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Climate tracking by mountain bumblebees across a century: Distribution retreats, small refugia and elevational shifts[☆]

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ABSTRACT

Cold-adapted species endangered by global change are crucial cases for understanding range dynamics and its interface with conservation and environmental decision-making. However, the study of their distribution change is either neglected or conducted at coarse resolutions at continental level, thus having little indicator value for regional and local conservation strategies. In view of climate change, it can be expected that cold-adapted insects should reduce distribution ranges by mainly concentric retreats and 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 at a 1 km-resolution, and we estimated elevation uphill and the year of elevation change with broken-line regressions. Results indicate that climate change will likely 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 '80 s 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 (2–60 % of current areas) and even vary regionally, 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 and elevation changes demonstrate that cold-adapted bumblebees can track climate change, reasons for it to be found in the specialist niches mainly requiring narrow temperature ranges and glacier presence. Overall, the distribution changes of cold specialist bumblebees driven by climate change demonstrate that conservation and policy makers should act upon the time dynamics and regional responses because future

[☆] Open Research statement: All relevant data are made public in online repository. The private link (for Editor and Referees) is <https://figshare.com/s/bcce5f3642b364cb11a2>This link includes the data used for modelling species distribution and calculating the altitudinal shift, available in a public repository (data resolution at 5 km, finer resolution available upon request due to ownership issues by government agencies).

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range contraction, the little availability of new areas and the movement uphill emerge as consistent patterns.

1. Introduction

Climate shapes biodiversity in natural and human-dominated landscapes (Biella et al., 2022; Peters et al., 2019; Wiczyński et al., 2019). The growing concern towards climate change is increasing the research efforts aimed at understanding its effects on global biodiversity in order to find adequate conservation strategies (Beaumont et al., 2019), which should take into account the pervasive and ubiquitous impacts of climate change. Among its most evident and readily detectable consequences there is the re-arrangement of species distribution, 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 both the thermophilic species, reported to generally expand northwards or uphill thanks to warmer winters (Biella et al., 2021b; Stiels et al., 2021; Zait et al., 2020), and also the cold-adapted species that are retreating due to climate warming (Marshall et al., 2020; McCain et al., 2021).

While patterns of this kind have been largely reported over large, continental scales, it remains urgent and novel to better understand responses at geographic scales that are close to policy makers and conservation practitioners, as well as to the scales of species ecology, such as the regional and local levels. According to this perspective, it is crucial to detect, protect and improve areas that will constitute refugia against climate change at fine spatial resolutions. Accounting for local scales will make possible long-term survival of species, for instance by integrating adaptive, climate-proof conservation strategies (Morelli et al., 2020). So far, this has been inadequately addressed in cold-adapted insects, whose responses to climate change are often predicted over large, continental scales, where responses to climate change are averaged across latitudes and ecosystems, and distribution changes homogenised in large geographic grids (e.g. Ghisbain et al., 2023). Conversely, only by studying species responses to climate change considering the environmental variability at local scales (e.g. at 1 km as in Lee et al., 2019; Suzuki-Ohno et al., 2020) and by focusing on the potential differences in responses among regions, it could be possible to provide a solid reference tool for conservation (e.g. Wiens and Bachelet, 2010).

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, which alter snow-cover and snow-melt patterns, reduce icy and snowy surfaces, provoke the expansion of forest at the expense of grasslands and the encroachment of species from lower elevational belts and latitudes. All those changes are altering community composition, competition patterns, trophic interactions and 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 (Bertini et al., 2021; Scharsack 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). 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 (Biella et al., 2017; Ormosa 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., 2017, 2016).

Bumblebees are crucial high-elevation pollinators (Biella et al., 2021a). However, many bumblebee species are facing negative population trends, range contraction and elevational shifts with climate change considered one main cause among others (Kerr et al., 2015; 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 thrives in many mountain regions. Their high sensitivity paired with the key role they play 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 closely track 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”); the prevalence of one of such patterns could be easily assessed by measuring the overlap between current and future suitable areas. A concentric retreat pattern could 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”). Furthermore, while assessing these hypotheses, it will also be possible to gain a critical view of feasible conservation actions of cold adapted species by evaluating the distribution of climate refugia. It should be noted that climate refugia for a given species are the areas where the distribution could remain relatively unaltered, in spite of the impacts of climate change (Ashcroft, 2010). Therefore, investigating their spatial relationship with protected areas is key to inform area prioritisation for conservation, under adaptive conservation strategies (Rannow et al., 2014). In fact, under adaptive

