

# Climate tracking by alpine insect distribution across a century: concentric retreats, small refugia and strong elevational shifts in bumblebees

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## Abstract

Cold-adapted species endangered by global change are crucial cases for understanding range dynamics and its interface with conservation. In view of climate change and their sensitivity, Alpine insects should modify their distribution by reducing ranges, while being unable of sufficient displacements and mostly moving uphill. To test these hypotheses, we targeted four threatened, high-altitude bumblebees differing in subgenera and elevation ranges, and covering the main central and south European mountains. We performed species distribution models including climate and habitat, and we described elevation uphill and the year of change with broken-line regressions. Results indicate that climate change will cause severe future range contractions across large areas, more in the Apennines (80% - 85% ca) than the Alps and Pyrenees (24 - 56% ca), with mostly concentric retreats as future extents will nearly entirely be included in the present ones. Remarkably, since the '80s elevation uplift has started by about 325 - 535 m, a period coinciding with the beginning of the main warming, and will continue. The size and distribution of climate refugia will challenge conservation: they will be small and context specific (2-60% of current areas), but while in the Apennines and Pyrenees they will be nearly entirely within Protected Areas, only a third will be so for the Alps. Such impressive distribution changes demonstrates that cold-adapted bumblebees can accurately track climate change and be precise sentinels of it, and these results link with the investigated species being specialists with specific habitat requirements of temperature and glacier presence. Overall, the distribution of cold specialist bumblebees driven by climate change demonstrates that conservation should act upon the dynamic realities of species ranges because their range reduction, the impossibility of finding new areas and the movement uphill emerge as consistent patterns.

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Keywords: Bombus; Threatened species of bees; Alpine habitat; Temperature climate warming; Conservation of high altitudes; Range change

## Introduction

Climate shapes biodiversity in natural and human-dominated landscapes (Peters et al. 2019, Wieczynski et al. 2019, Biella et al. 2022). The growing concern towards climate change is increasing the research efforts aimed at understanding its effects on global biodiversity, to apply conservation efforts and a strong focus has been given to ecosystem indicators like insects (Harvey et al. 2023). Climate change effects have been observed in any kind of habitat and species, from deserts to high elevations (Kimball et al. 2010, Koot et al. 2022). Among the most evident and readily detectable consequences, the species distribution is rearranged by the new Earth climate, showing negative, positive or neutral range trends, with expansion or contraction patterns depending mostly on species thermal requirements (Hill et al. 2011, Williams and Blois 2018). Iconic cases are the thermophilic species, that have been reported to generally expand northwards or uphill thanks to warmer winters (Zait et al. 2020, Biella et al. 2021a, Stiels et al. 2021), but also the cold-adapted species that are retreating ranges due to climate warming (Marshall et al. 2020, McCain et al. 2021). While patterns of this kind have been widely detected, it remains urgent to better understand what are the underlying environmental features contributing the most to species trends and how this global change interplays with habitat features and species ecology (Stuhldreher et al. 2014). Under this view, it is crucial to detect, protect and improve areas that will constitute refugia against climate change and disturbance (Brambilla et al. 2022).

Climate change is especially stressing cold-adapted life forms (McCain et al. 2021, Seaborn et al. 2021) and the negative impacts are particularly acute in the arctic and alpine biomes (Pearson et al. 2013). The “cold biodiversity” is threatened by temperature warming and changes in precipitation regimes especially because of the melting of ice and snow surfaces, the expansion of forest at the expense of grasslands and the encroachment of species from lower elevational belts and latitudes, altering competition, causing changes in trophic interactions, reducing available resources (Brambilla et al. 2020, Körner and Hiltbrunner 2021, Kuo et al. 2021). Furthermore, in high-mountain areas, climate is changing faster than the global average (Nogués-Bravo et al. 2007). This warming is harmful because it accelerates the metabolisms of ectothermic organisms and it also increases the activity of harmful fungi and parasites (Scharsack et al. 2021, Bertini et al. 2021) or impacts survival and fecundity in different taxa (Irwin and Lee 2000, Williams et al. 2003), including cold-adapted bumblebees (Martinet et al. 2021, Ghisbain et al. 2023). These phenomena are often reflected by large population declines occurring in many species and, even more strikingly, by retreats towards the highest elevation, as for the case of orophylic bumblebees in the Alps and Pyrenees (Ornosa et al. 2017, Biella et al. 2017). Therefore, the spatial patterns of distribution changes due to climatic variations have the potential to diagnose the climatic sensitivity of biodiversity and warn towards a biodiversity-friendly management of cold areas (Brambilla et al. 2016, 2017).

Bumblebees are crucial high-altitude pollinators (Biella et al. 2021b). However, many bumblebee species are

facing negative population trends, range contraction and altitude shifts with climate change considered one main cause among others (Kerr et al. 2015, Biella et al. 2017, Marshall et al. 2018). Moreover, laboratory tests indicated a high sensitivity to high and extreme temperatures (Oyen et al. 2016) and field observations detected body alterations due to heat islands in urban areas (Tommasi et al. 2022). In fact, bumblebees are mostly linked to fresh and cold habitats (Condamine and Hines 2015) and their diversity thrive in many mountain regions. Their high sensitivity and key role for ecosystem functioning make these organisms an ideal model to investigate the effects of climate change on mountain biodiversity and ecosystems.

