distribution.

Changes in species elevation range

We explored the trend in the 10th, 50th and 90th percentile of the species altitudinal distribution over the years by means of a weighted linear regression, using as weight the number of sampling units within each year, obtained from the unbiased sample. From this analysis, we could expect a significant and consistent change in all the three percentiles or a significant change in only one or two of the three percentiles. This would configure an altitudinal range shift or a range contraction/expansion, respectively. Otherwise, we could also find a not significant trend in all the three percentiles, which would indicate a substantial unchanged species range.

Habitat and climate as drivers of species range shift

For each bird species we performed multiple regression models in order to understand the relative contribution of temperature (climate) and woodland cover (habitat) in affecting changes of the species' altitudinal distribution. We used as a response variable the yearly average of the 200-bootstrapped value of the 10th, 50th and 90th percentile of the elevation of the species occurrence and as explanatory variables, the yearly average of the maximum temperature of late breeding season and the percentage of woodland cover. As climate and habitat data for the 10th, 50th and 90th percentile, we considered yearly average extracted from all the sampling points (not only those of species occurrence) within the limits defined by the minimum and the maximum reached by each percentile within the historical series.

Species adaptation to altitudinal shift drivers

In order to understand how bird species responded to the main drivers of altitudinal changes (habitat and climate), we analysed the trend of the temperature and the woodland cover in the species occurrence points only, using a weighted linear regression.

We then configured two main species responses pointed out by the relationship between temperature variations in species occurrence points and species altitudinal range changes, measured at the three percentiles. i) A non-statistically significant variation of the temperature at the species presence points, in the case of a significant variations in the percentiles of the species altitudinal distribution, would mean that the species has shifted upwards, maintaining its climate envelope. ii) On the contrary, a statistically significant variation of the temperature at the species presence points would suggest that the species did not maintain its climate envelope.

The altitudinal woodland cover changes might affect the species range change too. Following the same conceptual framework used for the temperature variation at the species occurrence points in relation to the altitudinal range changes, we could define two main species responses to the woodland cover changes. i) If non-significant woodland cover changes occurred in bird presence points, simultaneously to bird altitudinal range changes, could mean that the species moved in order to maintain its habitat structure. ii) Conversely, if woodland cover increased or decreased significantly in species occurrence points and the species changed its altitudinal range, could reveal that species did not maintain its habitat structure.

We summarized the species' adaptations, comparing the conservation of the climate envelope and the habitat niche in relation to the significant drivers affecting the 10th, 50th and 90th altitudinal changes of each species. If the climate envelope or habitat structure maintenance matched with the drivers (habitat or climate) affecting the relative percentile of the altitudinal ranges (10th, 50th and 90th) we considered the species response as efficient.

2.4 Results

Changes in species elevation range

We considered the results of the bird species for which it has been possible to assess the altitudinal changes per each percentile (10th, 50th and 90th). Thus, we selected 26 bird species belonging to three different breeding habitat groups (woodland, edge, grassland): ten woodland, seven edge and nine grassland birds.

Eight out of the 26 bird species shifted upwards, 12 contracted their lower altitudinal boundary and three expanded the upper altitudinal boundary, whilst three did not show any altitudinal change (Table 1). Considering the breeding habitat groups, we detected some consistencies in pattern of altitudinal changes within them. In particular, we observed that 50% of woodland species and 85% of the edge species shifted or expanded upwards, while most of the grassland species (78%) contracted the lower portion of their altitudinal distribution.

Habitat and climate as drivers of species range shift

Almost all the species showed a significant positive effect of the temperature and/or the woodland cover on the upward shift of the 10th, 50th and 90th percentile of their altitudinal range (Table 2). Only four bird species did not show any significant relationship between altitudinal changes and the two covariates. Concerning habitat groups, we observed that eight out of the ten woodland species showed a positive significant effect of climate in at least one out of the three percentile of the altitudinal distribution, while for one species the woodland cover is the only important driver at the 10th percentile of the altitudinal distribution. For six out of the seven edge species the temperature resulted the most important driver in at least one of the three percentile. One species was positively affected by either climate or habitat for the 10th percentile of the altitudinal distribution, while another species for the 10th and 50th percentile. The temperature is the most important driver of altitudinal changes for almost all the grassland species too (seven out of the nine species). However, habitat variable increased its relevance in this ecological group mainly at the lower portion of the altitudinal range (10th percentile). Two species were positively affected by either climate or habitat for the 10th percentile of the altitudinal range, while in two species we observed an isolated and positive effect of woodland cover on the 10th percentile of the distribution.

Species adaptation to altitudinal shift drivers

Temperature variability and woodland cover changes in bird occurrence points are quite dissimilar between species (Table 3, Table 4). However, within habitat groups, we found some consistencies in bird responses to climate and habitat drivers (Table 5).

As mentioned above, the main driver affecting the upward shift of woodland species is the climate. However, although woodland species moved towards higher altitudes stimulated by rising temperatures, most of them did not succeed in adapting their altitudinal range according to the climate warming. Considering the eight woodland species for which climate is the main driver at the upper part of the altitudinal distribution (90th percentile), six did not maintain their climate envelope. Conversely, among the five species for which climate is the main driver at the lower part of the altitudinal range (10th percentile), three species did not suffer temperature warming. Overall the framework is negative, since only two out of the 10 woodland species conserved their climatic envelope in the whole altitudinal range.

Four out of the five edge species for which climate or habitat is the significant driver at the lower portion of the altitudinal distribution maintained their climatic envelope or habitat niche, while in the upper part of their range most of the edge species did not find new suitable climatic or habitat conditions. Considering only the 90th percentile, the framework become more dramatic, since all the species for which climate is the main driver suffered the temperature warming. No edge species succeeded in maintaining their climatic or habitat requirements considering the whole altitudinal range.

For the grassland species, six out of the eight species that moved upwards the lower part of the altitudinal range (10th percentile) succeeded in conserving their climate envelope or habitat structure. Also for the 50th percentile, three out of the five grassland species moved upward, maintaining their temperature requirements (Table 5).

2.5 Discussion

Almost all the birds considered in the study (23 out of the 26) moved upwards their altitudinal distributions during the 34-years study period. These evidences are coherent with recent studies that demonstrated important altitudinal changes for mountain birds in the last decades (Maggini et al. 2011, Reif and Flousek 2012, Rocchia et al. *submitted*).

However, the patterns of change in bird's altitudinal ranges are not universal (e.g. Chamberlain et al. 2012) and the drivers of those changes vary between geographic contexts (Archaux 2004, Reif and Flousek 2012, Rocchia et al. *submitted*). The aim of this research was to disentangle the role of the two considered drivers (climate and habitat) in the changes occurred in bird altitudinal ranges in the Italian central Alps.

Our findings revealed that climate is the main driver of bird altitudinal changes for most of the investigated species. This result is consistent with some researches on mountain bird's altitudinal changes. In particular, Reif and Flousek (2012) reported significant upward shifts during a 20 years period for the birds of Giant Mountains (Czech Republic), probably linked to the temperature increase recorded for that study site in the same time period. In the United States and southern Canada, Auer et al. (2014) found that 40 passerine birds moved towards higher altitudes during a 30-years period while simultaneously summer temperatures increased in the region over the same period. By contrast, during a temporal extent similar to our research (about 30 years), in two sites of the French Alps, Archaux (2004) reported no significant altitudinal changes for mountain birds although temperature became warmer.

Focusing on habitat groups we observed an overall preponderant effect of climate. However, for two ecoloigcal groups (edge and grassland) we found an increasing importance of habitat in driving altitudinal shift.

The altitudinal shifts of woodland species were mainly affected by temperature warming. Some researches pointed out that woodland birds displacements were mainly determined by the forest expansion (Laiolo et al. 2004, Rolando et al. 2014) or by forest expansion in concert with climate (Rocchia et al. *submitted*). Our results suggest that climate stimulated some woodland birds to move upwards where, probably, forests were previuosly vacant or where new woodland habitats are now available due to forest expansion. As reported in the chapter 1 (Rocchia et al. *submitted*), the central Alps experienced a huge forest regrowth in the eighties and nineties, providing new potential habitat niches for the woodland birds. The woodland species considered for this study were forced to colonize new altitudinal zones, mainly for climatic requirements, but, fortunately, they found new suitable woodland habitats to settle. For the edge species we observed an overall effect of climate too. However, they showed a weak but increasing importance of the forest cover in driving contaction the low border (10th percentile) of the altitudinal range. The edge species require habitats characterized by fragmented woodland cover with clearings and shrubs. The increasing forest expansion at lower altitudes might compromise these habitat requirements, forcing several edge species to move upwards in order to stray from areas interested from forest encroachment. Also the altitudinal shifts of grassland species were mainly affected by climate. However, even in this case, the effect of forest cover is still important at the lower boundary of the altitudinal range. Many studies have demonstrated that tree line shifted upwards because of the forest regrowth enhanced by the abandonment of pastures and meadows (Tasser et al. 2007, Pellissier et al. 2012, Lasanta et al. 2016). Furthermore, the additional effect of climate warming could have accelerated the tree line advancement (Gherig-Fasel et al. 2007). This process led to a loss of open habitats, constraining bird grassland species to abandon the lower altitudinal areas of their range. Therefore, our results confirmed that alpine species moved the 10th percentile towards higher altitudes both to follow their climate envelope and to escape from tree line rise.

Species adaptation to climatic or habitat drivers varies among habitat groups and according to the portion of altitudinal range considered (10th, 50th and 90th). Most of the woodland species did not conserve their climate envelope for almost all the percentiles, showing a not efficient response to the climatic driver. Stimulated by the rising temperatures, they moved upwards probably reaching a trade-off between habitat availability and climate constraints, mediated by the biological traits, such as the species-specific colonization ability. Moreover, for high altitude forest species (e.g. for strictly coniferous bird species), even the habitat availability at the higher boundaries of forest represent a physical constraint beyond which they could obviously not move. This barrier might have forced woodland birds in remaining at lower altitudes suffering temperature warming. Anyway, we should consider biotic interactions as a likely limiting factor in woodland species upward shift too (Lenoir et al. 2010). Probably, the ten species considered for the study might also suffered interspecific competition that prevented them to colonize new forest habitats upwards.

The edge species showed efficient responses both respect to climate and habitat changes at their lower distribution boundary (10th percentile), while at the medium and upper part of the altitudinal range (50th, 90th) they did not succeed in adapting to the climate warming, which is the prevailing driver at higher elevations. This process could be caused by the different edge habitat availability at the different portions of their altitudinal distribution. At the lower part of their altitudinal range, the edge species may have found suitable upward habitats to colonize, responding to the climate and habitat drivers. At higher altitudes (50th, 90th percentile) suitable habitats were increasingly scarce, preventing edge species to move upwards enough thus suffering the temperature increase.

For the grassland group, we observed an overall noticeable response to both climate and habitat drivers as they moved upward the lower and central portions (10th and 50th percentile) of their altitudinal range. However, these species did not shift upwards the 90th percentile of the altitudinal range probably because they did not have more suitable grassland habitats to colonize upwards. Indeed, the 78% of the grassland species did not conserve climate envelope at the 90th percentile. Thus, they might be stimulated in shifting upwards by increasing temperatures but they are blocked by physical limitations. The lower boundary contraction allowed grassland species to temporally adapt to climate and habitat drivers, however, if we simultaneously consider the lower contraction of the altitudinal range with the impossibility to move the upper boundary upwards, the grassland species will face a negative future scenario.

Our results suggest that edge species and grassland species are the most threatened group mainly considering the upper part of their altitudinal distribution. Both ecological groups suffered the temperature warming because they could not move upwards due to a probable limitation in habitats availability. Under a conservation perspective the two groups needs *ad hoc* management actions in order to counteract this negative trends. Climate warming is a global and widespread negative process that could be mitigated only with global consistent policies among countries. Anyway, some effective local actions could be put in place in order to counteract the global threat. For the edge species, isolated trees and shrubs as well as forest clearings are fundamental. Local policies that sustain grazing activities are crucial for maintaining and increasing edge habitats and clearings that could act as refuges for the species that suffer at the upper part of their altitudinal range and thus, they might find suitable habitat at lower altitudes. Therefore, other than preventing the forest expansion and the tree line growth with the above mention measures, for grassland specie conservation it's fundamental counteract habitat threats deriving form high altitude tourism and sports (e.g. ski slopes management) in order to limit as much as possible the stress factors on species and habitat in an serious global warming scenario.