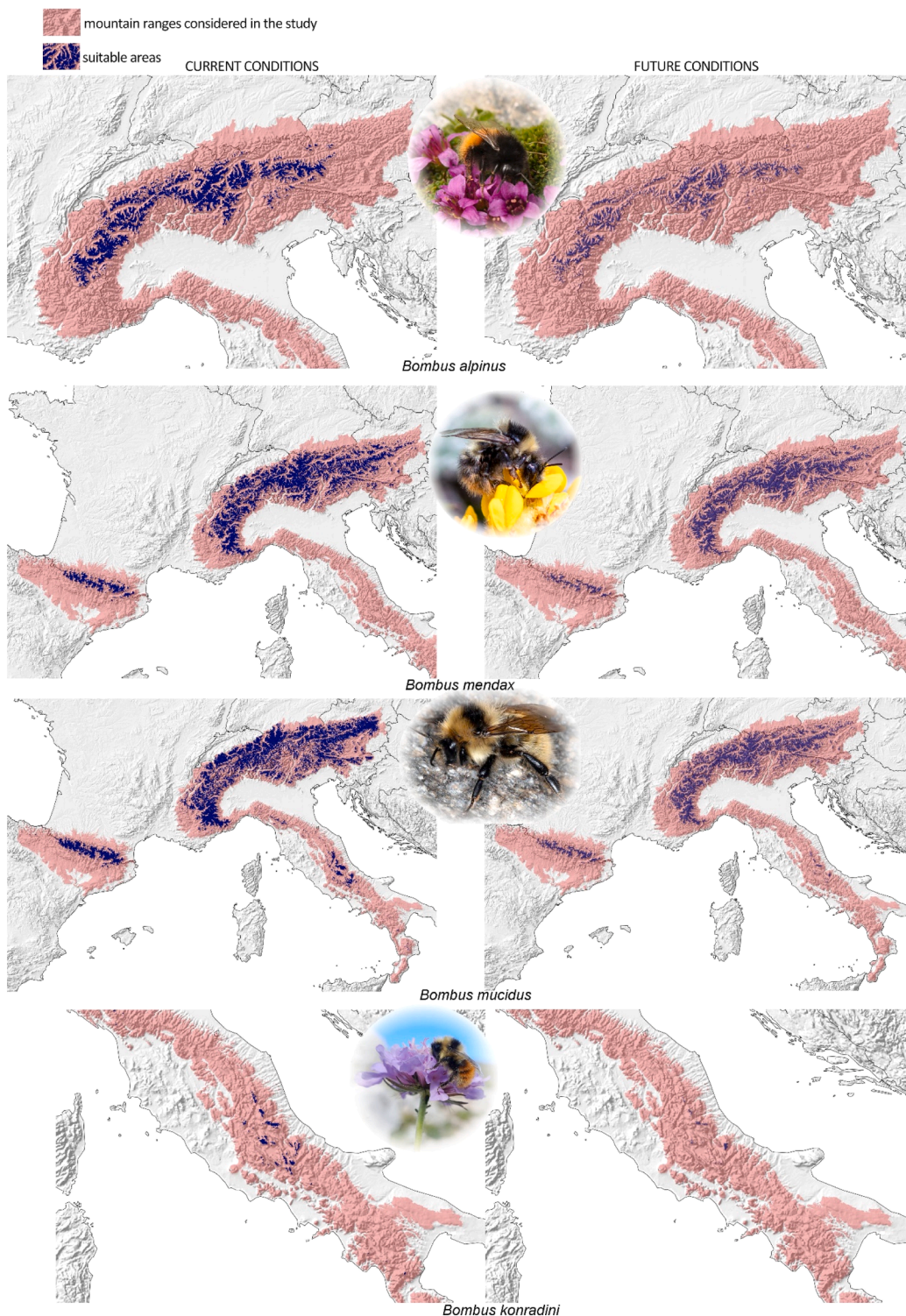


Fig. 1. Current and future distribution of four cold-adapted bumblebees. The maps outline the suitable predicted distribution under current (left) and future (right) climate, indicated by blue, with darker colour when the predictions of four alternative future climates overlap. The pink colour shows the mountain ranges considered by the study. Bumblebee photos are taken from the authors, except for *Bombus mendax* that was taken by Sophie Girien and licensed under the Creative Commons Attribution-Share Alike 4.0 International license.