Based on their sensitivity to climate and especially to temperature (Ghisbain et al. 2023), bumblebees should possess a high ability of tracking thermocline variation over time. Therefore, in face of the past and future climate change, we expect bumblebee species of cold areas to suffer range contraction: considering the realised and predicted magnitude of climate change, such variations should be evident when comparing the current patterns with both the past and future ones (Hypothesis 1, “H1”). Moreover, in the case of range variation, we hypothesise that such changes could happen mainly by concentric retreats (i.e., abandoning peripheral areas) rather than by displacement (i.e., by colonising new areas in the future) (Hypothesis 2, “H2”). This pattern can be expected because mountain orography and uneven distribution of cold microhabitat could limit dispersal (Ceresa et al. 2023), in particular when the species are habitat specialists (Alessandrini et al. 2022). Furthermore, by tracking their optimal thermal niche under a changing climate (Harvey et al. 2023), cold-adapted bumblebees should also undergo a strong upward shift in the average elevation of their occurrence sites and range (Hypothesis 3, “H3”). In this concerning scenarios, the critical study of the distribution of climate refugia and their spatial relation with protected areas will also inform area prioritisation for conservation, under adaptive conservation strategies (Rannow et al. 2014).

To test the three hypotheses formulated above and critically investigate the conservation challenges posed by ongoing and future distribution patterns of cold adapted species, this study focuses on four bumblebee species occurring on mountain areas in the southern and central part of Europe, differing in mountain chain orientation, mean elevation and extent (Kapos et al. 2000). Given these differences, we expected to see idiosyncratic responses to climate change by area at the regional level, i.e. the bumblebee ranges in different chains showing responses of different magnitude to climate change. Acknowledging these regional patterns is crucial for effective and ‘realistic’ conservation strategies, tailoring area-specific actions.

We focus on four cold-adapted bumblebee species and consider (i) the changes in occurrence elevation over past decades and in the future, (ii) the predicted distribution of suitable areas at present and under future climate, to highlight patterns of distribution change at the regional level, (iii) the distribution of climate refugia in relation to the Protected Area Network. Because the four species are often difficult to detect, either because of their rarity or because they occur in areas of difficult accessibility (i.e. high mountains), we combined approaches based on known occurrences and on Species Distribution Modelling integrating environmental variables of habitat and climate. In this way, we obviated the lack of complete knowledge on their distribution and retrieved clear ecological patterns that will aid conservation efforts of these species.

## Methods

### *Species, study area & species locations*

Four species are particularly known for their link to cold areas and for their rarity: *Bombus alpinus helleri*, *Bombus mendax*, *Bombus mucidus* and *Bombus konradini*. *Bombus (Alpinobombus) alpinus* (Linnaeus, 1758) has a disjoint distribution, as the subspecies *alpinus* occurs in the high Fennoscandia and *helleri* occurs in the Alps at the highest elevation and formerly in the Carpathians, where it is now considered extinct (Rasmont et al. 2015, Biella et al. 2017). *Bombus (Mendacibombus) mendax* Gerstaecker, 1869 occurs at the highest elevation of the Alps with the subspecies *mendax* (Amiet et al. 2017) and of the Pyrenees with the subspecies *latofasciatus* Vogt 1909 (Ornosa et al. 2017), with a few more records on the Cantabrian mountains (Santamaría et al. 2011). *Bombus (Mucidobombus) mucidus* Gerstaecker, 1869 occupies the middle and high elevations of the Alps and of the Apennines (Manino et al. 2007), it occurs in the Pyrenees and it occurs also locally on the Cantabrian Range (Ornosa et al. 2017) and patchily in the Balkans and the

Carpathians (Rasmont et al. 2015). *Bombus (Pyrobombus) konradini* Reinig 1965 (i.e. the central Apennines populations of the formerly known *Bombus monticola konradini*) occurs exclusively at the high elevations of the central section of the Apennines and little is known on its ecology (Ricciardelli D’Albore and Piatti 2003).

The study area encompasses the Alps, the Apennines and the Pyrenees. Occurrence locations were retrieved from the literature, private and museum collections, with details available in supporting text A1. The coordinates of the records were visually validated with satellite images (i.e. corresponding to alpine areas in a broad sense and within the known elevational range of the species); unlabelled, inconsistent, dubious or duplicated data were excluded. Cumulatively, 1771 data were available for the analyses: 172 for *B. alpinus*, 722 for *B. mendax*, 826 of *B. mucidus* and 50 of *B. konradini* from the Alps, Apennines and Pyrenees study areas (we excluded the Cantabrian Range and Balkans because of too scattered and mostly old records available from there). As the investigated species are large and conspicuous, they are unlikely to go undetected and these available records are representative for describing the distribution with sufficient accuracy. The datasets used in the analyses constitute the most comprehensive ones available for the study species.