Species	**Habitat**	**β 10th Elevation**	**Pr(>|t|)**	**β 50th Elevation**	**Pr(>|t|)**	**β 90th Elevation**	**Pr(>|t|)**	**Range change**
Alauda arvensis	Grassland	24.511	**<0.001**	17.114	**<0.001**	11.439	**<0.001**	Upward shift
Anthus trivialis	Edge	8.327	**0.001**	11.496	**<0.001**	4.796	**0.005**	Upward shift
Anthus spinoletta	Grassland	8.022	**0.001**	3.727	**0.006**	-0.862	0.624	Lower boundary contraction
Prunella modularis	edge	17.628	**<0.001**	11.784	**<0.001**	5.494	**0.002**	Upward shift
Prunella collaris	Grassland	19.195	**0.010**	6.577	0.179	-4.272	0.352	Lower boundary contraction
Phoenicurus ochrurus	Grassland	10.971	**0.004**	4.784	**0.045**	0.782	0.631	Lower boundary contraction
Saxicola rubetra	Grassland	15.107	**0.002**	12.008	**0.001**	5.946	**0.026**	Lower boundary contraction
Oenanthe oenanthe	Grassland	13.706	**<0.001**	5.174	**<0.001**	-0.429	0.838	Lower boundary contraction
Monticola saxatilis	Grassland	26.283	**0.004**	15.172	**0.008**	7.424	**0.037**	Upward shift
Turdus torquatus	Edge	11.786	**0.015**	1.728	0.265	-3.648	0.084	Lower boundary contraction
Turdus viscivorus	Woodland	6.235	0.058	4.729	0.056	-0.442	0.838	No change
Sylvia curruca	Edge	12.295	**<0.001**	6.127	**0.016**	4.072	**0.016**	Upward shift
Regulus regulus	Woodland	-0.849	0.803	2.459	0.228	5.348	**0.014**	Upper boundary expansion
Periparus montanus	Woodland	15.479	**<0.001**	11.830	**<0.001**	7.347	**<0.001**	Upward shift
Periparus ater	Woodland	-0.153	0.927	5.016	**0.003**	4.443	**0.025**	Upper boundary expansion
Lophophanes cristatus	Woodland	-2.068	0.499	3.541	0.245	5.574	0.077	No change
Certhia familiaris	Woodland	-5.751	0.141	-5.152	0.075	-2.110	0.530	No change
Nucifraga caryocatactes	Woodland	10.457	**0.009**	7.575	**0.010**	3.276	0.144	Lower boundary contraction
Montifringilla nivalis	Grassland	17.990	**0.031**	15.271	0.105	12.580	0.055	Lower boundary contraction
Serinus citrinella	Grassland	16.336	**0.006**	13.081	**0.010**	8.308	0.083	Lower boundary contraction
Carduelis spinus	Woodland	12.580	**0.049**	12.158	0.078	12.246	0.099	Lower boundary contraction
Carduelis cannabina	Edge	6.215	0.102	7.877	**0.001**	5.162	**0.039**	Upper boundary expansion
Carduelis flammea	Edge	10.526	**<0.001**	4.380	**0.005**	2.227	0.178	Lower boundary contraction
Loxia curvirostra	Woodland	21.960	**0.006**	13.215	**0.007**	8.536	**0.024**	Upward shift
Pyrrhula pyrrhula	Woodland	8.954	**<0.001**	5.869	**0.001**	5.499	**0.022**	Upward shift
Emberiza citrinella	Edge	15.618	**<0.001**	17.329	**<0.001**	7.804	**0.002**	Upward shift

Table1: Altitudinal changes of bird species. We reported from left to right: the species name, the habitat breeding preference (woodland, edge, grassland), β values of the lower, medium and upper altitudinal distribution (β 10th Elevation, β 50th Elevation, β 90th Elevation) and the relative significance level (Pr(>|t|)), the altitudinal range changes (Lower boundary contraction, Upper boundary expansion, Upward shift).

Species	Habitat	Drivers 10th	Drivers 50th	Drivers 90th
Alauda arvensis	Grassland	Clim	Clim	-
Anthus trivialis	Edge	Clim + Habitat	Clim + Habitat	Clim
Anthus spinoletta	Grassland	Clim + Habitat	Clim	-
Prunella modularis	Edge	Clim + Habitat	Clim	Clim
Prunella collaris	Grassland	Clim	-	-
Phoenicurus ochrurus	Grassland	Habitat	-	-
Saxicola rubetra	Grassland	Clim + Habitat	Clim	Clim
Oenanthe oenanthe	Grassland	Habitat	Clim	-
Monticola saxatilis	Grassland	Clim	-	-
Turdus torquatus	Edge	-	-	-
Turdus viscivorus	Woodland	-	-	-
Sylvia curruca	Edge	Clim	Clim	Clim
Regulus regulus	Woodland	-	-	Clim
Periparus montanus	Woodland	Habitat	Clim	Clim
Periparus ater	Woodland	-	Clim	Clim
Lophophanes cristatus	Woodland	-	-	Clim
Certhia familiaris	Woodland	-	-	-
Nucifraga caryocatactes	Woodland	Clim	Clim	Clim
Montifringilla nivalis	Grassland	-	-	-
Serinus citrinella	Grassland	Clim	Clim	-
Carduelis spinus	Woodland	Clim	Clim	Clim
Carduelis cannabina	Edge	Clim	Clim	Clim
Carduelis flammea	Edge	Clim	Clim	
Loxia curvirostra	Woodland	Clim	-	Clim
Pyrrhula pyrrhula	Woodland	Clim	-	Clim
Emberiza citrinella	Edge	-	Clim	-

Table 2: Drivers of the altitudinal shifts at the lower, medium and upper altitudinal range. We reported from left to right: the species name, the habitat breeding preference (woodland, edge, grassland), the significant driver for each percentile of the altitudinal distribution (Drivers 10th, Drivers 50th, Drivers 90th). We reported only the significant variables estimated with the multiple regressions. All the significant coefficients were positively related with altitude (see Supplmentary material). “Clim” means average maximum temperature of late breeding season (May-June) while “Habitat” means average forest cover (%).

Species	habitat	pattern of change	β 10th Temp	Pr(>|t|)	β 50th Temp	Pr(>|t|)	β 90th Temp	Pr(>|t|)	Climate envelope conservation
Alauda arvensis	Grassland	Upward shift	-7,306	0,067	1,136	0,725	6,129	0,174	YES
Anthus trivialis	Edge	Upward shift	7,825	**0,020**	2,238	0,439	11,830	**<0.001**	NO
Anthus spinoletta	Grassland	Lower boundary contraction	8,524	**0,008**	10,236	**0,002**	13,750	**0,001**	NO
Prunella modularis	Edge	Upward shift	-1,576	0,678	4,096	0,199	8,967	**0,005**	NO
Prunella collaris	Grassland	Lower boundary contraction	-0,982	0,891	5,450	0,391	14,773	**0,049**	NO
Phoenicurus ochrurus	Grassland	Lower boundary contraction	2,741	0,487	9,585	**0,025**	11,767	**0,002**	NO
Saxicola rubetra	Grassland	Lower boundary contraction	-0,242	0,946	1,555	0,640	7,948	**0,025**	NO
Oenanthe oenanthe	Grassland	Lower boundary contraction	2,172	0,616	11,172	**0,001**	13,325	**0,001**	NO
Monticola saxatilis	Grassland	Upward shift	-7,106	0,335	3,113	0,595	9,231	**0,048**	NO
Turdus torquatus	Edge	Lower boundary contraction	2,736	0,511	12,440	**0,001**	16,380	**0,001**	NO
Turdus viscivorus	Woodland	No change	7,377	0,052	9,274	**0,019**	13,911	**0,001**	NO
Sylvia curruca	Edge	Upward shift	4,707	0,142	11,012	**0,006**	10,373	**0,005**	NO
Regulus regulus	Woodland	Upper boundary expansion	13,510	**0,001**	10,190	**0,002**	9,150	**0,007**	NO
Periparus montanus	Woodland	Upward shift	-0,515	0,910	4,128	0,294	8,927	**0,010**	NO
Periparus ater	Woodland	Upper boundary expansion	12,675	**<0.001**	8,025	**0,003**	10,591	**0,001**	NO
Lophophanes cristatus	Woodland	No change	13,438	**0,001**	9,521	**0,029**	8,742	**0,046**	NO
Certhia familiaris	Woodland	No change	17,380	**0,005**	15,811	**0,001**	12,398	**0,004**	NO
Nucifraga caryocatactes	Woodland	Lower boundary contraction	2,828	0,514	8,470	**0,036**	10,634	**0,004**	NO
Montifringilla nivalis	Grassland	Lower boundary contraction	6,585	0,108	8,719	0,064	17,019	**0,003**	NO
Serinus citrinella	Grassland	Lower boundary contraction	3,549	0,498	6,866	0,264	15,101	0,164	YES
Carduelis spinus	Woodland	Lower boundary contraction	4,786	0,326	4,307	0,318	6,737	0,105	YES
Carduelis cannabina	Edge	Upper boundary expansion	7,812	**0,031**	8,464	**0,001**	12,406	**0,002**	NO
Carduelis flammea	Edge	Lower boundary contraction	3,604	0,258	11,388	**0,001**	12,970	**<0.001**	NO
Loxia curvirostra	Woodland	Upward shift	-5,663	0,392	3,923	0,510	7,751	0,053	YES
Pyrrhula pyrrhula	Woodland	Upward shift	7,195	**0,023**	7,455	**0,008**	10,514	**0,004**	NO
Emberiza citrinella	Edge	Upward shift	2,514	0,552	0,183	0,960	6,766	0,080	YES

Table3: Temperature changes at bird occurrence points. We reported from left to right: the species name, the habitat breeding preference (woodland, edge, grassland), the altitudinal range changes (Lower boundary contraction, Upper boundary expansion, Upward shift), β values of the temperature percentile (β 10th Temp, β 50th Temp, β 90th Temp) and the relative significance level (Pr(>|t|), climate envelope conservation ("YES", "NO").

Species	habitat	pattern of change	β 10th Forest cover	Pr(>|t|)	β 50th Forest cover	Pr(>|t|)	β 90th Forest cover	Pr(>|t|)	Habitat conservation
Alauda arvensis	Grassland	Upward shift	-0,005	0,188	-0,006	**<0.001**	-0,003	**0,020**	NO
Anthus trivialis	Edge	Upward shift	-0,001	0,767	-0,008	**0,004**	-0,006	0,066	NO
Anthus spinoletta	Grassland	Lower boundary contraction	-0,005	**<0.001**	-0,001	0,330	0,000	0,358	NO
Prunella modularis	Edge	Upward shift	-0,001	0,747	-0,011	**0,002**	-0,006	**0,001**	NO
Prunella collaris	Grassland	Lower boundary contraction	-0,002	0,791	0,002	0,611	0,000	0,302	YES
Phoenicurus ochrurus	Grassland	Lower boundary contraction	0,003	0,197	-0,006	**0,001**	0,001	0,193	NO
Saxicola rubetra	Grassland	Lower boundary contraction	-0,004	0,224	-0,005	**0,003**	-0,002	0,481	NO
Oenanthe oenanthe	Grassland	Lower boundary contraction	-0,006	**0,002**	-0,002	0,087	0,000	0,475	NO
Monticola saxatilis	Grassland	Upward shift	-0,011	**0,024**	-0,010	**0,022**	-0,002	0,169	NO
Turdus torquatus	Edge	Lower boundary contraction	-0,012	**0,012**	-0,008	**<0.001**	0,002	0,325	NO
Turdus viscivorus	Woodland	No change	0,000	0,962	0,000	0,921	0,000	0,958	YES
Sylvia curruca	Edge	Upward shift	-0,009	**0,028**	-0,003	0,241	-0,008	**0,002**	NO
Regulus regulus	Woodland	Upper boundary expansion	0,000	0,964	-0,002	0,374	0,000	0,972	YES
Periparus montanus	Woodland	Upward shift	-0,008	**0,005**	-0,010	**0,019**	-0,007	0,057	NO
Periparus ater	Woodland	Upper boundary expansion	0,001	0,659	-0,001	0,522	-0,005	0,309	YES
Lophophanes cristatus	Woodland	No change	-0,002	0,366	0,001	0,805	-0,002	0,715	YES
Certhia familiaris	Woodland	No change	0,008	**0,005**	0,001	0,510	0,008	**0,048**	NO
Nucifraga caryocatactes	Woodland	Lower boundary contraction	-0,007	0,052	-0,010	**0,030**	0,003	0,403	NO
Montifringilla nivalis	Grassland	Lower boundary contraction	1,066	0,893	-0,001	0,970	4,915	0,575	YES
Serinus citrinella	Grassland	Lower boundary contraction	-0,021	0,073	-0,011	0,154	-0,004	0,575	YES
Carduelis spinus	Woodland	Lower boundary contraction	0,002	0,793	-0,005	0,382	-0,009	0,088	YES
Carduelis cannabina	Edge	Upper boundary expansion	-0,004	0,270	-0,001	0,581	-0,002	**0,014**	NO
Carduelis flammea	Edge	Lower boundary contraction	-0,011	**0,001**	-0,005	0,083	0,000	0,912	NO
Loxia curvirostra	Woodland	Upward shift	-0,015	**0,035**	-0,014	**0,030**	-0,011	0,106	NO
Pyrrhula pyrrhula	Woodland	Upward shift	0,007	**0,021**	0,001	0,835	-0,004	0,244	NO
Emberiza citrinella	Edge	Upward shift	-0,003	0,392	-0,010	**<0.001**	-0,007	**0,006**	NO

Table 4: Forest cover changes at bird occurrence points. We reported from left to right: the species name, the habitat breeding preference (woodland, edge, grassland), the altitudinal range changes (Lower boundary contraction, Upper boundary expansion, Upward shift), β values of the forest cover percentile (β 10th Forest cover, β 50th Forest cover, β 90th Forest cover) and the relative significance level (Pr(>|t|), habitat niche conservation (“YES”, “NO”).