management, it would be desirable for protected areas to ‘track’ species distribution changes and other effects of climate change (Tanner-McAllister et al., 2017). To obtain this, one of the available tools is to define “in-situ” and “ex-situ” refugia. The in-situ ones are areas suitable under current climatic conditions that will be so also in the future, while ex-situ refugia are sites that will be suitable under future climatic scenarios although they are not so at the moment (Beaumont et al., 2019). Preserving these refugia is key to species conservation, as in-situ refugia are fundamental for population resistance over time, and ex-situ ones play a key role in allowing future redistribution and hence are key to population resilience (Brambilla et al., 2022).

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 southern and central Europe, across mountain systems differing in terms of 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, with bumblebee ranges in different mountain systems 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 a 1 km-resolution under present and future climatic conditions, 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 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.

2. Methods

2.1. Species, study area & species locations

Four taxa species are renowned for their link to cold areas and rarity: *Bombus alpinus helleri*, *Bombus mendax*, *Bombus mucidus* and *Bombus konradini*. *Bombus (Alpinobombus) alpinus* (Linnaeus, 1758) has a disjointed 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 (Biella et al., 2017; Rasmont et al., 2015). *Bombus (Mendacibombus) mendax* Gerstaecker, 1869 occurs at high-elevation environments 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), and occurs also in the Pyrenees and locally in the Cantabrians (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 taxon formerly known as *Bombus monticola konradini*) occurs exclusively at high elevation in the central Apennines, and little is known about its ecology (Ricciardelli D’Albore and Piatti, 2003).

The study area encompasses the Alps, the Apennines and the Pyrenees as in Fig. 1 (in pink colour), and only occurrences and predictions within this area are considered here (we excluded the Cantabrian Range and Balkans because of severely scattered and very old records available, causing problems of low representativeness). Occurrence locations were retrieved from the literature, private and museum collections, with details available in Supporting text A1 in the Supplementary Information. The record position was visually validated with satellite images (i.e., occurrence sites corresponding to alpine areas in a broad sense, and within the known elevational range of the species); records deriving from specimens that were unlabelled, with inconsistent information, dubious toponyms or duplicated with other data (i.e., belonging to the same cell used for modelling) were excluded. Cumulatively, 1771 occurrence records were available for the analyses: 172 for *B. alpinus*, 722 for *B. mendax*, 826 for *B. mucidus* and 50 for *B. konradini* from the study area, see Supplementary Figure S1. The datasets used in the analyses constitute the most comprehensive ones ever assembled for these taxa so far.

2.2. Climatic and land-use variables: present and future

From the species distribution modelling we excluded the records before 1970 and those without date (hence, using only the time range: 1970–2018, but for *konradini* 1960–2020 due to the few data available) to avoid possible mismatches between observations and climatic variables. 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., 2021, 2017), and were the following ones: mean annual 2-m air temperature, annual range in 2-m air temperature, sum of annual precipitation, precipitation seasonality, on the basis of their importance in explaining species distribution (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, from the product EU-DEM v1.0 of European Environment Agency, <https://sdi.eea.europa.eu/catalogue/srv/api/records/19cff95e-61ac-45ed-8ee3-c43220d709cf>). Finally, LULC variables were worked out from the CORINE land cover map (from the European Environment Agency, version 2018 <https://sdi.eea.europa.eu/catalogue/copernicus/api/records/71c95a07-e296-44fc-b22b-415f42acfd0>). All variables were then estimated for 1×1 km² 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 in the Supplementary Information). In

addition, we calculated over raster layers the distance of each cell from the closest glacier, which was entered as a further predictor, considering its potential importance for high-elevation bumblebees (Biella et al., 2017). The variables so worked out showed relatively modest correlations ($r < |.7|$; Grimmitt et al., 2020).