#### *Climatic and land-use variables, present and future scenarios*

To avoid possible mismatches between observations and climatic variables, we excluded from the analysis the records before 1970 and those without date (time range: 1970–2018, but for *konradini* 1960–2020 due to the few data available). Three different categories of possible environmental drivers were considered: climate, topography, and land-use/land-cover (LULC). Climatic variables were derived from the database CHELSA V2.1 (Karger et al. 2017, 2021), and were the following ones: mean annual 2-m air temperature, annual range in 2-m air temperature, sum of annual precipitation, precipitation seasonality (Thuiller et al. 2019), all calculated for the period 1981–2010. Topographic variables were computed starting from a fine-scale digital elevation model (25 m-resolution; EU-DEM v1.0, publicly available from the European Environment Agency). Finally, LULC variables were obtained from the CORINE land cover map (*Corine Land Cover — European Environment Agency*, 2018). All variables were then estimated for  $1 \times 1 \text{ km}^2$  cells, as average values (climate and topography), or as proportional cover (LULC). When needed (climatic variables), raster resampling was carried out by bilinear interpolation. LULC categories with negligible cover were excluded, while some other categories poorly represented were merged (Supporting text A2). The variables so worked out showed relatively modest correlations ( $r < |.7|$ ; Grimmer et al. 2020).

To describe possible alternative future climates on the medium-term, we relied on the downscaled CMIP6 (Coupled Model Intercomparison Project Phase 6) data, choosing the period 2041–2070, and two alternative climate models (a ‘warmer’ one and a ‘colder’ alternative) as provided by ISIMIP (Intersectoral Impact model Intercomparison Project; Warszawski et al., 2014): GFDL-ESM4 and UKESM1-0-LL. Those data are tailored for such a kind of application. For both climate models, we picked the ‘worst case’ scenario SSP585 and the moderate change one SSP370 (Eyring et al. 2016). Therefore, we based our assessment on four alternative climatic conditions for the future, based on the combination between two very different climate models and on two different scenarios. Also those data were retrieved from the CHELSA V 2.1 database.

#### *Species distribution models*

To work out species distribution models (SDMs), we relied on the method proposed by Brambilla et al. (2022). Such an approach involves building maximum entropy models using MaxEnt (Phillips et al. 2006) in the software R (R Core Team 2020) by combining different packages. We used only MaxEnt because of the many advantages it offers advantages over alternative methods: it is the commonest algorithm for SDMs, it limits the potential undesired effects of false absences (Jiménez-Valverde et al. 2008, Elith et al. 2011), often performs better than other methods or ensemble modelling (Kaky et al. 2020), and has been already used to model distribution and potential changes for other species on similar same mountain ranges (Brambilla et al. 2022). We scattered 79393 background points (the highest possible number of independent locations) within a 10-km buffer drawn around all bumblebee records, to ensure that background points are placed in areas actually sampled or close to sampled ones, to adequately represent sampled environmental conditions

(Brambilla et al. 2020).

By means of the ‘checkerboard 2’ method of the ENMeval package (Muscarella et al. 2014), occurrence data of each species were partitioned into two spatially independent datasets. In case of records of the same species overlapping within the same grid cell, they were considered as duplicates and only one was retained for the analyses. Training datasets included occurrences from three partitions, and testing datasets those from the remaining fourth one. We only fitted linear and quadratic relationships to reduce possible overfitting. The regularization multiplier was first selected by testing 0.5-increase values between 0.5 and 5, and that leading to the lowest AICc was chosen to build a base model.

Then, all the variables showing lambda equal to 0 (i.e., no tangible effect on species distribution) were discarded. A variable selection procedure was then carried out by leaving out one variable at a time according to increasing value of permutation importance, until the model’s AICc increased. We thus identified a most supported model, which was then subject to further tuning. Linear and quadratic features and the value of the regularization multiplier were checked again, if needed changed (always according to AICc), and a final model was thus produced and used for model evaluation and distribution prediction. The Area Under the Receiver Operating Characteristic (ROC) Curve (AUC), as well as the True Skills Statistics (TSS), were computed over training and testing data sets and used for model evaluation, together with the computation of the omission rates over the test dataset, both at the 10<sup>th</sup> percentile and at the minimum training presence, both computed on the training presence dataset. The two omission rates should be close to 0.1 and to 0, respectively, whereas AUC and TSS should be similar over the training and testing datasets as their absolute value is poorly informative (Lobo et al. 2008). The final model was used to predict a species’ environmental suitability according to its *cloglog* outputs. For further details, see Brambilla et al. (2022).

The distribution models obtained according to the above procedure were then used to predict environmental suitability over current and future conditions. From each map of predicted suitability, we derived a potential range by considering as suitable for a species all cells with an environmental suitability value higher than the tenth percentile threshold, considering the *cloglog*-transformed output. We selected such a threshold over the possible other ones as its use led to the results most consistent with the known actual distribution of the target species (Brambilla et al., 2022). To estimate the extent of the relative range under current and future conditions, the potential distribution so obtained had been overlapped with the extent of the mountain ranges respectively occupied by each studied species. Since mountain ranges were not available in public repositories as shapefiles, each mountain range was identified by selecting areas above 300 m a.s.l. (elevation threshold was taken from Kapos et al., 2000) within the commonly recognized geographic boundaries of Alps, Apennines and Pyrenees.