Species	Habitat	Drivers 10th		Drivers 50th		Drivers 90th	
		Clim	**Habitat**	**Clim**	**Habitat**	**Clim**	**Habitat**
Alauda arvensis	Grassland	YES	-	YES	-	-	-
Anthus trivialis	Edge	NO	YES	YES	NO	NO	-
Anthus spinoletta	Grassland	NO	NO	NO	-	-	-
Prunella modularis	Edge	YES	YES	YES	-	NO	-
Prunella collaris	Grassland	YES	-	-	-	-	-
Phoenicurus ochrurus	Grassland	YES	-	-	-	-	-
Saxicola rubetra	Grassland	YES	YES	YES	-	NO	-
Oenanthe oenanthe	Grassland	NO	-	NO	-	-	-
Monticola saxatilis	Grassland	YES	-	-	-	-	-
Turdus torquatus	Edge	-	-	-	-	-	-
Turdus viscivorus	Woodland	-	-	-	-	-	-
Sylvia curruca	Edge	YES	-	NO	-	NO	-
Regulus regulus	Woodland	-	-	-	-	NO	-
Periparus montanus	Woodland	-	NO	YES	-	NO	-
Periparus ater	Woodland	-	-	NO	-	NO	-
Lophophanes cristatus	Woodland	-	-	-	-	NO	-
Certhia familiaris	Woodland	-	-	-	-	-	-
Nucifraga caryocatactes	Woodland	YES	-	NO	-	NO	-
Montifringilla nivalis	Grassland	-	-	-	-	-	-
Serinus citrinella	Grassland	YES	-	YES	-	-	-
Carduelis spinus	Woodland	YES	-	YES	-	YES	-
Carduelis cannabina	Edge	NO	-	NO	-	NO	-
Carduelis flammea	Edge	YES	-	NO	-	-	-
Loxia curvirostra	Woodland	YES	-	-	-	YES	-
Pyrrhula pyrrhula	Woodland	NO	-	-	-	NO	-
Emberiza citrinella	Edge	-	-	YES	-	-	-

Table 5: Species adaptation to the drivers of altitudinal shifts. We reported from left to right: the species name, the habitat breeding preference (woodland, edge, grassland) and the potential drivers acting at the different portions of the altitudinal range (Drivers 10th – clim and habitat, Drivers 50th - clim and habitat, Drivers 90th- clim and habitat). “YES” means that the species adapted to the drivers conserving the climate envelope or the habitat niche. Conversely, “NO” means that the species did not adapt to the drivers and thus it did not conserve climate envelope or habitat niche.

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2.7 Supplementary material

Species	Habitat			Estimate	SE	t	Pr(>|t|)	Adj. R^2	F- statistic	p-value
Alauda arvensis	Open	90th perc.	(Intercept)	1702,06	213,23	7,982	<0.001	0,154	3,915	0,067
			Forest cover (%)							
			temperature (°C)	37,81	19,11	1,979	0,067			
		50th perc.	(Intercept)	872,54	230,33	3,788	0,002	0,503	17,170	0,001
			Forest cover (%)							
			temperature (°C)	72,07	17,39	4,143	0,001			
		10th perc.	(Intercept)	-208,80	406,10	-0,514	0,615	0,519	18,250	0,001
			Forest cover (%)							
			temperature (°C)	105,50	24,70	4,272	0,001			
Anthus trivialis	Forest	90th perc.	(Intercept)	1588,93	100,51	15,809	<0.001	0,336	12,140	0,002
			Forest cover (%)							
			temperature (°C)	28,30	8,12	3,484	0,002			
		50th perc.	(Intercept)	285,06	200,65	1,421	0,171	0,670	23,370	<0.001
			Forest cover (%)	10,46	3,11	3,361	0,003			
			temperature (°C)	51,13	9,07	5,640	<0.001			
		10th perc.	(Intercept)	31,98	289,43	0,111	0,913	0,390	8,023	0,003
			Forest cover (%)	8,24	3,84	2,149	0,044			
			temperature (°C)	35,45	12,59	2,816	0,011			
Anthus spinoletta	Open	90th perc.	(Intercept)	2437,45	68,29	35,696	<0.001	0,083	2,726	0,116
			Forest cover (%)							
			temperature (°C)	-13,16	7,97	-1,651	0,116			

		50th perc.	(Intercept)	1892,70	75,66	25,015	<0.001	0,159	4,981	0,037
			Forest cover (%)							
			temperature (°C)	15,83	7,095	2,232	0,037			
		10th perc.	(Intercept)	914,45	170,98	5,348	0,000	0,520	12,380	<0.001
			Forest cover (%)	12,29	3,71	3,309	0,004			
			temperature (°C)	31,58	10,20	3,097	0,006			
Prunella modularis	Shrub	90th perc.	(Intercept)	1734,55	98,30	17,645	<0.001	0,297	10,280	0,004
			Forest cover (%)							
			temperature (°C)	28,24	8,81	3,206	0,004			
		50th perc.	(Intercept)	773,06	262,15	2,949	0,008	0,404	8,455	0,002
			Forest cover (%)	6,64	4,48	1,482	0,154			
			temperature (°C)	49,10	13,15	3,734	0,001			
		10th perc.	(Intercept)	-678,27	545,39	-1,244	0,228	0,359	7,169	0,004
			Forest cover (%)	15,91	7,76	2,050	0,050			
			temperature (°C)	60,69	22,83	2,659	0,015			
Prunella collaris	Open	90th perc.	(Intercept)							-
			Forest cover (%)							
			temperature (°C)							
		50th perc.	(Intercept)							-
			Forest cover (%)							
			temperature (°C)							
		10th perc.	(Intercept)	1443,86	236,81	6,097	<0.001	0,348	6,327	0,033
			Forest cover (%)							
			temperature (°C)	55,78	22,17	2,515	0,033			

Phoenicurus ochrurus	Open	90th perc.	(Intercept)							-
			Forest cover (%)							
			temperature (°C)							
		50th perc.	(Intercept)							-
			Forest cover (%)							
			temperature (°C)							
		10th perc.	(Intercept)	-650,48	332,45	-1,957	0,065	0,597	17,260	<0.001
			Forest cover (%)	24,61	4,96	4,966	<0.001			
			temperature (°C)	26,23	14,59	1,798	0,087			
Saxicola rubetra	Open	90th perc.	(Intercept)	1149,15	284,80	4,035	0,001	0,242	4,035	0,037
			Forest cover (%)	10,47	5,69	1,839	0,083			
			temperature (°C)	34,38	15,55	2,210	0,041			
		50th perc.	(Intercept)	344,14	410,33	0,839	0,413	0,332	5,717	0,013
			Forest cover (%)	9,98	6,56	1,521	0,147			
			temperature (°C)	59,03	20,50	2,880	0,010			
		10th perc.	(Intercept)	-1084,12	479,31	-2,262	0,037	0,540	12,160	0,001
			Forest cover (%)	23,31	7,66	3,043	0,007			
			temperature (°C)	58,33	24,53	2,377	0,029			
Oenanthe oenanthe	Open	90th perc.	(Intercept)							-
			Forest cover (%)							
			temperature (°C)							
		50th perc.	(Intercept)	1754,31	85,50	20,519	<0.001	0,170	5,497	0,029
			Forest cover (%)							
			temperature (°C)	23,04	7,40	3,114	0,005			
		10th perc.	(Intercept)	-61,92	522,21	-0,119	0,907	0,192	3,618	0,046

			Forest cover (%)	20,78	8,88	2,341	0,030			
			temperature (°C)	36,48	23,95	1,523	0,144			
Monticola saxatilis	Open	90th perc.	(Intercept)							-
			Forest cover (%)							
			temperature (°C)							
		50th perc.	(Intercept)							
			Forest cover (%)							
			temperature (°C)							
		10th perc.	(Intercept)	-1022,91	784,38	-1,304	0,215	0,397	10,210	0,007
			Forest cover (%)							
			temperature (°C)	160,49	50,24	3,195	0,007			
Turdus torquatus	Open	90th perc.	(Intercept)							-
			Forest cover (%)							
			temperature (°C)							
		50th perc.	(Intercept)							-
			Forest cover (%)							
			temperature (°C)							
		10th perc.	(Intercept)	572,93	432,67	1,324	0,207	0,260	6,272	0,025
			Forest cover (%)							
			temperature (°C)	74,06	29,57	2,504	0,025			
Sylvia curruca	Shrub	90th perc.	(Intercept)	1837,03	79,78	23,026	<0.001	0,318	9,391	0,007
			Forest cover (%)							
			temperature (°C)	23,73	7,75	3,064	0,007			
		50th perc.	(Intercept)	1531,03	157,32	9,732	<0.001	0,165	4,565	0,047
			Forest cover							

			(%)							
			temperature (°C)	26,84	12,56	2,136	0,048			
		10th perc.	(Intercept)	643,63	210,29	3,061	0,007	0,488	18,150	0,001
			Forest cover (%)							
			temperature (°C)	62,34	14,63	4,260	0,001			
Regulus regulus	Forest	90th perc.	(Intercept)	1354,44	142,05	9,535	<0.001	0,233	7,675	0,011
			Forest cover (%)							
			temperature (°C)	29,51	10,65	2,770	0,012			
		50th perc.	(Intercept)							
			Forest cover (%)							
			temperature (°C)							
		10th perc.	(Intercept)							-
			Forest cover (%)							
			temperature (°C)							
Periparus ater	Forest	90th perc.	(Intercept)	1491,83	114,85	12,990	<0.001	0,299	10,370	0,004
			Forest cover (%)							
			temperature (°C)	29,38	9,13	3,220	0,004			
		50th perc.	(Intercept)	828,81	119,17	6,955	<0.001	0,450	19,030	<0.001
			Forest cover (%)							
			temperature (°C)	32,03	7,34	4,362	<0.001			
		10th perc.	(Intercept)							
			Forest cover (%)							
			temperature (°C)							
Lophophanes cristatus	Forest	90th perc.	(Intercept)	1259,48	231,74	5,435	<0.001	0,163	5,269	0,032
			Forest cover (%)							

			temperature (°C)	37,16	16,19	2,295	0,032			
		50th perc.	(Intercept)							
			Forest cover (%)							
			temperature (°C)							
		10th perc.	(Intercept)							
			Forest cover (%)							
			temperature (°C)							
Nucifraga caryocatactes	Forest	90th perc.	(Intercept)	1782,06	127,38	13,990	<0.001	0,154	4,449	0,049
			Forest cover (%)							
			temperature (°C)	24,11	11,43	2,109	0,049			
		50th perc.	(Intercept)	1302,40	192,82	6,755	<0.001	0,222	6,435	0,021
			Forest cover (%)							
			temperature (°C)	37,72	14,87	2,537	0,021			
		10th perc.	(Intercept)	663,74	336,77	1,971	0,064	0,162	4,666	0,044
			Forest cover (%)							
			temperature (°C)	46,87	21,70	2,160	0,045			
Serinus citrinella	Open	90th perc.	(Intercept)							
			Forest cover (%)							
			temperature (°C)							
		50th perc.	(Intercept)	1120,84	184,58	6,072	0,002	0,641	11,720	0,019
			Forest cover (%)							
			temperature (°C)	53,56	15,64	3,424	0,019			
		10th perc.	(Intercept)	55,90	452,62	0,123	0,908	0,771	11,070	0,023
			Forest cover (%)	19,81	10,72	1,848	0,138			
			temperature	66,63	15,38	4,333	0,012			