To describe possible alternative future climates, we relied on the downscaled CMIP6 (Coupled Model Intercomparison Project Phase 6) data. We chose the period 2041–2070, and two alternative climate general circulation models (a ‘warmer’ one, and a ‘colder’ alternative) as defined by ISIMIP (Intersectoral Impact model Intercomparison Project; Warszawski et al., 2014): GFDL-ESM4 and UKESM1–0-LL. Those data are specifically recommended for such a kind of application. For both climate models, we picked the ‘worst case’ greenhouse gas emission scenario SSP585 and the moderate change one SSP370 (Eyring et al., 2016) and downloaded the same climatic variables used for modelling current distribution. 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 greenhouse gas emission scenarios. Also those data were retrieved from the CHELSA V 2.1 database. We did not consider changes in LULC in our future estimations: although this is unlikely per se, it should be considered that habitat changes at high elevation may take long time to become perceptible and management is a key in shaping future LULC in a given site; therefore, keeping LULC fixed, it should be considered as a conservative approach in estimating the potential effect of climate change on the species distribution, as it could be even stronger because of associated changes in land-use.

2.3. Species distribution models

We built species distribution models (SDMs) by means of maximum entropy models using MaxEnt (Phillips et al., 2006) in the software R (R Core Team 2020) by combining different packages, following the method proposed by Brambilla et al. (2022). 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 (Elith et al., 2011; Jiménez-Valverde et al., 2008), leads to ecologically reliable models when properly tuned and often performs better than other methods or ensemble modelling (Brambilla et al., 2023; 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 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 were used to develop models; testing datasets included the records from the remaining fourth partition, and were used only to test models.

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 conducted by leaving out one variable at a time according to increasing value of permutation importance (calculated using the *varImp* command in SDMTune and 10 permutations; Vignali et al., 2020), 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), which plots the true positive rate against the false positive rate as well as the True Skills Statistics (TSS; a modified version of Cohen’s kappa to lessen its dependence on prevalence, (Allouche et al., 2006) 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 10th 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 (Leroy et al., 2018). Evaluation statistics for all models were good or acceptable (see Supplementary table S1). The final model was used to predict a species’ environmental suitability according to its *cloglog* outputs.

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 (cf. Brambilla et al., 2022), on the basis of a visual evaluation of the correspondence between the distribution of the species in the areas mostly known by the authors, and the outcomes of the thresholding. The obtained potential distribution had been overlapped with the extent of the mountain ranges respectively occupied by each studied species to estimate the extent of the relative range under current and future conditions. 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. For the estimation of suitable areas, for each species, we considered only the mountain range of known real presence (e.g. for *B. konradini* only the Apennines are considered).

We calculated in-situ and ex-situ refugia from the distribution inferred from the above models and projections. For each target species and mountain region, we defined “refugia” as areas that are suitable now and will remain suitable in the future (in-situ refugia),

or that are not suitable under current conditions but will become suited for a species under any future condition considered (ex-situ refugia), following previous approaches (Beaumont et al., 2019; Brambilla et al., 2022). Considering all future climates for such an assessment allowed us to identify areas that will be important for a target species whatever the future climate will be, and hence that are crucial for a species' conservation in the face of a changing climate. Moreover, the refugia were overlapped with the current Protected Area network, obtained by merging Natura 2000 sites with the European inventory of nationally designated Protected Areas (Nationally designated areas; CDDA), updated in 2020 (<https://www.eea.europa.eu/data-and-maps/data/nationally-designated-areas-national-cdda-15>; accessed on the 2nd February 2021).

2.4. Elevation profile of bumblebee occurrences over time

Elevation was analysed with a segmented regression with the elevation as response and year of record as predictor, in order to evaluate and highlight the presence of times of significant change in the elevation occurrence and later discuss co-occurring events that might have impacted. The best-fit breakpoint value was retrieved using the function *davies.test* in the *segmented* library in R (Mugge, 2003). The same procedure was applied to each time frame previously detected and supported, to test the possible presence of additional break-points. Subsequently, on each identified interval from the breakpoint analysis, linear regressions were performed and, to test if the slopes were significantly different, a t-test was applied. For these analyses, we included only the records older than the year 1949, to have evenly distributed data over time. Only for *B. konradini* a different analysis was performed: as the few available 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 and record elevation was compared across the three groups with a post-hoc test after a linear regression.

After these analyses, we considered the oldest 40 observations in each group and calculated the difference in the 25 % quantile elevation estimate of each cluster, this was done to calculate the uphill shift and also considering that is more evident in the lower ranges of the elevation than in the upper ones especially in some high elevation species. We also calculated the differences also with other quantiles for comparison.