We calculated in-situ and ex-situ refugia from the distribution inferred from the above models and projections. We defined “refugia” the areas that probably will be suitable “in-situ” or “ex-situ” for each target species and region, following Brambilla et al. (2017): (1) “in-situ” areas suitable under current and all future conditions, (2) “ex-situ” potential areas, currently unsuitable for a species, but suitable under all future models. While “in-situ” refugia are fundamental for population resistance, “ex-situ” ones are key sites for future redistribution and resilience. Moreover, the refugia were overlapped with the current Protected Area network, obtained by merging Natura 2000 sites with the European inventory of nationally designated PAs (Nationally designated areas; CDDA), updated in 2020 (<https://www.eea.europa.eu/data-and-maps/data/nationally-designated-areas-national-cdda-15>; accessed 2 Feb 2021).

#### *Elevation use over time*

Changes in elevation were analysed by applying a “segmented” (or “broken-line”) regression model with record elevation as a response, and the year as a predictor. We obtained the best-fit breakpoint value with the *davies.test* function of the ‘segmented’ library in R (Muggeo 2003). Additional break-points were tested by applying the *davies.test* to each time frame previously detected. Linear regressions were performed on the two obtained intervals (namely to the left and to right of the breakpoint value), a t-test was applied to compare the two regression slopes. For these analyses, we included observations older than 1949 in order

to include data evenly distributed over time. Only for *B. konradini* different analysis was used: as the few records are unevenly distributed over time, we grouped them in three ranges: “1960s” from 1961-1963, “1980s-1990s” from 1984 to 1998, “2010s-2020” from 2011 to 2020. To calculate the uphill shift, we considered the difference in 25% quantile elevation values of the oldest 40 observations in the recent and the older time group, although we calculated the differences also with other quantiles too for comparison.

## Results

### *Models of present and future distribution*

*B. konradini* is the bumblebee with the narrowest suitable range of only 767 km<sup>2</sup>, while *B. mucidus* and *B. mendax* are estimated to occur in the study areas over 80445 and 56716 km<sup>2</sup>, respectively, and *B. alpinus* in 21875 km<sup>2</sup> (Figure 1). Regionally, the current suitable areas of the studied species are largest in the Alps, while Pyrenees and Apennines harbour much smaller suitable extents: *B. mucidus* has ca 20 times smaller range in the Apennines and 2.6 times on the Pyrenees compared to that of the Alps, while *B. mendax* has ca 8 times smaller range in the Pyrenees compared to that of the Alps.

These bumblebees occur in areas with specific climates and habitats, as all species demonstrate a narrow or very narrow thermal range; average temperature stands out as the most important driver of distribution in all species but *B. konradini* (for which average temperature is anyway important). In addition, the distance from glacier edge and forests were important predictors for some of the studied species. The importance of variables included in the model for each species is reported in Table 1, and the main effects of the most relevant ones are shown in Supplementary Figure S1.

In future, all studied species are expected to shrink their distribution (Figure 1), confirming our first hypothesis (H1), although with different magnitude depending on the climatic model and on the mountain chain (Table 2); the future suitable areas will correspond to 6-80% of the current suitable extent according to the different combinations of species / area / climate model (Supplementary table S1). Under models predicting severe warming, future areas resulted in higher contraction and therefore less overlap between present and future distribution, compared to those predicting moderate warming (Table 2). Specifically, on average across models, the Apennines part of *B. mucidus* and *B. konradini* range will contract dramatically (ca 80%, but up to ca 94% in specific models), and Alps and Pyrenees will host severe contractions by about 40-56% in most cases, while only the Alpine range of *B. mendax* will shrink by 24%.

Most of the future areas will be within the current suitable range: on average 60-100 % of future areas will be included in present ones (Supplementary table S2). However, only a small fraction of future areas will constitute in-situ or ex-situ refugia (Table 3): only 2-6% of the present suitable areas in the Apennines, 23 and 35% ca of currently suitable areas in Alps and Pyrenees in most cases, and about 60% in the Alps for *B. mendax*. On the other side, while only about one third fall within current protected areas in the Alps, those from the Apennines and Pyrenees are almost entirely included. Ex-situ refugia are extremely small compared to in-situ refugia, and only *B. konradini* will have broader ex-situ refugia; their percentage of protection follows what is observed for in-situ refugia. Therefore, our second hypothesis H2 was largely confirmed, with the partial exception of *B. konradini*.

### *Elevation use over time*

All bumblebees tested for elevation shift over time have significantly changed their altitude from a given year or time range. *Bombus alpinus*, *mendax* and *mucidus* have uplifted since the ‘80s and similarly *B. konradini* changed sometime between the 1960s and the 1980s considering that the data are unevenly distributed in time (Figure 2, Table 4). In *B. alpinus*, *mendax* and *mucidus*, the year of record was a significant predictor in the most recent time interval, but not in the older time interval and the slopes of the regression lines at both sides were significantly different (Table 4). In *B. konradini*, the records from the 60s were significantly different in elevation from the more recent year groups, which were not different from each other (Table 4). The estimated elevation uplift resulted large in all species, between ca 325 and 535 m, but it is important to note that occasional records were present also below the calculated elevation range and that the estimate

changes depending on the chosen quartile (Supplementary table S3). Under future scenarios, the elevational shift is predicted to continue considerably, based on the distribution of the suitable patches (Supplementary table s4). Hypothesis H3 was therefore fully confirmed by the observed and predicted shifts.