			(°C)							
Carduelis spinus	Forest	90th perc.	(Intercept)	565,67	413,74	1,367	0,214	0,409	6,545	0,038
			Forest cover (%)							
			temperature (°C)	81,38	31,81	2,558	0,038			
		50th perc.	(Intercept)	215,29	465,69	0,462	0,658	0,399	6,321	0,040
			Forest cover (%)							
			temperature (°C)	79,57	31,65	2,514	0,040			
		10th perc.	(Intercept)	-282,60	428,60	-0,659	0,531	0,553	10,910	0,013
			Forest cover (%)							
			temperature (°C)	84,20	25,50	3,303	0,013			
Carduelis cannabina	Open	90th perc.	(Intercept)	1647,76	161,43	10,208	<0.001		3,338	0,060
			Forest cover (%)	6,70	4,88	1,373	0,188			
			temperature (°C)	25,17	13,08	1,924	0,071			
		50th perc.	(Intercept)	1248,19	118,51	10,533	<0.001		23,080	0,000
			Forest cover (%)							
			temperature (°C)	44,69	9,30	4,804	<0.001			
		10th perc.	(Intercept)		748,35	298,880	2,504	0,022	5,939	0,025
			Forest cover (%)							
			temperature (°C)	46,43	19,05	2,437	0,025			
Carduelis flammea	Open	90th perc.	(Intercept)							
			Forest cover (%)							
			temperature (°C)							
		50th perc.	(Intercept)	1680,07	87,90	19,112	0,928	0,256	8,550	0,008
			Forest cover (%)							

			temperature (°C)	22,37	7,65	2,925	0,008			
		10th perc.	(Intercept)	970,50	219,49	4,422	<0.001	0,271	9,192	0,006
			Forest cover (%)							
			temperature (°C)	46,16	15,23	3,032	0,006			
Loxia curvirostra	Forest	90th perc.	(Intercept)	1344,97	159,47	8,434	<0.001		13,860	0,004
			Forest cover (%)							
			temperature (°C)	49,80	13,38	3,724	0,004			
		50th perc.	(Intercept)		2058,35	814,830	2,526	0,032	3,548	0,073
			Forest cover (%)	-25,62	17,90	-1,431	0,186			
			temperature (°C)	48,31	23,01	2,100	0,065			
		10th perc.	(Intercept)	-49,75	605,87	-0,082	0,936		5,327	0,044
			Forest cover (%)							
			temperature (°C)	90,66	39,28	2,308	0,044			
Pyrrhula pyrrhula	Forest	90th perc.	(Intercept)	1397,86	164,62	8,491	<0.001	0,186	5,800	0,026
			Forest cover (%)							
			temperature (°C)	29,10	12,08	2,408	0,026			
		50th perc.	(Intercept)	902,52	156,41	5,770	<0.001	0,302	10,090	0,005
			Forest cover (%)							
			temperature (°C)	29,42	9,26	3,176	1,000			
		10th perc.	(Intercept)	173,21	242,64	0,714	0,484	0,307	10,310	0,004
			Forest cover (%)							
			temperature (°C)	39,30	12,24	3.2120	0,004			
Emberiza citrinella	Open	90th perc.	(Intercept)	1351,71	187,20	7,221	<0.001		4,348	0,050
			Forest cover (%)							
			temperature		28,83	13,82	2,085	0,050		

	(°C)			0			
50th perc.	(Intercept)	489,13	303,47	1,612	0,123	9,404	0,006
	Forest cover (%) temperature (°C)	60,390	19,690	3,067	0,006		
10th perc.	(Intercept)	-347,632	484,407	-0,718	0,482	4,831	0,020
	Forest cover (%)	11,463	7,616	1,505	0,149		
	temperature (°C)	45,572	21,769	2,093	0,050		

Chapter 3 – Multi taxa distribution along altitude: 5 years data from the Western Alps.

3.1 Introduction

Climate warming and land use changes are considered among the main threats to biodiversity (Sala et al. 2000, Lemoine et al. 2007). Other drivers may also interact with climate change and land use changes to impact biodiversity (Brook et al. 2008) however, substantial changes in terrestrial species' populations and distributions have already been detected world-wide mainly in response to both of these impacts (Mantyka-Pringle et al. 2012). Most of the researches focused on the isolated effect of climate change (Parmesan et al. 1999, Parmesan and Yohe 2003, Chen et al. 2011) and habitat loss or alteration (Spiegelberger et al. 2006, Dirnbock et al. 2011) not considering the likely combined effects of the two factors (Mantyka-Pringle et al. 2012, Oliver and Morecroft 2014).

Mountain ranges are very sensitive to environmental changes and climate warming (Huber et al. 2005, Beniston 2006). It's widely known that the Alps experienced a temperature increase in the last century (Beniston 2003, Brunetti et al. 2009) especially at higher altitudes (Acquaotta et al. 2014). In addition, to the climate warming, the alpine chain suffered and it is still suffering an evident process of habitat loss as a consequence of forest expansion (Hunziker 1995, Gellrich et al. 2007) deriving from the abandonment of traditional land use practices (Hinojosa et al. 2016). Therefore, the Alps have already suffered noticeable loss of habitat and species (Pauli et al. 2007) and they are particularly under threat because these negative changes will probably continue in the future (Nogués-Bravo et al. 2007, Chamberlain et al. 2013, Pellissier et al. 2013). The alpine biodiversity has already responded to these adverse factors. Upward shifts of alpine plants (Walther et al. 2005, Pauli et al. 2012), butterflies (Vittoz et al. 2013) and mountain birds (Popy et al. 2010, Maggini et al. 2011) are documented. Also community composition changed at high alpine sites (Keller and Körner 2003) with an accelerating increase of species richness (Walther et al. 2005, Pauli et al. 2007). Even if some responses are evident, few researches focused on alpine biodiversity temporal changes. As mentioned above, alpine environments are under threat, therefore more information is needed to understand how the main adverse factors (climate warming and habitat loss) affected or are affecting the alpine biodiversity along altitude in time.

Exploring temporal patterns of biodiversity is of great significance because future warming and related environmental changes are expected to cause substantial changes not only in spatial distribution of species but also in species turnover in time (Korhonen et al. 2010).

Thus, long-term monitoring programs are fundamental tools to assessing and monitoring temporal changes of biodiversity. However, long time series are rarely available. Therefore, it could be intriguing meanwhile to focus on short-time scales, for investigating short-term biodiversity responses and understanding if there is a beginning of biodiversity temporal patterns or just a temporal fluctuation. Moreover, short-term responses could vary among different taxa, therefore, is fundamental to use a multi-taxa approach in order to investigate consistencies or dissimilarities between faunal groups.

The first aim of the research consisted in assessing the altitudinal changes of three different taxa (butterflies, ground beetles and birds) between two sampling periods (1st sampling period, 2006-2007, and 2nd sampling period, 2012-2013). Secondly, we investigated the temporal variation (1st vs 2nd sampling period) of species richness and of community composition for each target groups.

3.2 Study area and sampling design

The study was carried out in three protected areas in the northwestern Italian Alps (Piedmont and Aosta Valley regions): Gran Paradiso National Park (720 km^2; 44°25’N - 7°34’E), Orsiera Rocciavrè Natural Park (110 km^2; 44°75’N - 6°90’E) and Veglia Devero Natural Park (86,2 km^2; 46°18' N - 8°13' E). All areas are characterized by mountain and alpine conditions with vegetation ranging from mixed forest to rocky meadows and glaciers. The three parks have similar mean elevation values and vegetation characteristics, but display slight differences in terms of climatic regime (highest monthly precipitation and lowest annual mean temperature in Veglia Devero Natural Park) (figure 1).

Twelve altitudinal transects were set (one for each valley for each of the three parks) covering an altitudinal range of 1000 m, chosen from 500 to 2700 m a.s.l. and interesting three vegetation belts (montane, subalpine, alpine). Each transect is composed of 4-7 sampling units (plots) separated by an altitude range of 200 m, to allow for independence of sampled data, for a total of 69 plots. Sampling units are circular plots with a radius of 100 m, where monitoring activities have been carried out to provide presence/absence and relative abundance data of species belonging to investigated taxa (figure 1).

3.3 Faunal data

Data about butterflies, birds, and ground beetles, were collected in 2006-2007 and in 2012-2013, from April to October using, for each taxon, semi-quantitative census techniques that are, as much as possible, easy to apply, standardized, cheap and repeatable.

Birds were census by means of point counts with infinite counting range (Bibby et al. 1992). Counts lasted 20 minutes and birds were identified using acoustic and morphological characteristics. Each plot was visited twice during the reproductive season.

We sampled butterflies using walking transects along the diameter of the plot (200 m in length), walked at uniform speed. Following Pollard (1977), we recorded all butterflies seen within an imaginary 5 x 5 m square. Sampling was limited to sunny condition, under calm to light wind. Each plot was visited once a month from June to September. Individuals were captured and released after specific identification, except for specimens of difficult identification, retained for further determination.

We collected ground beetles using pitfall traps (plastic cups, diameter of 7 cm, filled with 10 ml of white vinegar). For each plot, the traps were set along the diameter, in a single row of five traps at a distance of 50 m from each other. The traps were collected and refilled every two weeks from May to October (figure 1).

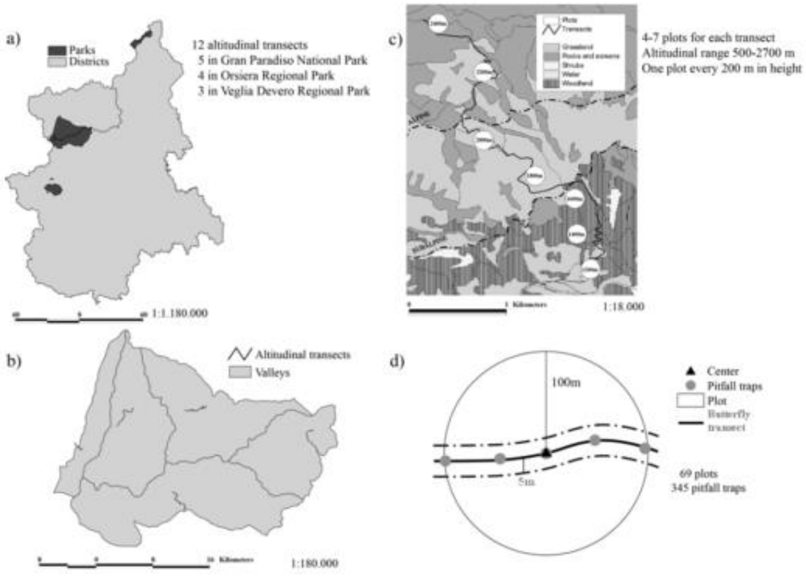

Figure 1. Description of sampling design. In 3 protected areas in the northwestern Italian Alps (a), data were collected along 12 altitudinal transects (b). Each altitudinal transect covers an altitudinal range of 800-1400 meters and three vegetation belts (boundaries are represented as dashed lines). Sampling areas are located every 200 m in height (c). The sampling unit is a circular plot, with horizontal radius of 100 m, where data on 5 different taxonomic groups have been collected (d).

3.4 Temperature data

Microclimatic conditions were measured by data-loggers (Thermochron iButton, DS1922, Maxim, Sunnyvale, CA, U.S.), located in each sampling plot, programmed to record air temperature every hour throughout the field season. Raw data were used to calculate following parameters: mean, maximum, minimum and standard deviation of daily measurements. Daily data were aggregate to obtain seasonal mean values for each parameters. Each sampling unit was also characterized by mean altitude

3.5 Land management and habitat data

We considered as land management data three categorical variable: grazing or mowing presence/absence and no activities. Data were noted during each sampling session for each plot.

Habitat data were obtained from an analysis of the main land cover types per plot, using aerial photos and the relative field validation (Agroselvilter 2009, Meloni et al. 2009). Data were collected during 2007-2008. Then, following the main habitat cover type, we classified each plot according to four categories of land cover: woodland, ecotone, grassland and rocks.

3.6 Data analysis

Changes in plot occupancy

To understand if and how species' distribution changes through time and explore the existence of a common pattern among the species of each taxonomic group, we analysed changes in occupancy between time periods. We defined occupancy as the number of plots occupied by each species in each sampling session (1st vs 2nd) and compared it by using a *t*-test for paired samples (significance level assessed after 999 randomizations, following Legendre and Legendre 2012).

To identify which group of species changes the most through time, we analysed if the occupancy equally increase/decrease between functional groups. We compared the changes in the number of plot per species (delta plot, the number of plots in the 2nd sampling session *minus* the number of plots in the 1st sampling session), among the ecological groups of conservation interest, identified independently for each taxonomic group, by using non-parametric test (Kruskal-Wallis or Mann-Whitney tests, depending on the number of ecological categories).

For butterflies we classified each species following the classification proposed by Balletto et al. (2016). We took into account the feeding specialization (from polyphagous to monophagous), the altitudinal range (generalist, medium altitude, specialised), the membership in the group of alpine species, the light preferences ("shade loving", "sun loving"), the temperature and water preferences, the dispersal capacity, habitat preferences (woodland, ecotone, open areas, screes), the length of flight period, the voltinism (monovoltine, multivoltine), and the hibernation strategy (egg, larva, pupa, adult).

For carabids, we classified each species in relation to feeding habits (predator and omnivorous, whereas we did not considered phytophagous because we found only three species belonging to this category), the dispersal capacity (short-winged, long-winged, species with both characteristics), habitat preferences (woodland, open areas, strictly hygrophilus species).

For birds, we considered the following categories: migratory behaviour (resident, short range, long range), altitudinal range (generalist, medium altitude, specialised), habitat preferences (woodland, ecotone, grassland), European population trend (increasing, decreasing, stable).