3. Results

3.1. Models of present and future distribution

The analyses provided an estimation of the current suitable ranges and habitat use. For what concerns the current extent of suitable areas, *B. konradini* is the bumblebee with the narrowest suitable range of only 767 km², while *B. mucidus* and *B. mendax* are estimated to occur in the study areas over 80445 and 56716 km², respectively, and *B. alpinus* in 21875 km² (Fig. 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 S2.

Regarding the first hypothesis, all studied species are expected to shrink their distribution in the coming future (Fig. 1), confirming our first hypothesis (H1), although with different magnitude depending on the climatic model and on the mountain system (Table 2); the future suitable areas will contract considerably, by ca 15–75 % of the current suitable extent as an average across mountain range

Table 1

Permutation importance of environmental variables (VPI) 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 in the Supplementary Information.

Variable code	Variable	<i>B. alpinus</i>	<i>B. konradini</i>	<i>B. mendax</i>	<i>B. mucidus</i>
bio1	mean annual air temperature (°C)	61.3 ± 0.032	28.4 ± 0.04	51.2 ± 0.014	57.8 ± 0.013
dis_gla	distance from glacier edge (m)	15.5 ± 0.011		5.3 ± 0.003	14.2 ± 0.004
conif_forest	coniferous forest (proportional cover)	7.9 ± 0.008	45.9 ± 0.06	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 (proportional cover)	2.5 ± 0.003		1.5 ± 0.002	1.4 ± 0.003
bio12	annual precipitation amount (kg/m ²)		13.6 ± 0.026		2.3 ± 0.002
mixed_forest	mixed forest (proportional cover)		11.3 ± 0.029	3.6 ± 0.003	
low_veg	low vegetation (proportional cover)		0.8 ± 0.001	6.3 ± 0.004	
broadleaved_forest	broad-leaved forest (proportional cover)			4.4 ± 0.005	3.2 ± 0.003
solar_radiation	total solar radiation (kWh/m ²)			3.4 ± 0.002	
bio7	annual range of air temperature (°C)			3.0 ± 0.003	0.4 ± 0.001
bio15	precipitation seasonality (kg/m ²)			2.7 ± 0.003	6.8 ± 0.003
grassland	grassland (proportional cover)			1.4 ± 0.001	7.9 ± 0.004
shrubland	shrubland (proportional cover)			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 variation in the potential distribution (within brackets below the extent of suitable areas) are obtained from the combination of two climate general circulation models and two greenhouse gas emission 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. Variation 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-WS)	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

and climate projection for each species (range 6–80 % again across mountain ranges and climate projection, see details in [Supplementary table S2](#)), with the lowest extent of suitable areas predicted for the Apennines, and the larger ones in the Alps. Moreover, under climate models predicting severe warming, future areas resulted in higher contraction and less overlap between present and future distribution, compared to those predicting moderate warming ([Table 2](#)). Specifically, on average across climate projections, the Apennines part of *B. mucidus* and *B. konradini* range will contract dramatically (ca 80 %, but up to ca 94 % in some cases), and Alps and Pyrenees will host severe contractions by about 40–56 %; only the Alpine range of *B. mendax* will shrink by a relatively modest 24 %.

Regarding the second hypothesis, most of the future areas will overlap with the current suitable range by on average 60–100 % ([Supplementary table S3](#)). However, only a small fraction of currently suitable areas will constitute in-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, and about 60 % in the Alps for *B. mendax*. The high overlap of future suitable areas with current ones means that ex-situ refugia are extremely small compared to in-situ refugia, and only *B. konradini* will have larger ex-situ refugia. Therefore, our second hypothesis H2 was largely confirmed, with the partial exception of *B. konradini*. 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.

3.2. Elevation use over time

Regarding the third hypothesis, all bumblebees underwent an upward elevational shift. *Bombus alpinus*, *mendax* and *mucidus* have uplifted since the '80 s and similarly *B. konradini* changed between the 1960 s and the 1980s (the data for that species were unevenly distributed in time; [Fig. 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 60 s were significantly different in elevation from the more recent year groups, which were not different from each other ([Table 4](#)).

The estimated elevation uplift was between ca 325 and 535 m between time frames (before vs. after the breakpoint value), but it is important to note that occasional records were present also below the calculated elevation range and that the estimate changed depending on the chosen quartile ([Supplementary table S4](#)). Under future projections of the distribution, the elevational shift is predicted to continue considerably, based on the distribution of the suitable patches ([Supplementary table S5](#)). Hypothesis H3 was therefore fully confirmed by the observed and predicted shifts.