## Discussion

We tested three hypotheses concerning climate change and alpine insects, by exploring the responses to climate change of four bumblebee species currently inhabiting cold areas of the mountains of southern and central Europe, a part of the world under severe, unprecedented warming and climate change. Here, we explored the environmental features associated with the species distribution, modelled the present distribution to infer future occurrences under realistic climatic conditions, identified the distribution refugia constituting priority areas for conservation and estimated the elevational shift over time.

### *Responses to future climates and conservation*

The four cold-adapted bumblebees will dramatically shrink their ranges as the distribution models unanimously predicted negative responses to future climate change, despite their different geography and different subgenera, thus fulfilling our hypothesis H1. The severe range contractions predicted for the 2070s are particularly alarming as these bumblebees are already enlisted in categories of extinction risk from what had been observed in recent times (Nieto et al. 2014, Quaranta et al. 2018) and our study shows that future climate dynamics will add up to the current negative trends and threats. Responses as these are expected and observed in a range of cold-adapted insects (Koot et al. 2022) and, to some extent, also on endotherms organisms in the same contexts (de Gabriel Hernando et al. 2021, Brambilla et al. 2022), making it very likely that H1 is a general rule for animals of cold areas.

The severe future range shrinkage will likely be “concentric”, because most future areas are predicted to occur within the current suitable ones, while large surfaces will turn into inhospitable land. This result supports the hypothesis H2 and adds evidence to what was observed in previous studies in North America that clarified the determinant role of changing temperature in causing range loss in bumblebees (Jackson et al. 2022). Similar results were obtained in alpine grasshoppers and are concordant with other bumblebee species (Martínez-López et al. 2021, Koot et al. 2022). Therefore, it is clear that the strong future alteration of the current distribution pattern will further imperil the lasting of these pollinators. Furthermore, our study demonstrated that refugia areas estimated suitable by all scenarios will be of small size, especially in the Apennines. Thus, the remaining patches will be important refuges for the four bumblebee species studies, and conservation measures should be strengthened there.

Some differences in shrinkage amount were detected among mountain ranges, with the conditions in the Apennines being particularly harsh in the future for the two studied bumblebees occurring there. For instance, *B. mucidus*, which occurs in all the three mountain ranges, will decrease on the Apennines by a percentage almost twice those of the other ranges. Likewise, the Apennines endemic *B. konradini* will largely shrink its distribution. A similar scenario is expected for other local elements of fauna and flora of this mountain range. The Apennines range of two high-elevation butterflies will be considerably small and even possibly disappear in future years (Sistri et al. 2022, Bonifacino et al. 2022). Likewise, the area occupied by some Apennines rare plants will considerably shrink (Di Musciano et al. 2020). We suspect that differences in orientation, elevation range, general climate and in diversity and extent of microhabitats among the three massifs investigated here could explain these differential responses, although without affecting the validity of H2. However, future research efforts on understanding why the Apennines seems to be so subjected to distribution loss in cold adapted species are clearly a priority, given that this region will also pose important conservation challenges for preserving its cold adapted fauna and flora.

Unfortunately, considering the unprecedented and fast rate of climate change, it is difficult to estimate the efficacy of conservation measures. Nevertheless, in a previous study, Biella et al. (2017) suggested applying conservation measures for decreasing the non-climatic stresses often associated with mountain environments, such as the impacting tourist activities and the competition by domestic grazers. Future, additional, efforts and studies could integrate physiological aspects into conservation by valorizing potentially different response

abilities to heating in different populations, as previously proposed for reptiles (Besson and Cree 2011). A critical consideration regards refugia: it is surely a promising measure to protect and apply mitigation strategies within areas that represent in-situ refugia (shared by present and future scenarios) and also ex-situ ones (only in future scenario) under a dynamic view of area conservation. Given that climate refugia are key areas for the endurance of species facing challenges by global change as these are likely to preserve suitable environments (Brambilla et al. 2022), they must be considered as priority areas for targeted conservation efforts. The fact that in certain parts of the ranges a high proportion of refugia lies within the Protected Area network could promote the implementation of conservation measures.

#### *Current distribution and environmental relationships*

Our study demonstrates that the four cold-adapted bumblebees occupy a rather narrow environmental niche as the higher environmental suitability for each species is associated with a rather narrow range of climatic and habitat variables, that could be the mechanism why H2 holds true in the context of cold-adapted animals. Thus, by being specialists, they are usually rare in the field and will suffer from severe range contraction in future. In other words, environmental variations over time, between years or due to weather extreme events are likely to affect the populations and therefore the distribution, as observed for the population density fluctuations in *Bombus alpinus* (Rasmont et al. 2015). Moreover, previous studies suspected that heat waves could exert a strong impact on bumblebees (Iserbyt and Rasmont 2012), which seems realistic also for cold-adapted bumblebees considering their ecological niche. Of particular concern are the temperature and glacier dependencies of the environmental niches, given the temperature warming and especially the dramatic ongoing glacier contraction (Zemp et al. 2015). Therefore, especially the warming and the glacier melting rate seriously imperils the fate of the alpine ecosystem and the cold-adapted bumblebees.