Altitudinal Range

We described the altitudinal range of each species with the following parameters:

- altitudinal optimum (mean and median of the altitude at occurrence plots);
- higher limit (absolute maximum, 90th percentile of the altitude at occurrence plots);
- lower limit (absolute minimum, 10th percentile of the altitude at occurrence plots).

To quantify the amount of change for each taxonomic groups, we compared these parameters between sampling periods with *t*-test for paired samples (significance level assessed after 999 randomizations, following Legendre and Legendre 2012). As in the case of occupancy rates, we also compared the changes in altitudinal range among the ecological groups.

Species richness

To analyse how species richness per plot changed through time, we compared it between sampling periods with *t*-test for paired samples (significance level assessed after 999 randomizations, following Legendre and Legendre 2012).

To understand if changes in species richness were mainly related to specific plot characteristics, we analysed it as a function of the following variables: altitude, temperature, geographic location, dominant vegetation cover (habitat type), dominant land use. We considered as dependent variable the rate-of-change (hereinafter *ROC*), defined as the differences in species richness between sampling sessions, divided per the species richness of the first sampling session. We analysed ROC through linear regression and we compared variables in a multi-model context, according to two criteria: (i) avoiding the simultaneous use in the same model of highly correlated predictors (Spearman's rs >0.5); (ii) choosing predictors to represent biologically meaningful combinations of predictive variables and consequently avoiding data dredging. All models were compared with the null model (intercept only) and all continuous variables were standardised, to permit comparisons among variables. The multivariate model selection was performed using Akaike information criterion, in its form corrected for small samples (AICc). As measures of goodness of fit, we calculated the adjusted R^2. These analyses were performed by R package *MuMIn* 1.7.2 (Barton 2012).

Community composition

We analysed community compositions by testing both for changes in location (significant changes in community composition per site over time) and dispersion over the years (significant changes in observed differences in community composition among sites, over time).

Changes in location were tested by applying non-parametric MANOVA to Bray-Curtis distance matrixes, to test if the multivariate centroids of species composition were, or were not, similar in the two groups (Anderson 2001; McArdle and Anderson 2001). Non-parametric MANOVA is an analysis of variance using distance matrixes and was performed by the function *adonis* of the *vegan* package (Oksanen et al. 2012). The significance of the test was assessed by using *F*-tests based on sequential sums of squares obtained from permutations of the raw data (999 permutations). Since we had to keep in mind the temporal structure and the spatial dependencies of our sampling design (62 sites at 2 points in time), we applied a restricted randomisation, which did not allow for permutations across samples.

Changes in dispersion were tested by the *betadisper* function of the package *vegan*, a multivariate analogous of the Levene's test for comparing group variances (Anderson 2001). Non-Euclidean distances between objects and group centroids were handled by reducing the original distances to principal coordinates. To test for significance, we applied a similar randomisation approach, as previously explained.

3.7 Results

Descriptive data

Butterflies. 150 species (133 of which found in both sampling session, 5 and 12 exclusive of the first and the second sampling session, respectively)

Carabids. 120 species (100 of which found in both sampling session, 9 and 11 exclusive of the first and the second sampling session, respectively)

Birds. 59 species (50 of which found in both sampling session, 3 and 6 exclusive of the first and the second sampling session, respectively)

Changes in plot occupancy

Butterflies. We observed a general increase in mean occupancy levels (n = 150, t = -8.15, p = 0.001; plot/species 1st = 8.85 ± 0.74, 2nd = 12.50 ± 0.96, change = 3.65 ± 0.45).

The occupancy did not change equally among ecological groups. Concerning feeding specialisation, specialised (monophagous) species differed from the other feeding groups (KW test, χ^2 = 9.82, df = 3, p = 0.020), even showing a slight decrease in the number of plot per species (polyphagous = 3.26 ± 0.99, one family = 4.10 ± 0.59, one genus = 3.68 ± 1.05, monophagous = -1.17 ± 0.98). We also recorded significant differences regarding the relationship with altitude. Altitudinal specialists increased less than the altitudinal generalists (KW test, χ^2 = 13.13, df = 2, p = 0.001; generalists = 6.12 ± 1.03, medium = 3.04 ± 0.48, specialists = 2.32 ± 1.55) and also high altitude species showed a significant less marked increase (MW test, W = 1070, p = 0.013, high altitude = 1.76 ± 1.32, others = 4.02 ± 0.46). "*Shade loving*" species showed on the opposite the highest increase in mean occupancy levels (MW test, W = 2269, p = 0.041, "shade loving" = 4.53 ± 0.67, "sun loving" = 2.71 ± 0.57).

Carabids. We observed a slight, but not significant, decrease in mean occupancy levels (n = 120, t = 1.84, p = 0.074; plot/species, 1st = 5.47 ± 0.56, 2nd = 5.17 ± 0.58, change = -0.31 ± 0.17).

We observed significant differences in mean occupancy levels between species with different feeding habits. In particular, the predators were stable through time, while the omnivorous species, and the few phytophagous one, showed a slight decrease in the number of plot/species (KW test, χ^2 = 9.28, df = 2, p = 0.010; predators = -0.01 ± 0.20, omnivorous = -0.83 ± 0.30, phytophagous = -2.00 ± 0.58). Also concerning habitat associations, we observed significant differences with the hygrophilus and woodland species remaining stable, while the species associated with open herbaceous habitats showed a significant lower delta plot (KW test, χ^2 = 7.39, df = 2, p = 0.025; hygrophilous = 0.00 ± 0.42, woodland = 0.41 ± 0.35, herbaceous = -0.62 ± 0.21).

Birds. We observed a slight increase in mean occupancy levels (n = 59, t = -2.56, p = 0.02; plot/species, 1st = 11.19 ± 1.37, 2nd = 12.15 ± 1.37, change = 0.97 ± 0.38), but we detected no significant differences in mean occupancy levels among ecological groups.

Analysis of the altitudinal range

Butterflies. We observed significant changes both at the minimum and at the maximum boundary of species' altitudinal range. At the lower altitudinal limit, we observed a significant decrease in the absolute minimum value (*t*-test, n = 133, *t* = 3.03, p = 0.004, change = -96.62 ± 31.85). At the higher one, we observed an increase in both the absolute maximum (*t*-test, n = 133, *t* = -3.08, p = 0.006, change = -75.19 ± 24.01) and in the 90th percentile (*t*-test, n = 133, *t* = -2.63, p = 0.014, change = 55.15 ± 20.97). We also observed significant differences in the altitudinal range changes between ecological groups. In particular "high altitude" species, compared to the others, showed a significant increase in the mean (MW test, W = 1657.5, p = 0.041; high altitude = 59.21 ± 21.24, others = -11.07 ± 18.09), the median (MW test, W = 1657, p = 0.040; high altitude = 59.37 ± 19.90, others = -8.72 ± 17.58) and 10th percentile (MW test, W = 1737, p = 0.012; high altitude = 68.12 ± 50.24, others = -72.11 ± 28.05) of the altitude at occurrence plot. "Shade loving" species, compared to the "sun loving" one, lowered their minimum (MW test, W = 2738.5, p = 0.014; shade = -164.18 ± 45.34, sun = -28.03 ± 43.47) and 10th percentile values (MW test, W = 2702, p = 0.027; shade = -74.10 ± 36.66, sun = -19.09 ± 34.14). Strongly vagile species increased their minimum boundary, while the others lowered it (KW test, χ^2 = 8.34, df = 2, p = 0.015; high = 139.29 ± 110.22, medium = -103.49 ± 37.93, low = -178.79 ± 62.12).

Birds. We observed no significant differences in the altitudinal limits of bird species, both considering them as a whole, both comparing groups of species with different ecological specialisation.

Carabids. We observed a significant increase at the lower boundary, both considering the minimum absolute value (t-test, n = 100, t = -2.83, p = 0.005, change = 81.00 ± 28.61) both the 10th percentile (t-test, n = 100, t = -2.03, p = 0.047, change = 38.10 ± 18.74). In spite of this, we observed no significant differences among the ecological categories.

Species richness

Butterflies. Species richness significantly increased from the first to the second sampling season (*t*-test, n = 62, *t* = -9.76, p = 0.001, change = 8.82 ± 0.90). The analysis of the ROC showed a significant effect of both land cover and land use: wooded habitats and managed plots increased the most (Table 1).

Birds. Differences in species richness among years are nearly significant (*t*-test, n = 62, *t* = -1.96, p = 0.055, change = 0.15 ± 0.05). Surprisingly, we observed a different rate of change depending on the geographic location of our plots. The plots located in the Cottian Alps (PNOR), representing the area with a milder climate, showed the highest ROC (Table 1).

Carabids. We observed no significant changes in mean species richness between sampling years. In the case of carabids, we observed an inverse relationship between the rate of change and the minimum temperature, but with a lower R^2 value if compared to the other taxonomic groups (Table 1).

	alt	**alt^2**	**park**		**rme**	**rmi**	**vegetation**		**use**		**Tmin**	**R-squared adj.**
butterflies							ecotone	-0.415 ± 0.137 ***	yes	0.284 ± 0.100 **	0.109 ± 0.124 *	24.64
							meadows	-0.192 ± 0.124 **				
							rock	-0.179 ± 0.199				
birds			foresto	0.290 ± 0.179								35.03
			pnor	0.619 ± 0.104 ***								
			pnvd	0.148 ± 0.115								
carabids											-0.157 ± 0.051 **	12.11

Table 1. Best linear regression model for each taxon. In the cells are indicated the coefficients (± standard error) of the selected variables. Adjusted r squared is indicated as a measure of goodness of fit. alt = altitude; alt^2 = altitude (second order); park = geographic location; rme = change in mean temperature; rmi = change in minimum temperature; vegetation = dominant cover type (land cover); use = land use; Tmin = mean seasonal minimum temperature during the first season. adj r^2 = adjusted R^2. *** $p < 0.001$; ** p = 0.01; * p = 0.05 .

Community composition

Butterflies. All the variables significantly influenced butterfly community composition, but focusing on the R-squared, geographic location (park) and altitude showed the most important role (Table 2). The interaction of season and each variables is significant but, in all cases, of low importance. Interestingly, we observed a significant changes in dispersion between season, with a lower dispersion around the median during the second sampling session (indicating a tendency towards homogenisation).

Variable	**Sampling sessions**	**F-value**	**R-squared**	**p**	**p (dispersion)**
season		5.87	1.91	0.001	0.001
park	**first**	5.31	21.54	0.001	0.006
	second	7.1	26.85	0.001	
	***season**	1.93	1.88	0.001	
altitude	**first**	8.14	29.63	0.001	0.015
	second	10.16	34.44	0.001	
	***season**	1.57	1.56	0.002	
vegetation	**first**	4.59	19.19	0.001	0.206
	second	4.82	19.96	0.001	
	*season	1.18	1.19	0.076	
use	**first**	2.11	3.39	0.029	0.001
	second	1.99	3.21	0.045	
	***season**	1.69	0.57	0.006	

Table 2. Results of the non-parametric MANOVA for the butterflies. We showed the relative role (expressed as R-squared) of sampling season and of categorical variables in determining community composition. For each categorical variable, we showed its effects during the first and the second sampling season, and its interaction through time. To represent the importance of each variable, we indicated the F-value, the p-values (after 999 randomisations) and the R squared of the variable. For each variable, we also indicate if the multivariate dispersion was significantly different among categories. Significant variables ($p < 0.005$) are indicated in bold.

Birds. In the case of birds, we observed a pattern similar to that of butterflies, but with an lower seasonal effect and no changes in multivariate dispersion through time (Table 3).

Variables	**Sampling periods**	**F-value**	**R-squared**	***p***	***p* (dispersion)**
Season		1.6063	0.40	0.039	0.715
park	**first**	3.0151	13.49	0.004	0.003
	second	3.5782	15.62	0.002	
	*season	1.8241	1.37	0.004	
altitude	**first**	13.947	41.91	0.001	0.006
	second	14.739	43.26	0.001	
	*season	1.7612	1.33	0.001	
vegetation	**first**	6.5631	25.34	0.001	0.044
	second	7.4582	27.84	0.001	
	*season	1.4291	1.09	0.034	
land-use	**first**	1.4001	2.28	0.198	0.001
	second	1.5114	2.46	0.188	
	*season	1.3884	0.36	0.093	

Table 3. Results of the non-parametric MANOVA for the birds. We showed the relative role (expressed as R squared) of sampling season and of categorical variables in determining community composition. For each categorical variable, we showed its effects during the first and the second sampling season, and its interaction through time. To represent the importance of each variable, we indicated the F-value, the p-values (after 999 randomisations) and the R squared of the variable. For each variable, we also indicate if the multivariate dispersion was significantly different among categories. Significant variables ($p < 0.005$) are indicated in bold.