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 km² 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 current distribution acting as in-situ refugia
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

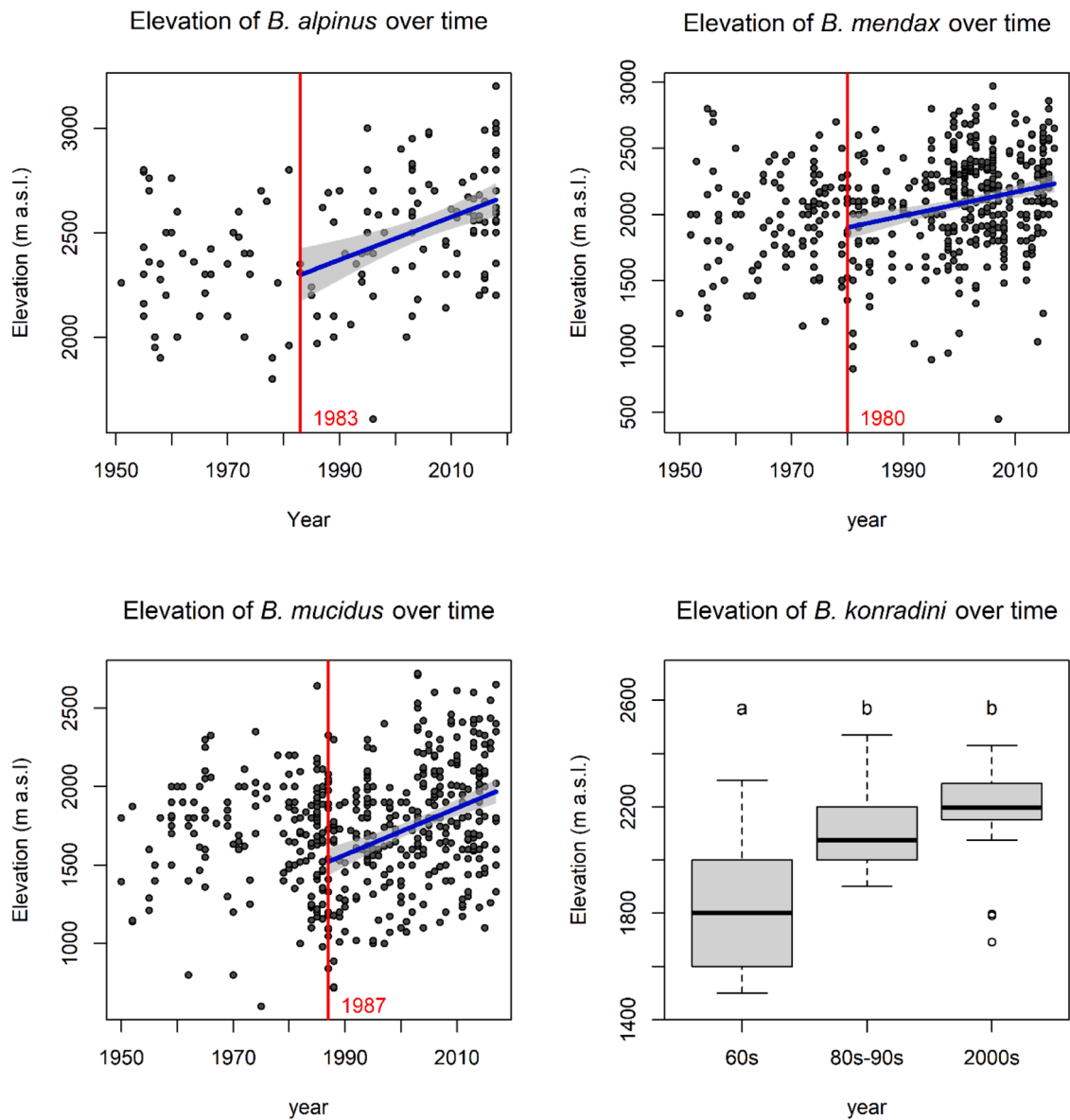


Fig. 2. Altitudinal shifts of the four studied bumblebees. Linear regressions and 95 % confidence intervals are shown (grey polygons). The red vertical line shows the breakpoint year of changing slope. In the plot of *B. konradini*, that is different from the other plots because the records are unevenly distributed over time, the letters indicate significant differences with the compact letter display (i.e., different groups are denoted by different letters).