#### *Elevation shifts and the fate of cold-adapted bumblebees*

Average elevation of occurrence sites by the four bumblebees had considerably moved up, thus validating hypothesis H3: for all species the altitude shift so far occurred and predicted to happen in future is very high, although with varying estimates depending on the species. A unifying element is also the fact that the up-hill trend has started since the mid 1980s for all species, and will continue in future. Changes in elevation have been already observed in a number of bumblebees (Manino et al. 2007, Ornos et al. 2017, Biella et al. 2017). The beginning of the elevational shift (the 1980s) is not surprising considering previous results on an alpine bumblebee (Biella et al. 2017) and that also thermophilic lowland bumblebees started expanding their range exactly from the 1980s (Biella et al. 2021a). This is confirmed by climatic data indicating that since the 1980s the warmest period of the last 800 years has started in the Northern Hemisphere (IPCC, Intergovernmental Panel on Climate, 2014), warming high elevation areas as twice as the global average during the 1980s and 1990s at a rate of 0.4 °C/decade (Pepin and Seidel 2005). In cold-adapted bumblebees occurring at high elevation, a continuous uphill shift of elevation range raises serious concerns for their fate, considering both the upper limit of the mountains and the reduction of land surface as elevation increases in pyramidally shaped mountains. These concerns are fuelled by the fact that future climate will particularly warm high elevation areas (Thuiller et al. 2005). Therefore, investigating and identifying possible microrefugia is a valuable option for further research that could eventually inform conservation practices, and for the fine-scale designation and management of priority areas.

## **Conclusions**

Bumblebees of cold environments in the main European mountains act as sentinels and respond in a similar way to global climate change by shrinking their distribution and shifting uphill in elevation, in spite of having different distributions and life histories. This will likely lead to issues such as habitat loss, reduced surfaces for acquiring resources and finding mates. Furthermore, it is possible that future scenarios will also contribute to the erosion of genetic diversity, as a low genetic diversity has been found in declining bumblebees (Cameron et al. 2011) and also in other high-elevation specialist species (Bauert et al. 1998, Rubidge et al. 2012). This scenario challenges dramatically any conservation effort but attention should be directed towards the dynamic realities of species ranges.

The narrow future ranges and small refugia will lead to conservation issues for cold-adapted bumblebees. However, conservation should take in full consideration the dynamic realities of species ranges over time and that refugium areas may be target of conservation priority considering in situ and ex situ locations. Moreover, a useful tool could be updating the country- and continental-level Red Lists in light of the results presented in this study, and the different responses among mountain ranges highlight the need for regional lists at smaller scales. Furthermore, protecting and keeping high habitat quality and microhabitat diversity in current and in refugium areas will be the first pillar for any reasonable conservation plan. Other future conservation actions could also integrate biogeographical and genetic evidence in order to further tailor the design of conservation priority areas and therefore help outlining specific measures to preserve these species.

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## Tables –

Table 1. Permutation importance of environmental variables (VIP) included in the selected distribution models for each bumblebee species. In bold the cases > 10 VPI. The variable codes are further explained in the Supporting text A2.

Variable code	Variable	B. alpinus	B. konradini	B. mendax	B. mucidus
bio1	mean annual air temperature (°C)	<b>61.3 ± 0.032</b>	<b>28.4 ± 0.04</b>	<b>51.2 ± 0.014</b>	<b>57.8 ± 0.014</b>
dis_gla	distance from glacier edge (m)	<b>15.5 ± 0.011</b>		5.3 ± 0.003	<b>14.2 ± 0.011</b>
conif_forest	coniferous forest (m <sup>2</sup> )	7.9 ± 0.008	<b>45.9 ± 0.06</b>	8.6 ± 0.004	3.8 ± 0.003
slope	slope (°)	7.5 ± 0.007		7.7 ± 0.003	0.4 ± 0.001
glaciers	glaciers and perpetual snow (m <sup>2</sup> )	2.5 ± 0.003		1.5 ± 0.002	1.4 ± 0.003
bio12	annual precipitation amount (kg/m <sup>2</sup> )		<b>13.6 ± 0.026</b>		2.3 ± 0.002
Mixed_forest	mixed forest (m <sup>2</sup> )		<b>11.3 ± 0.029</b>	3.6 ± 0.003	
low_veg	low vegetation (m <sup>2</sup> )		0.8 ± 0.001	6.3 ± 0.004	
broadleaved_forest	broad-leaved forest (m <sup>2</sup> )			4.4 ± 0.005	3.2 ± 0.003
solar_radiation	total solar radiation (kWh/m <sup>2</sup> )			3.4 ± 0.002	
bio7	annual range of air temperature (°C)			3.0 ± 0.003	0.4 ± 0.001
bio15	precipitation seasonality (kg/m <sup>2</sup> )			2.7 ± 0.003	6.8 ± 0.003
grassland	grassland (m <sup>2</sup> )			1.4 ± 0.001	7.9 ± 0.004
shrubland	shrubland (m <sup>2</sup> )			0.7 ± 0.002	1.8 ± 0.002