Variables		**F-value**	**R-squared**	***p***	***p* (dispersion)**
season		1.45	0.32	0.057	0.559
park	**first**	6.36	24.76	0.001	0.142
	second	5.38	21.77	0.001	
	*season	1.62	1.09	0.172	
altitude	**first**	3.72	16.15	0.001	0.641
	second	3.56	15.55	0.001	
	*season	1.93	1.32	0.351	
vegetation	**first**	2.29	10.6	0.001	0.001
	second	2.83	12.79	0.001	
	*season	0.99	0.72	0.329	
land-use	**first**	2.22	3.56	0.013	0.841
	second	1.8	2.91	0.045	
	***season**	1.43	0.34	0.046	

Table 4. Results of the non-parametric MANOVA for the carabids. We showed the relative role (expressed as R squared) of sampling season and of categorical variables in determining community composition. For each categorical variable, we showed its effects during the first and the second sampling season, and its interaction through time. To represent the importance of each variable, we indicated the F-value, the p-values (after 999

randomisations) and the R squared of the variable. For each variable, we also indicate if the multivariate dispersion was significantly different among categories. Significant variables ($p < 0.005$) are indicated in bold.

Carabids. We observed a significant effect of each considered parameter in determining community composition, but no changes between sampling seasons. The effect of land use, and its changes through seasons, can be considered negligible due to the low R-squared (Table 4).

Temperature

Field temperature records indicated significant differences between sampling seasons, in particular concerning the monthly mean and minimum temperature observed during July, August and September (Table 5). Consequently, we can assert that the second sampling session was significantly warmer than the first one.

Temp	**Month**	**Intercept**	**Altitude**	**Year**	**Altitude*Year**	**R^2**
Mean	June	11.43	-2.46			80.2
	July	13.22	-2.72	0.11		91.9
	August	12.65	-2.62	0.2		87.8
	September	8.39	-2.45	0.28		89.2
Max	June	17.08	-1.76			46.8
	July	20.16	-2.03	-0.14		50.5
	August	19.35	-1.92			53.8
	September	15.38	-1.50			42.4
Min	June	7.33	-2.88			83.7
	July	8.3	-3.08	0.25		96
	August	8.29	-2.96	0.26		90.6
	September	4.22	--2.88	0.37		95.9

Table 5. Results from the best linear model indicating the role of altitude and year (and their interaction) in determining differences between sampling season for each month and temperature parameters.

3.8 Discussion

A long-term monitoring, periodically and systematically repeated through time (usually decades), is crucial to correctly understand the variables and the mechanisms determining species distribution responses and patterns of community composition as a consequence of climate and land use changes (Magurran et al. 2010, Magurran and Henderson 2010 Legendre and Gauthier 2013).

Recent studies have however proved how significant changes can happen also in shorter periods, highlighting the importance of verifying distributional and community changes at temporal interval lower than 10 years (short-term changes). Roth et al. (2014), in the Swiss Alps, described changes in community composition of birds, butterflies and plants along an altitudinal gradient in only 8 years. Erschbamer and Kiebacher (2008) showed how plant species richness in the Dolomites was significantly higher after 5 years only.

In this framework, our work on multi-taxa composition and distribution along altitudinal gradients in the NW Italian Alps represents an important step towards a better comprehension of biodiversity pattern in mountain ecosystems, even if restricted to a short time frame (2006-2007 vs 2012-2013). Indeed, understanding the spatial and temporal dynamics of species-rich communities is critical to understanding how environmental change will affect biodiversity (McCann 2007).

Drivers of change

Also in such a short time-frame, it is important to consider the role of potential drivers of change, analysing climatic and land cover changes (whenever occurring) as explicative predictors.

Concerning variations in temperature between sampling sessions (2006-2007 vs 2012-2013), we observed how the second sampling session had significantly higher minimum (+1.22 °C) and mean (+0.83°C) temperatures. Even if we cannot obviously refer these changes to a climate change in such a short period, the observed differences are coherent with the trend recorded by Beniston (2006) for the Alps. Indeed, he observed an increase in minimum and mean temperatures, but no trend in the maximum. Looking at the official weather stations of the Regional Meteorological Service, we moreover observed an interesting pattern in snow cover, characterised by a reduction in the number of days with snow and by a seasonal shift in snow cover towards the spring, in particular since 2005. This trend correspond to a common pattern for all the Alpine chain (Scherrer et al. 2015). Thus, our meteo-climatic parameters, showed significant differences between sampling sessions, because the second time frame

(2012-2013) occurs at the end of a period of increase in temperature and of variations in the seasonal distribution of snow cover. Such conditions should have determine a warmer climate, with lower differences between minimum and maximum temperatures.

Land cover changes, due to the natural evolution of vegetation following climatic changes and land abandonment, can be considered as minimal because of the short time frame of analysis. Indeed, we considered the main habitat type (dominant land cover) as a constant variable through time. Land use changes and habitat alteration can instead be considered absent, due to the status of protected areas of our study sites and considering that one of the main function of protected areas is to guarantee the stability of habitats and ecosystems (Gaston et al. 2008).

Species distribution (plot occupancy, altitudinal range)

Birds and butterflies showed a significant increase in mean occupancy levels, heavily more marked for butterflies than for birds, while carabids showed no clear pattern through time. This result is consistent with most of the patterns observed on these taxonomic groups over longer periods. Indeed, butterflies respond faster than birds (Devictor et al. 2012) and carabids in many cases showed no clear patterns through space and time (Kotze et al. 2011). Even if carabids are one of the most studied insect groups, the spatial scale at which they relate to resources is not completely understood (Kotze et al. 2011). However, they are usually known to perceive the environment at fine-scales of micro-climate and micro-habitat, selecting niches accordingly (Niemelä et al. 1992, Kotze et al. 2011).

Ecological and life-history traits may be good predictors of species distributional changes and shifts in their upper-elevation boundaries. However, few studies to date have examined their explanatory value, and results thus far are equivocal (Angert et al. 2011, Buckley and Kingsolver 2012).

Concerning butterflies, monophagous, altitudinal specialists and high-altitude species appeared to be more limited than the others were. Such categories comprehend species with high level of specialisation, consequently less prone to colonise new environments, even if climatic or environmental constraints will be relaxed. In particular, monophagous species are strictly limited by the presence and the quality of their single larval host plant and are already observed and also predicted to be highly vulnerable to climatic/environmental changes (Blois et al. 2013; Romo et al. 2014). Our results concerning butterfly specialisation are quite interesting and mirror what has been observed in central Europe concerning habitat specialisation, where a decrease of specialised and low vagile species has been observed along with an increase of generalist and good disperser (Habel et al. 2016).

Finally, high-altitude species are already limited in their distribution. Their presence is, in many cases, limited by minimum temperatures (Pellisier et al. 2013) and, consequently, they cannot lower their altitudinal range, neither in many cases, raise it, due to drastic changes in vegetation cover (a high occurrence in rock cover and a strong reduction of the availability of herbs and grasses). Moreover, the permafrost reduction, which is a relatively new and rapid phenomenon, make instable high altitude rock and screes, preventing the colonisation by plant species (Cannone et al. 2007). Indeed, high altitude species also showed a significantly higher increase in their mean, median and 10th percentile altitudinal parameters, corresponding to a reduction in their lower altitudinal boundary and in the surface available. However, we should also consider a limit of our sampling design, as we do not consider plots above 2700 m a.s.l., consequently reducing our possibility to observe an expansion toward higher altitude and a colonisation of new plots by high altitude species.

A significant higher increase in plot occupancy by "shade-loving" species compared to the others can be associated to a tendency towards a higher coverage of shrubs in the open areas at low and medium altitude. In the European Alps, the effect of climate change is regionally confused by human activities. Cattle grazing in the alpine pastures has been decreasing throughout the last century, allowing a fast recolonization by trees and shrubs, where the treeline had been artificially lowered (e.g., Vittoz et al. 2008b, EEA 2010).

Concerning carabids, we observed a decrease in phytophagous/omnivorous species and in species associated to open herbaceous habitats. A higher sensibility of species associated to open herbaceous habitats has been observed also in medium- and long-term studies, carried out in other environments. For example, in the UK, Bowler et al. (2015) observed that species associated with woodland and hedgerows were more stable than species related to upland pasture. Kotze and O'Hara (2003), in Belgium, observed that populations of large carabids associated with coastal, woodland or riparian habitat types were less prone to decline than populations of large carabids associated with open or grassland habitat types. Also in a recent research in the eastern Alps, a comparison of sites sampled through a time frame of 30 years, has been reported a stronger decline in the open sites above the treeline compared to the forest sites (Pizzolotto et al. 2014).

Concerning birds, we observed a slight increase in plot occupancy, but no changes along the altitudinal gradient. This is in part contrasting with some other European trends, where also in a short time period, altitudinal changes has been observed. In particular, in Switzerland, 64% of the bird species experienced altitudinal changes inside a short-time period (9 years, 1999-2007; Maggini et al. 2011). For the Italian Alps (Val Sessera, Piedmont), Popy et al. (2010)

did not find any significant shift at the community level, although most species showed an increment in altitude between 1992 and 2005. Also more recent studies, carried out in other geographic contexts, demonstrated that bird altitudinal ranges had changed over time (Auer et al. 2014; Massimino et al. 2015). Moreover, some recent studies have demonstrated the important role of species ecological traits in shaping the altitudinal changes of birds (Reif and Flousek 2012; Auer et al. 2014; Hovick et al. 2016), but we did not observe any differences among ecological groups. Our contrasting results can be partially explained by the short time period analysed and the stability in land cover, guarantee by the presence of protected areas as safeguard of habitat alteration.

Species richness

Only butterflies showed significant changes in species richness per plot inside the analysed period, while birds and carabids remained mainly stable. Butterfly communities are known to quickly change their arrangement because of environmental changes (New 1997; Thomas 2005), and previous studies indicated that butterflies might be responding faster than birds (Devictor et al. 2012). Indeed, it has been observed that birds respond relatively fast to contemporary environmental changes (in particular the climatic ones), but firstly through changes in abundances patterns, and more time is necessary to observe changes at the community level (Lindstrom 2013).

Moreover, birds and carabids stability through time can also be another clue that, inside the parks, the protection of the territory can guarantee more stabile ecosystems, safeguarded by short-term anthropic pressures. Many studies have indeed found a correlation between a reduction in species richness with high level of anthropic disturbance and/or habitat fragmentation, both in carabids and in birds (Brandmayr et al. 2007, Caprio et al. 2011 Wamser et al. 2012, Camargo et al. 2012,).

We observed a clear and significant increase in species richness within our temporal frame, mainly related to land cover and land management. The highest rate of change was clearly observed in the wooded areas, while ecotonal places (transitional areas, dominated by shrubs and mainly located inside the subalpine belts) showed the lowest rate. Also other authors observed similar results, although mainly related to individual species abundances. For instance, they observed a higher increase in species abundances simultaneously to an increase of temperature within forest areas respect to elsewhere (Sgardeli et al. 2016). Indeed, in days with high temperature and solar radiation, wooded areas can exert a tampon effects, protecting the individuals from extreme temperature and reducing temperature leaps, on the opposite of what happen in the open areas where they are exacerbated (Oliver and Morecrof 2014).

In the grazed areas, we observed an increase in species richness twice as much as in the unmanaged one. This can be probably explained with the low intensity, sustainable grazing we had there. Indeed, it has been already observed that grazing can increase the presence of plant species belonging to Poaceae and Fabaceae (Fischer and Wipf 2002), which represent the most used plant families as larval host plant by many butterfly species. Moreover, grazing maintains woodland clearings and open herbaceous areas below the tree line, which without management activities would be fast colonised by shrubs and trees (Nagy and Grabherr 2009).

Bird rate of change was related to the geographic location of the study site: we observed different rate of change, depending on the portion of the Alps in which we sampled. The highest rate of change was observed in the Cottian Alps, the warmer study place (except of the xerothermic area), characterised by the highest percentage of decidous woodlands. This can be easily justified because of the highest expansion, within the original altitudinal band, of woodland species related.

Carabids rate of change was the most difficult to be explained (lower adjusted R-squared) and resulted inversely related to plot minimum temperature. This means that the colder areas showed the highest relative increase in species richness.

Community composition

Even if we observed a quite huge amount of differences between our sampling seasons (for butterflies in particular), we did not observe substantial differences in community composition for none of the analysed taxonomic groups. These results were expected due to the short time frame of analysis.

Works that demonstrated variation in butterfly community composition take into account clearly longer time frames (e.g., Habel et al. 2016) and, at our knowledge, no works observe significant changes in community composition in such a short time frame. Also in birds has been observed that relatively short time frame are not enough to detect changes in community composition, as suggested by Lindstrom et al. (2012).

Concerning carabids, very little is known about the changes of ground beetle assemblages in the last few decades in the Alps (Pizzolotto et al. 2014).