4. 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 warming and climate change. Here, we estimated the elevation uphill shifts with a precise tracking over time for the first time for these species, providing crucial knowledge that previous studies did not provide. Moreover, we explored the environmental features associated with the species distribution, modelled the present distribution to infer future occurrences under climatic conditions and identified the distribution refugia constituting priority areas for conservation. We did so by considering regional estimates and variables at fine spatial resolution (1 km x 1 km), thus differently from the main previous studies covering considering continental scales and relatively coarse resolutions (Ghisbain et al., 2023; Kerr et al., 2015).

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
<i>mucidus</i>	1987	$B_{t1} = -1.33$ ($p = 0.52$); $B_{t2} = 14.90$ ($p < 0.01$)	$t1$ vs $t2 < 0.001$	325.00
<i>alpinus</i>	1983	$B_{t1} = -1.903$ ($p = 0.67$); $B_{t2} = 10.256$ ($p < 0.01$)	$t1$ vs $t2 < 0.001$	400.00
<i>mendax</i>	1980	$B_{t1} = 3.07$ ($p = 0.46$); $B_{t2} = 8.94$ ($p < 0.01$)	$t1$ vs $t2 < 0.001$	416.25
<i>konradini</i>	likely between 60 s and 80 s	$Mt1(1960s) = 1850$; $Mt2(1980s-90 s) = 2129$; $Mt3(2010s-20 s) = 2183.75$	$t1$ vs $t2 < 0.01$; $t1$ vs $t3 < 0.001$; $t2$ vs $t3 = 0.70$	535.77

4.1. Species 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 ranges and different taxonomic subgenera, thus fulfilling our hypothesis H1 (i.e., future range contraction). The severe range contractions predicted for the 2070 s are particularly alarming as these bumblebees are already enlisted as threatened of extinction from what had been observed in recent times and reported in continental and regional red lists (Nieto et al., 2014; Quaranta et al., 2018). 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 (Brambilla et al., 2022; de Gabriel Hernandez et al., 2021), highlighting how similar concerning patterns might interest many animal species of cold areas, which have not yet been properly investigated.

The severe future shrinkage in distribution range will likely be concentric in the study areas, because most future areas are predicted to occur within the current suitable ones, or very close to them (Fig. 1), while large surfaces will turn into inhospitable lands. This result supports the hypothesis H2 (i.e., future concentric retreats) 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 (Koot et al., 2022; Martínez-López et al., 2021). Therefore, the strong future alteration of the current distribution pattern will further imperil the survival of these pollinators. Furthermore, our study demonstrated that refugia areas estimated suitable by all climatic projections will be of small size, especially in the Apennines. Thus, the remaining patches will be important refuges for the four bumblebee species studied, and conservation measures should be strengthened there. While we do not have any information about dispersal in the model species, and symptoms of isolation and restriction to gene flow in mountain environments had been reported also for highly mobile species (Ceresa et al., 2024, 2023), climate refugia for the bumblebees we investigated are mostly located within or very close to currently suitable areas (Fig. 1). This suggests that dispersal limitations are unlikely to hinder the ability of our study species to colonise refugia.

Some differences in shrinkage amount were detected among mountain ranges, with the conditions in the Apennines (the lowest and most southern mountain system considered here) 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 that of the other ranges. Likewise, the Apennines' endemic *B. konradini* will largely shrink its distribution. Studies highlight that similar modifications in future distribution ranges will be expected for other local elements of fauna and flora of this mountain range. Examples of this are the Apennines range of two high-elevation butterflies that will be considerably small and even possibly disappear in future years (Bonifacino et al., 2022; Sistri et al., 2022). Likewise, the area occupied by some Apennines rare plants will considerably shrink (Di Musciano et al., 2020). Differences in orientation, elevation range and general climate, as well as diversity and extent of habitats, among the three mountain massifs investigated here, could explain these differential responses, although without affecting the validity of H2. However, future research efforts on understanding why the Apennines seem 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. It is possible that the low overall altitude and the low latitude of this region compared to the Alps and Pyrenees could contribute to understanding the severe range contraction trend in the Apennine.