Table 2. Present and future distribution of four cold-adapted bumblebees. Future extent sizes and percentages of contractions are obtained from four climatic models and scenarios coded (as MC-MS: mild climate model - moderate scenario; WC-MS: worst climate model - moderate scenario; MC-WS: mild climate model - worst scenario; WC-WS: worst climate model - worst scenario). Contraction refers to the percentage of current suitable areas that will not be so in the future.

species	mountain	present extent	gfdl_esm4_-ssp370 (MC-MS)	ukesm1.0_-ll_ssp370 (WC-MS)	gfdl_esm4_-ssp585 (MC-WS)	ukesm1.0_-ll_ssp585 (WC-S)	Mean contraction %
mucidus	Apennines	3374	701 (79.22 %)	329 (90.25 %)	831 (75.37 %)	212 (93.72 %)	84.64
mucidus	Alps	68641	48314 (29.61 %)	38654 (43.69 %)	45504 (33.71 %)	30811 (55.11 %)	40.53
mucidus	Pyrenees	8440	4963 (41.20 %)	3347 (60.34 %)	4946 (41.40 %)	2324 (72.46 %)	53.85
alpinus	Alps	21875	13546 (38.08 %)	7913 (63.83 %)	12200 (44.23 %)	5200 (76.23 %)	55.59
mendax	Alps	51243	41076 (19.84 %)	37415 (26.99 %)	40911 (20.16 %)	35387 (30.94 %)	24.48
mendax	Pyrenees	5473	3301 (39.69 %)	2260 (58.71 %)	3257 (40.49 %)	1919 (64.94 %)	50.95
konradini	Apennines	757	230 (69.62 %)	91 (87.98 %)	231 (69.48 %)	58 (92.34 %)	79.85

Table 3. In- and Ex- situ refugia by bumblebee species, where in-situ refugia represents suitable areas both in the current and in all possible periods, ex-situ refers to refugia that will be available only in future. All values are in km<sup>2</sup> unless for the percentages.

Species	Area	Size of protected ex-situ refugia	Size of protected in-situ refugia	Size of ex-situ refugia	Size of in-situ refugia	Percentage of ex-situ refugia being protected	Percentage of in-situ refugia being protected	Percentage of in-situ refugia present
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mucidus	Apennines	0	211	0	212	-	99.53	6.28
mucidus	Alps	2457	6849	7284	19508	33.73	35.11	28.42
mucidus	Pyrenees	31	1914	31	2291	100.00	83.54	27.14
alpinus	Alps	59	1906	135	5064	43.70	37.64	23.15
mendax	Alps	1553	11311	3520	30554	44.12	37.02	59.63
mendax	Pyrenees	2	1592	2	1913	100.00	83.22	34.95
konradini	Apennines	40	18	40	18	100.00	100.00	2.38

Table 4 - Elevation shifts over time in four cold adapted bumblebees, including the year of change in elevation, the estimated regression slopes or means of each period, the significance of the difference in slopes or mean change and the elevation uplift as differences between 25% quantiles.

	Year of change	Estimated slopes (B) or means (M) per period $t$	P value between periods $t$	Elevation uplift
mucidus	1987	$B_{t1} = -1.33$ ( $p=0.52$ ); $B_{t2} = 14.90$ ( $p<0.01$ )	$t1$ vs $t2 < 0.001$	325.00
alpinus	1983	$B_{t1} = -1.903$ ( $p=0.67$ ); $B_{t2} = 10.256$ ( $p<0.01$ )	$t1$ vs $t2 < 0.001$	400.00
mendax	1980	$B_{t1} = 3.07$ ( $p=0.46$ ); $B_{t2} = 8.94$ ( $p<0.01$ )	$t1$ vs $t2 < 0.001$	416.25
konradini	likely between 60s and 80s	$M_{t1(1960s)} = 1850$ ; $M_{t2(1980s-90s)} = 2129$ ; $M_{t3(2010s-20s)} = 2183.75$	$t1$ vs $t2 < 0.01$ ; $t1$ vs $t3 < 0.001$ ; $t2$ vs $t3 = 0.70$	535.77