Anyway, we interestingly noticed a tendency towards biotic homogenization in butterfly community composition. With the term biotic homogenization, we refer to the increase in biological similarity among communities, a replacement process leading to a decrease in distinctiveness in community composition over time, as a result of the replacement of some specialist species with other generalists, which become more uniformly distributed across previously different assemblages (Olden and Rooney 2006). Indeed, species respond individually to the changing environmental conditions, depending mainly on their physiological characteristics and habitat requirements (Davis et al. 1998; Parmesan 2006; Wilson and Gutierrez 2012). This determines new species assemblages, which can be appreciated only by the examination of the entire communities throughout time (e.g., Wilson et al. al 2007; LeRoux and McGeoch 2008; Walther 2010).

For example, a similar change in community composition over time, accompanied by an increase in community similarity, has been observed in the analysis of data from the UK Butterfly Monitoring Scheme through a period of 20 years (Gonzalez-Megias et al. 2008).

This tendency towards biotic homogenisation has been observed during the last decades in different taxa, following land cover and climatic changes (e.g., Eskildsen et al. 2015; Buhler and Roth 2011). Such phenomena often determine an increase in the generalist and highly vagile species, to the detriment of the others (e.g., Menéndez et al. 2006; Bonelli et al. 2011).

3.9 Conclusions

Appropriate management strategies require a deep understanding of the mechanism controlling losses and changes of biodiversity and of functional important taxa (Purvis and Hector 2000).

Over the last few decades, changes in species' distribution and communities' composition have already been analysed in some parts of the Alps. Nevertheless, data are usually referred to plants (e.g. Grabherr et al. 1994; Pauli et al. 2001; Vittoz et al. 2008a, 200b), or birds (Archaux 2004; Popy et al. 2010), with very little information deriving from other taxonomic groups, and mainly concerning changes in the distribution of single species (e.g., Battisti et al. 2005).

Responses to climate and habitat changes vary widely among species in the same communities. Consequently it is now interesting understanding the heterogeneity of species responses and the implications of the changes in communities' composition that follow (Wilson and Gutierrez 2012). Moreover, many previous studies that aimed at understanding changes over time in communities' composition, relied on the comparison of contemporary with historical data (atlases, collection specimens), which were often collected in a non-standardized way and/or referred to a much coarser spatial grain (Wilson and Gutierrez 2012).

Sampling units placed in well-specified areas represent a more appropriate tool (e.g., Archaux 2004; Viterbi et al. 2013) and our data from the Italian Alps, taken on exactly the same sites at a 4-years intervals, represent a first trial to try and fulfil these gaps, focusing on multi-taxa changes in mountain ecosystems and mainly considering community level responses.

Interestingly, and partly alarming, our results suggest that, even if the time-frame under analysis is relatively short, we already observed a huge amount of changes (mainly for butterflies), in particular considering that we are working in protected areas, where habitat alteration by direct human effects is strongly reduced. Considering these results, it is now even more important to continue our monitoring to understand in the next future if the observed patterns represent only transient changes or are the first signals of an imminent and worrying trend.

3.10 References

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Chapter 4 – Morphometric variation of ground beetles along an altitudinal gradient.

4.1 Introduction

Climate warming could affect not only species distributions but also morphological traits and their clines along altitude. Thus, the measure of the phenotypic variability along altitude could be a good proxy to assess the possible effects of climate change (Gardner et al. 2011).

Variation in body size could affect abundance and structure of populations, dynamics of communities, geographic distribution of species and their interactions and physical performance (Hildrew et al. 2007, Fisher et al. 2010, Chown and Gaston 2010). Moreover, body size directly affects the energy and water requirements for thermoregulation (Porter & Kearney 2009; McKechnie & Wolf, 2010), mass acquisition, metabolic rates (Koijman, 2010) and life-history characteristics (Roff 2002).

Therefore, understanding the mechanistic links between body size and environmental heterogeneity will allow identifying key traits that shape the potential of a species to respond to climate change and provide insights concerning thermal tolerances, information that currently lack for most of the species (Kearney et al., 2009).

Much of the focus has been on the increase in size with latitude or altitude, which is sometimes also known as the temperature-size rule, owing to the tendency for organisms to develop to larger sizes when reared at lower temperatures, and which has also been called a puzzle for life historians (Chown & Gaston 2010).

The pattern of endotherms along latitudinal and altitudinal gradients is well documented and normally larger body sizes are found in cold environments because of better ability of conserving heat in cold climates (Millien et al. 2006, Macholán et al.2008). Nevertheless, fewer researches focused on the link between body size, altitude and temperature (Gardner et al. 2011) and how these relationships vary among different geographic areas and species. Since the relevance of body size variation in indicating climate variability (Gardner et al. 2011, Eweleit and Reinhold 2014) and the alarming temperature warming of mountain areas (Beniston 2006, Brunetti et al. 2009), there is a need to gain more insights into the body size variability along altitudinal and temperature gradients.

Moreover, no convincing general hypothesis in explaining insect body size patterns along climatic gradients is currently available (Brhem and Fiedler 2004, Shelomi 2012).

Nevertheless, the morphometrics studies should still be performed, particularly in understudied insect orders and in light of the evolution of clines over time and the effects climate change may have on clinal variables (Shelomi 2012).

In this context, our study aims to detect a potential cline of body size of five ground beetles species along elevation and in different geographic locations. In particular we analyze the intraspecific variation of body size for five different species to underline the relative role of different abiotic (altitude, temperature, seasonality, geographic location) and biotic factors (vegetation type, sex, species richness and abundance). In areas very sensitive to climate changes like mountain, it is of particular interest to understand the importance of physical drivers as well as competition in influencing life history traits.

Among insects, carabids are good candidates for this kind of analysis because they are predator, they show sexual dimorphism and they display different dispersal ability that could reflect different aptitude to react to external drivers.

Intraspecific body size frequency distributions constitute a central component of macroecology (Gaston and Blackburn, 2000) and are the outcome of the kinds of physiological and ecological interactions typically investigated to understand the causal basis for size variation (Stillwell et al., 2010), but they have not been widely documented for insects (Gouws et al., 2011). In particular, the sensitivity to various factors makes the carabids as good indicators of the environment, despite the intraspecific variation of body size in carabids is poorly investigated (Sukhodolskaya 2014).

4.2 Study areas and data collection

The study was carried out in three different protected areas: the Gran Paradiso National Park (GPNP; 44°25’N - 7°34’E), the Orsiera Rocciavrè Natural Park (ORNP; 44°75’N - 6°90’E) and the Veglia Devero Natural Park (VDNP; 46°18' N - 8°13' E) (Fig. 1).

We used ground beetles data collected during the Alpine Biodiversity Monitoring program, a multi-taxa project started in 2006 (Viterbi et al. 2013). The project sampling design is based on 12 altitudinal transects that cover an altitudinal range between 1150 m and 2700 m a.s.l.. Each altitudinal transect is composed of 4-7 sampling units (circular plots of 100 m radius) separated by an altitude range of 200 m, for a total of 69 plots. Ground beetles were sampled, in each plot, using pitfall traps (plastic cups, diameter of 7 cm, filled with 10 ml of white vinegar). The traps were set along the diameter, in a single row of five traps at a distance of 50 m from each other. The pitfall traps were collected and refilled every two weeks, from May to October, for a total of 10 to 12 samples per plot, depending on the starting date (Figure 1).

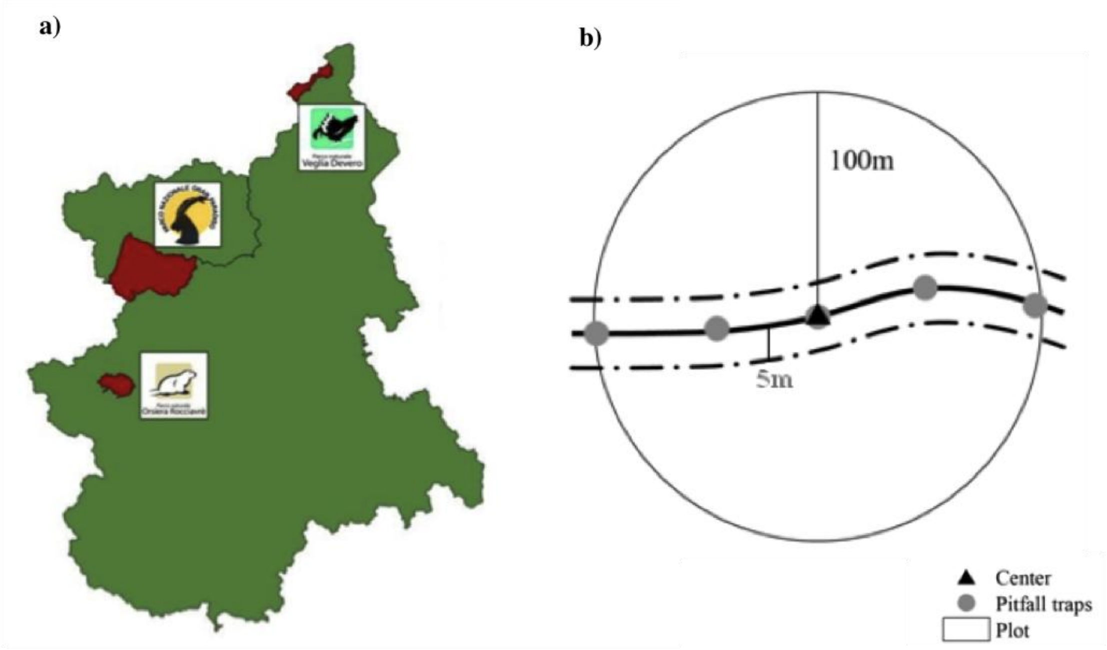

Figure 1. a) The three protected areas where the research were carried out. From north to south: Veglia Devero Natural Park, Gran Paradiso National Park, Orsiera Rocciavré Natural Park. b) Pitfall traps locations relatively to the sampling units (plot).

4.3 Morphometric data

For the study, we used ground beetles collected during the 2012 field season of the Alpine Biodiversity Monitoring program. In particular, we selected five ground beetles species that were equally distributed along the whole altitudinal gradient considered and among the three study sites: *Calathus melanocephalus*, *Carabus depressus*, *Pterostichus externepunctatus*, *Pterostichus multipunctatus* and *Pterostichus flavofemoratus*. For each specimen belonging to the five selected species, we measured seven morphometric traits and two body mass features:

- Total body length (TBL);
- Maximum length pronotum (MLP);
- Maximum width pronotum (MWP);
- Left elytra length (LEL);
- Right elytra length (REL);
- Maximum elytron width (MEW);
- Maximum thickness body (MTB);
- Left hinder femur length (LHFL);
- Right hinder femur length (RHFL);
- Ethanol-fresh mass (EFM);
- Ethanol-dry mass (EDM).

Using a binocular microscope (Leica 8x/25x), we took pictures of the anatomical traits for each specimen. Then, we measured six morphometric traits directly on pictures by using a specific software (LAS EZ version 3.0.0). Maximum Thickness Body was measured by means of electronic calipers with an accuracy of 0.01 mm. Each specimen was then placed on paper towel for 45 minutes and subsequently weighted on digital scale (0.0001 g) obtaining the ethanol-fresh mass value (EFM). For the ethanol-dry mass measures (EDM), we put the specimens previously weighted into an incubator set on 60°C for 48 hours. We then weighted them in order to obtain the EDM value.

Following this protocol, we measured morphological traits of 2176 specimens belonging to five species.

4.4 Data Analysis

We used the measured morphometric data to obtain four simplified "indices", describing carabid beetles mass and conditions. To assess the nutritional condition ("fatness") of carabid species, a *Condition Factor (CF)* has been calculated for each individual (Juliano 1986; Barone and Frank 2003). CF was obtained through the application of the relationship existing between body weight (EDM, ethanol dry mass, a more reliable measure than fresh weight to calculate CF, following Frank et al. 2007) and the elytra length (EL, the mean value between the right and the left elytra), expressed by this simple power function

$$\mathrm{EDM} = a * \mathrm{EL}^{b} \text{ (with a e b as constants)}$$

Resolving this regression curves, with the "*nls*" function of the "*stats*" package in R software (2016), we obtained the value of the constant "b" and consequently calculated CF using the following formula

$$\mathrm{CF} = \mathrm{EDM} / \mathrm{EL}^{b}$$

To identify the major axes of morphological and size variations, we applied a Principal Component Analysis to the 11 measured traits. We focused our attention on the first axis (*PCA*), which was highly correlated with most of the traits and accounted for a high percentage of variation in the data (Table 1) and can be consequently considered a synthetic measure of body size.

Traits	***Carabus depressus***	***Calathus melanocephalus***	***Pterostichus sp.***
Tbl	-0.959	-0.929	0.956
Mlp	-0.220	-0.92	0.902
Mwp	-0.668	-0.938	0.616
Lel	-0.952	-0.97	0.971
Rel	-0.949	-0.969	0.928
Lhfl	-0.813	-0.908	0.078
Rhfl	-0.776	-0.913	0.832
Mew	-0.899	-0.938	0.870
Mtb	-0.757	-0.659	0.855
Efm	-0.692	-0.604	0.648
Edm	-0.707	-0.738	0.700
% variation	62.23	75.92	63.66

Table 1. Correlation, expressed as Pearson correlation coefficient r, between the scores obtained by each individuals of each species along the first axis of a Principal Component Analysis and the morphometric traits, used in the analysis. Code of morphometric traits are explained in the main text. The percentage of variation in the original data, accounted for by the first PCA axis, is also shown.