Unfortunately, considering the unprecedented and fast rate of climate change, it is difficult to estimate the efficacy of conservation measures. It is very likely that microhabitat characteristics related to the flower richness of mountain meadows and the intensity of grazing, as well as the availability of nesting spots, could play a crucial role for conservation and could buffer the climatic effects. 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, studies could integrate species distribution modelling for conservation and the different physiological responses to heating by different populations, as previously proposed for reptiles (Besson and Cree, 2011). Furthermore, conservation efforts must incorporate the distribution and different types of refugia: it is surely a promising measure to protect and apply mitigation strategies to areas that are predicted to be in-situ refugia (shared by present and future climate conditions) and also ex-situ ones (only in future climate conditions), under an adaptive dynamic view of area conservation. Given that climate refugia are key areas for the survival 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, also thanks to the fine resolution of the distribution models that could allow to identify suitable lands in each Protected Areas.

4.2. Species 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 in the response curves, that could be the mechanism why H2 (*i.e.*, concentric retreats) holds true in the context of cold-adapted animals. Models revealed a relatively narrow range of suitable values of bioclimatic and habitat variables influencing the presence of the four cold-adapted bumblebees, despite the fact that we have pooled together records from a relatively broad time span. This implies that the stochastic 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 imperil the fate of the alpine ecosystem and the cold-adapted bumblebees.

4.3. Elevation shifts of cold-adapted bumblebees

Average elevation of occurrence sites by the four bumblebees had considerably moved up, thus validating hypothesis H3 (*i.e.*, elevation shift): 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 common feature is also the timing of elevation change, which has started since the mid 1980s for all species and will continue in future. This results provides a novel and precise estimation of the timing of these events, relevant for later searching possible causes. This is relevant because, although elevation changes in bumblebees are not uncommon and were observed on the Alps and Pyrenees (Marshall et al., 2020; Ormosa et al., 2017), those studies did not detect a precise knowledge of when the shift happens. Instead, in our study we found a time when the elevational shift started (the 1980s) that matches the timing of a previous estimate on an alpine bumblebee (Biella et al., 2017) and also the timing of a thermophilic lowland bumblebees that started expanding the range exactly from the 1980s (Biella et al., 2021a). By knowing the timing, the reasons for the distribution change in these bumblebees are to be searched in the chronology of the climatic data and the records of temperatures: in fact, since the 1980s the warmest period of the last 800 years has started (IPCC, Intergovernmental Panel on Climate, 2014), where the mountain areas were warming at a rate as twice as the global average (Pepin and Seidel, 2005). In cold-adapted bumblebees occurring at high elevation, a continuous uphill shift 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. Therefore, investigating and identifying possible microrefugia able to buffer against regional warming is a valuable option for further research that could eventually inform conservation practices, and for the fine-scale designation and management of priority areas.

5. Conclusions

Bumblebees of cold environments from 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. This scenario challenges dramatically any conservation effort but attention should be directed towards the dynamic realities of species ranges.

Starting from accurate distribution data and fine geographic resolutions, we detected narrow future ranges, small refugia and regional differences that will lead to conservation issues for cold-adapted bumblebees. Consequently, conservation should take full consideration of the dynamic realities of species ranges over time and that refugium areas may be targets of conservation priority, considering in situ and ex situ locations. Moreover, a useful tool for conservation could be to update 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 that could be fundamental tools for local conservation practitioners, *e.g.* the protected areas of the Pyrenees or of the Apennines. 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, for example by regulating the intensity of grazing that reduces flower availability, or the uphill shift of the treeline. 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.

CRediT authorship contribution statement

Paolo Biella: Conceptualization, Methodology, Formal analysis, Investigation, Data Curation, Validation, Resources, Writing - Original Draft. **Maurizio Cornalba:** Data curation, Writing - Review & Editing. **Pierre Rasmont:** Data curation, Writing - Review & Editing. **Johann Neumayer:** Data curation, Writing - Review & Editing. **Maurizio Mei:** Data curation, Writing - Review & Editing.

Mattia Brambilla: Conceptualization, Methodology, Formal analysis, Investigation, Writing - Original Draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All relevant data are made public in an online repository, available at the link: <http://figshare.com/s/bcce5f3642b364cb11a2>

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2024.e03163](https://doi.org/10.1016/j.gecco.2024.e03163).

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