**Figures –**

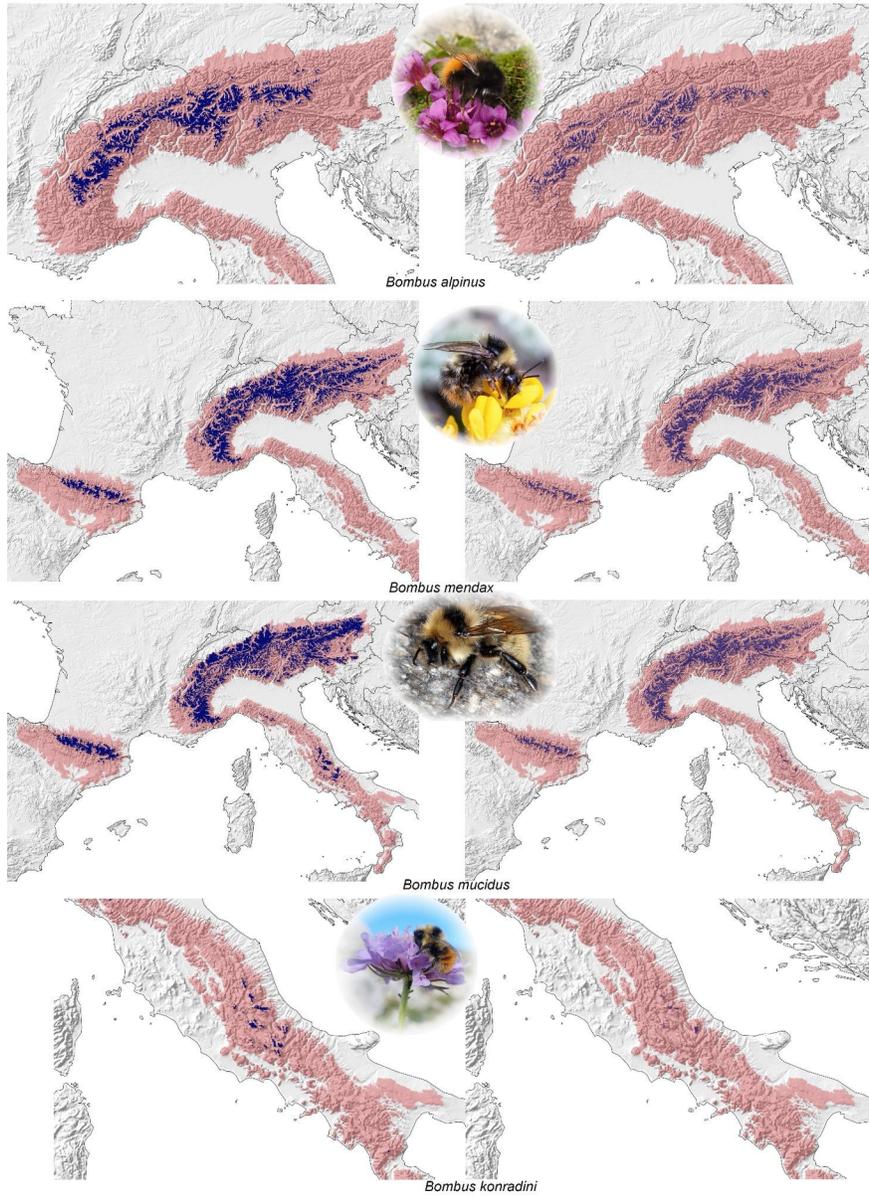


Figure 1 – Current and future distribution of cold-adapted bumblebees. The maps outline the distribution under current (left) and future climate, the latter indicated by darker color when the predictions of four climatic models and scenarios overlap.

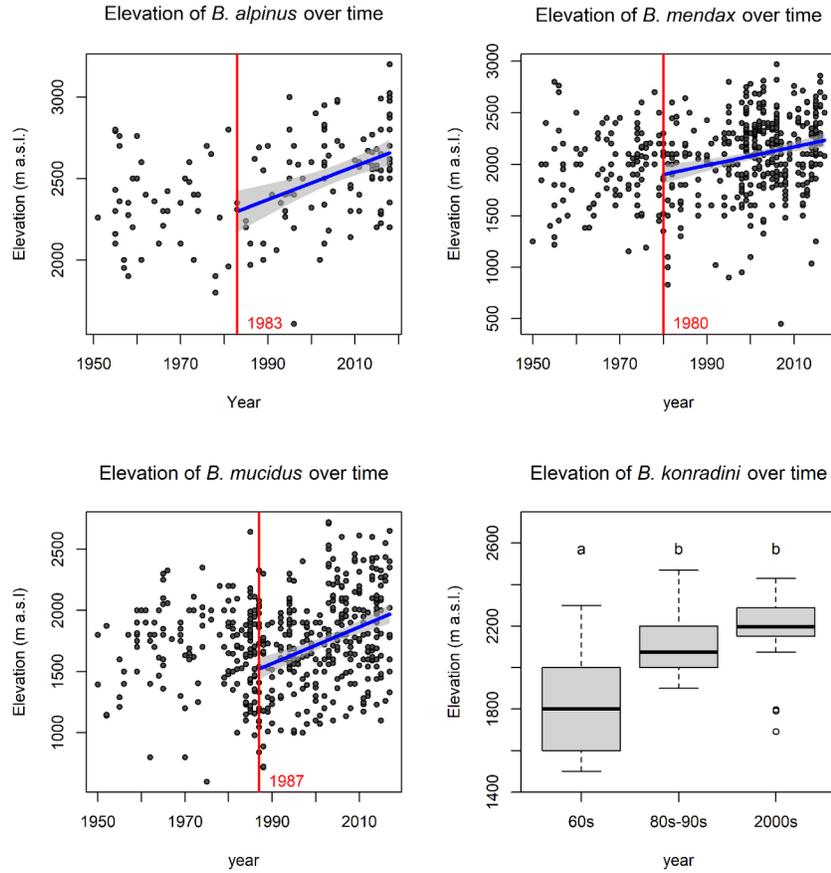


Figure 2 - Altitudinal shifts of the four studied bumblebees. Linear regressions and 95% confidence intervals are shown (grey polygons). The red vertical line shows the breakpoint year of changing slope. In the plot of *B. konradini*, the letters indicate significant differences with the compact letter display (i.e., different groups are denoted by different letters).