As a third measure of body size and condition, we simply considered the *Total Body Length (TBL)*.

Finally, to analyse a measure usually used to assess environmental quality, we quantified the *Fluctuating Asymmetry (FA)*, expressed as the absolute differences between the right and the left elytra. FA is defined as a non-directional derivation from bilateral symmetry and it is used as a measure of developmental stability. In general, bilateral traits should be symmetric, because they are products of the same genome, but stress during the development can result in deviations from the symmetry of the trait. Thus, asymmetry might be a sensitive indicator of habitat quality (Weller and Ganzhorn 2004).

Each of these indices has been analysed as a function of the following explicative variables, used as representing different biological hypotheses underlining body size variations in mountain ecosystems:

- altitude (first and second order), to merely identify pattern along the altitudinal gradient;
- mean, minimum and maximum spring/summer temperature, measured through field locations of temperature sensosrs (iButton) at each sampling location, during the carabids sampling season in June-September 2012;
- dominant vegetation type (main land cover typology at each sampling plot);
- geographic location (protected area in which the sampling was carried out, as an expression of different climatic and biogeographic conditions);
- season (spring, summer, autumn);

- sex, to identify systematic morphological dimorphisms;
- abundance and species richness of carabids in each sampled plot, to explore the potential role of competition on body size and mass.

We analysed each of the 4 response variables (CF, PCA, TBL, FA) for *Carabus depressus* and *Calathus melanocephalus*, through linear regression and we compared explicative variables in a multi-model context, according to two criteria: (i) avoiding the simultaneous use in the same model of highly correlated predictors (Spearman's $r>0.5$); (ii) choosing predictors to represent biologically meaningful combinations of predictive variables and consequently avoiding data dredging. All models were compared with the null model (intercept only). The multivariate model selection was performed using Akaike Information Criterion, corrected for small samples (AICc). As measures of goodness of fit, we calculated the adjusted R^2. Concerning the *Pterostichus* genus, we analysed the three species together in the same multi-model framework, but using linear-mixed effects models and considering the species as a random effect. These analyses were performed by the R packages "*MuMIn*" 1.15.6 (Barton 2016) and "*lme4*" (Bates et al. 2015).

4.5 Results

The best linear models for each morphometric parameters of *Carabus depressus* are shown in Table 2. We observed high congruency in data coming from the first axis of Principal Component Analysis (inversely related to the parameters describing body mass), Condition Factor and Total Body length. The role of altitude, even if significant, can be considered of scarce importance, due to the small size effects. Other variables are more important in explaining the observed pattern, in particular sex and geographic location. Indeed, females are systematically bigger than males and individuals from the Graian Alps (Gran Paradiso National Park) are significantly bigger than the others. Fluctuating Asymmetry is higher in the transitional, unstable habitat of the subalpine ecotone, but the R-squared is in all the cases really low, indicating a poor fit of the models.

		PCA	**CF**	**TBL**	**FA**
Intercept		-0.133 (0.013)***	1.231 (0.132)***	2.006 (0.293)***	-0.112 (0.091)
Altitude		$0.312*10^{-4}$ (0.000)***	$0.162*10^{-3}$ (0.000)***	-0.0003 (0.000)*	
Altitude^2					
Altitude*Sex				-0.0005 (0.000)*	
Sex					
	male	0.073 (0.0043)***	-0.302 (0.030)***	-0.500 (0.390)	
T mean					
T minimum					
T maximum					
Vegetation type	**ecotone**				0.500 (0.157)**
	meadow				0.058 (0.210)
	rock				-0.023 (0.210)
Geographic location	**pnor**	0.041 (0.005)***	-0.108 (0.037)**	-0.839 (0.090)***	
	pnvd	0.023 (0.006)***	0.011 (0.039)	-0.385 (0.102)***	
Season					
	Spring		0.249 (0.102)*		
	summer		0.362 (0.103)***		
Abundance					
Species richness		0.001 (0.000)***		-0.0164 (0.005)**	
Adjusted R squared		55.12	29.75	60.67	4.38

Table 2. Best linear regression models for each parameters in *Carabus depressus*. In the cells are indicated the coefficients (with standard errors in brackets) of the selected variables. Adjusted r squared is indicated as a measure of goodness of fit. PCA = fist axis of Principal Component Analysis; CF = Condition Factor; TBL = Total Body Lenght; FA = Fluctuating Asymmetry. *** $p < 0.001$; ** $p = 0.01$; * $p = 0.05$

Calathus melanocephalus showed patterns partially congruent with *Carabus depressus* (females significantly bigger than males) and partially opposite (Table 3). In particular, species richness showed a positive relationship with dimensions (in all the three considered parameters) and the coldest and most isolated geographic location (Lepontine Alps, Veglia Devero Natural Park).

		PCA	CF	TBL	FA
Intercept		0.009 (0.013)	1.141 (0.110)***	-0.237 (0.190)	0.216 (0.213)
Altitude					
Altitude^2					
Altitude*Sex					
Sex					
	male	0.045 (0.009)***	-0.301 (0.078)***	-0.694 (0.136)***	
T mean					
T minimum					
T maximum					
Vegetation type	**ecotone**				-0.544 (0.259)*
	meadow				-0.233 (0.229)
	rock				0.468 (0.313)
Geographic location	**pnor**	-0.025 (0.014)	0.130 (0.115)	0.318 (0.200)	
	pnvd	0.035 (0.009)***	-0.241 (0.075)*	-0.552 (0.130)***	
Season					
	spring				
	summer				
Abundance					
Species richness		-0.002 (0.001)**	0.014 (0.006)*	0.040 (0.010)***	
Adjusted R squared		23.61	17.42	27.83	4.99

Table 3. Best linear regression models for each parameters in *Calathus melanocephalus*. In the cells are indicated the coefficients (with standard errors in brackets) of the selected variables. Adjusted r squared is indicated as a measure of goodness of fit. PCA = fist axis of Principal Component Analysis; CF = Condition Factor; TBL = Total Body Lenght; FA = Fluctuating Asymmetry. *** $p < 0.001$; ** $p = 0.01$; * $p = 0.05$

Concerning the three *Pterostichus* species, we observed a less clear pattern, with more variables influencing body mass and dimensions (Table 4). In particular, sexual dimorphisms (females bigger than males) and differences between geographic locations (smaller individuals in the colder places) are observed. We also recorded bigger individuals within meadows, respect to forest areas and ecotones, in particular when considering the first PCA axis and the Condition Factor. Fluctuating Asymmetry cannot be described at the genus levels. Indeed, even if we found models performing better than the null one, the amount of explained variations was particularly low (adjusted R-squared < 1%).

		PCA	**CF**	**TBL**	**FA**
Intercept		0.009 (0.029)	1.281 (0.220)	-0.151 (1.312)	
Altitude		$0.388*10^{-6}$ (0.000)	$0.282*10^{-4}$ (0.000)	0.0004 (0.000)***	
Altitude^2					
Altitude*Sex					
Sex	**m**	-0.022 (0.001)***	-0.263 (0.016)***	-0.759 (0.029)***	
T mean					
T minimum					
T maximum					
Vegetation type	**ecotone**	0.001 (0.001)***	0.068 (0.023)***		
	meadow	0.006 (0.001)***	0.234 (0.030)***		
Geographic location	**pngp**	-0.013 (0.035)***	-0.222 (0.255)**	-0.492 (1.603)***	
	pnor	0.004 (0.003)***	0.005 (0.078)**	0.200 (0.137)***	
	pnvd	-0.021 (0.035)***	-0.346 (0.256)**	-0.858 (1.604)***	
Season	**spring**	0.001 (0.001)	-0.057 (0.026)		
	summer	-0.0003 (0.001)	-0.044 (0.025)		
Abundance				-0.0001 (0.000)***	
Species richness					
Adjusted R squared - Marginal		16.56	21.37	22.85	NA
Adjusted R squared - Conditional		83.89	43.61	72.91	NA

Table 4. Best linear mixed-effect regression models for each parameters in the genus *Pterostichus*. In the cells are indicated the coefficients (with standard errors in brackets) of the selected variables. Adjusted r squared is indicated as a measure of goodness of fit (both the marginal and the conditional one). PCA = fist axis of Principal Component Analysis; CF = Condition Factor; TBL = Total Body Lenght; FA = Fluctuating Asymmetry. *** $p < 0.001$; ** $p = 0.01$; * $p = 0.05$

4.6 Discussion

Patterns in body size variations, as a response to biotic and abiotic factors, strongly depend on the species life history and ecology. Therefore modification in body size among the individuals of the same species may be interpreted as an indicator of ecosystem state (McGeoch 1998; Niemi and McDonald 2004).

To identify potential common trends and vulnerability to environmental and climatic changes, we focused our attention on five carabid beetles, characterised by different levels of dispersal capacity and habitat specialisation. All of them are in any case well widespread inside the investigated altitudinal gradient (1150-2700 m a.s.l.). *Carabus depressus* and *Calathus melanocephalus* are common and widespread in the NW Italian Alps. On the opposite, the species of the genus *Pterostichus* are characterised by a high level of endemicity. Nonetheless, we analysed the three species belonging to this genus (*P. flavofemoratus*, *P. externepunctatus*, *P. multipunctatus*) in a common framework.

Our results, according to differences in ecology and life-history between the analysed taxa, showed different patterns among species. However, for all the taxa, the most influential variables were interestingly the same, showing how the important factors in determining body size can be considered common even among different entities.

First, we observed for all the taxonomic units, a clear sexual dimorphism in body size, with females clearly larger and heavier than males. Such a pattern has already been documented in literature, even if not observed in all the carabid species, in particular in harsh environment such as the mountain ecosystems, and can depend on costs related to reproduction.

Calathus melanocephalus, a generalist species with no specific preferences neither in terms of habitat nor in terms of feeding habits, has been observed to be influenced both by the geographic location and by the number of coexisting species in the same area. Concerning geographic location, we observed that the northern and colder area hosted the smallest individuals (Veglia Devero Natural Park in the Lepontine Alps, near the Swiss border), following a pattern well described by the inverse of Bergmann's rule, but no effect of altitude or local temperature has been observed. This is consistent with the vagility of this species. Indeed we cannot be sure that specimen collected at a specific altitude and micro-climatic condition have been developed exactly there, although the massif of origin cannot be changed.

Higher species richness correspond to bigger individuals. Probably local scale density is not enough to reach carrying capacity and generates strong intra- e inter-specific competition. In our case, higher species richness can be a proxy of higher micro-habitat heterogeneity, consequently representing an opportunity to have more diversified resources.

On the opposite, *Carabus depressus*, with lower dispersal ability and displaying specific habitat and feeding preferences, showed an inverse relationship with species richness, that highlight its lower competition ability if compared to more generalist species such as *C. melanocephalus*. Smaller individuals, in particular in term of synthetic morphological index (PCA) and of Total Body Length, have been recorded at higher altitude, even if such pattern is not fully clear (low explicative power and effect size of altitude) and reversed for the Condition Factor. Even the geographic location is important in determining body size variation in *Carabus depressus*, but we observed the biggest individuals in Gran Paradiso

National Park, within the Graian Alps. No clear explanation is currently available for such a pattern, but can be probably found in the historical biogeography of this massif.

Carabid body size largely depends on habitat conditions and food availability during larval development (Niemelä 1993; Schwerk and Szyszko 2006; Sota et al. 2000). Carabid larvae are weakly chitinised and less mobile if compared to the adults, consequently they are particularly sensitive to habitat changes (Grandchamp et al. 2002; Magura et al. 2006). Such characteristics make carabids larvae potentially sensitive to seasonality. Indeed, we observed significantly smaller individuals of *Carabus depressus* during the autumn samples.

The *Pterostichus* genus seemed to be the most influenced by topographic and geographic patterns. Indeed, we observed both significant differences along altitude (with a decrease in size along the altitudinal gradient) and between geographic locations (with smaller individuals in the colder massif). A negative effect of habitat type, with bigger individuals found in meadows, can indicate that, even if this group of species are usually considered generalist, differences in fitness and developmental rate can exist between habitat types. Moreover, we observed a negative effect of abundance on Total Body Length. The species of the genus *Pterostichus* can occur in highly disturbed environments, where densities of generalist species can be very high and they are not consequently considered as good indicators of habitat quality. The observed pattern can show that *Pterostichus* species may reach lower mean dimensions in disturbed environments, suffering the competition and habitat alteration, although this point should deserve further analyses.

Unfortunately, data related to Fluctuating Asymmetry are not well explained for any of the species, suggesting the need to more deeply analyse this important parameter.

4.7 References

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