Distribution patterns of the cold adapted bumblebee Bombus alpinus in the Alps and hints of an uphill shift (Insecta: Hymenoptera: Apidae)

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Distribution patterns of the cold adapted bumblebee *Bombus alpinus* in the Alps and hints of an uphill shift (Insecta: Hymenoptera: Apidae)

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Abstract

Climate change is threatening species and habitats. Altitudinal shifts uphill and negative population trends are commonly observed in altitude-related taxa. The bumblebee *Bombus alpinus* (Linnaeus, 1758) has a disjoint distribution restricted to Fennoscandia and the Alps, and is considered threatened. We studied the ecology and distribution of *B. alpinus* in the Alps, where the endemic subspecies *Bombus alpinus helleri* Dalla Torre 1882 is found, as a case-model because of its rarity, habitat, and mutual dependence with the ecosystem for pollination and resources. We developed species distribution models including both climatic and habitat variables to obtain the surface suitable for this subspecies and quantified its protected portion. Our analyses indicate that this bumblebee is restricted to the upper altitudes and has a narrow niche mainly related to the presence of glaciers, the cool temperature, a low temperature variation, and a specific range of precipitation. A strong altitudinal shift is also taking place probably due to climate change. After years of no changes in altitudinal distribution, its lowest altitudinal limit has moved up 479 m since the year 1984, while its upper altitudinal limit has remained unchanged. Over half of the suitable area in the Alps is included within protected areas, but conservation has not been planned yet. However, rare species with narrow niche, such as *B. alpinus*, are highly threatened by climate change. Potential short-term mitigation actions are discussed, including exchange of males between locations and integral protection of prairies in the vicinity of glaciers.

Keywords

Electronic supplementary material

The online version of this article (doi: 10.1007/s10841-017-9983-1) contains supplementary material, which is available to authorized users.

Introduction

Global change is currently threatening many species (Thomas et al. 2004). Together with land use change (Martins et al. 2014; Jha 2015), agricultural practices (Ollerton et al. 2014; Rundlöf et al. 2015), and new pathogens (Smith et al. 2006; Cameron et al. 2011), climate change affects the survival of endangered species and could even cause extinctions (e.g. Parmesan and Yohe 2003; Thomas et al. 2004). As pointed out by the International Panel on Climate Change (IPCC, Intergovernmental Panel on Climate Change 2014), atmospheric temperatures have increased since 1750, apparently due to rising concentrations of methane (CH_4, 150%), nitrous oxide (N_2O, 20%), and carbon dioxide (CO_2, 40%) during the same period (IPCC, Intergovernmental Panel on Climate Change 2014).

In mountainous areas, temperatures have warmed by 0.13 °C/decade since the 1950s (Pepin and Seidel 2005). Drought and the alteration of the chemical properties of soils are consequences of climate change that would largely impact the entire alpine ecosystem (Wu et al. 2013). Climate change also heavily impacts glaciers, which have lost about 50% and 30–40% of their historical volume and surface in the European Alps, respectively, since the 1950s (Haeberli and Beniston 1998); their melting rates in the early twenty-first century are unprecedented (Zemp et al. 2015).

Warming is particularly hostile to high-altitude species (Flousek et al. 2015), although habitat heterogeneity and microclimatic conditions might play a role against climate warming (Ashton et al. 2009; Anthelme et al. 2014). Species restricted to the higher altitudes show more negative trends than species of lower altitudes (Flousek et al. 2015). Therefore, range shifting could be a major threat to high-altitude species due to the loss of suitable refuges downhill (Monasterio et al. 2009) and to competition by lower altitude species which, favoured by warming, colonize new areas upwards (Tinner and Kaltenrieder 2005; Cannone and Pignatti 2014). High extinction rates might impact specialists from particular niches, for instance in the alpine environment where suitable habitats are unlikely to become available upwards (Sekercioglu et al. 2008).

The majority of the rare species are related to cold climatic niches, and areas with these conditions are expected to shrink under climate change (Ohlemüller et al. 2008; Viterbi et al. 2013). Therefore, rare species would face a higher extinction risk under climate change as a result of a decrease in habitat

availability (Thuiller et al. 2005). Thus, their conservation must be a priority. Knowing where species occur is a key aspect for their conservation, but in the case of rare species, a lack of knowledge about their distribution is often the rule due to their low detectability. By means of species distribution modelling (SDMs), this lack might be obviated by relating the known distribution to a set of ecological variables and therefore obtaining the potential suitable area of occurrence (Martins et al. 2014; Milanesi et al. 2016).

We chose *B. alpinus helleri* Dalla Torre 1882 as a model case, because: (i) it is a taxon occurring from the alpine altitudinal belt upwards (Amiet 1996; Neumayer and Paulus 1999; Biella 2015), and its habitat is among the most threatened (Franzén and Molander 2011); (ii) several research studies agree on a general decline of bumblebees (Cameron et al. 2011; Casey et al. 2015) with range losses and altitudinal shifts as a response to the recent climate warming (Kerr et al. 2015); (iii) mutual dependence links this taxon and its ecosystem, since bumblebees are key pollinators (Park et al. 2015) and their colonies need high quality pollen for their fitness (Francis et al. 2016); (iv) *B. alpinus helleri* is considered extinct in the Carpathians, a Southern European mountain chain, since old records have not been recently confirmed (Rasmont et al. 2015b), and it is therefore a priority to shed light on this taxa in another European mountain range, such as the Alps, while it is still present.

Thus, our aims are: (i) to estimate the suitable surface for the taxon with both habitat and bio-climatic variables; (ii) to calculate what proportion of suitable areas are included in protected areas, which would provide a direct estimation of the surface area that could be a target for direct management actions; (iii) to identify which environmental features are essential for the presence of the taxon and (iv) to detect and quantify any altitudinal shifts in its altitudinal range.

Materials and methods

The study area

Our study area (4°53′–16°28′E, 43°26′–48°22′N; Fig. S1) encompasses the entire Alps range as defined by the Alps Convention (http://www.alpconv.org). It includes a total surface of $\approx$191,146 km^2 overlapping the mountainous areas of seven countries (Austria, France, Germany, Italy, Liechtenstein, Slovenia, and Switzerland). The climate of the study area varies from continental to alpine, and the topography is mountainous (up to 4810 m a.s.l.).

The model taxon: *Bombus alpinus helleri*

Bombus (*Alpinobombus*) *alpinus* (Linnaeus, 1758) is the European arctic-alpine disjointed endemism, since the subspecies *B. alpinus alpinus* occurs in the high Fennoscandia while *B. alpinus helleri* occurs in the Alps (Rasmont et al. 2015a). In this latter area, no detailed information is available about its biology. However, single observations are available from Fennoscandia where rodent cavities are occupied and provided with hay and leaves. Pollen is obtained from several plant species (Løken 1973). Therefore, it is a polylectic species. Moreover, it seems that colony size could be smaller for *Alpinobombus* than for other temperate bumblebees, as supported by the low worker:queen ratio observed in the field (Stenström and Bergman 1998).
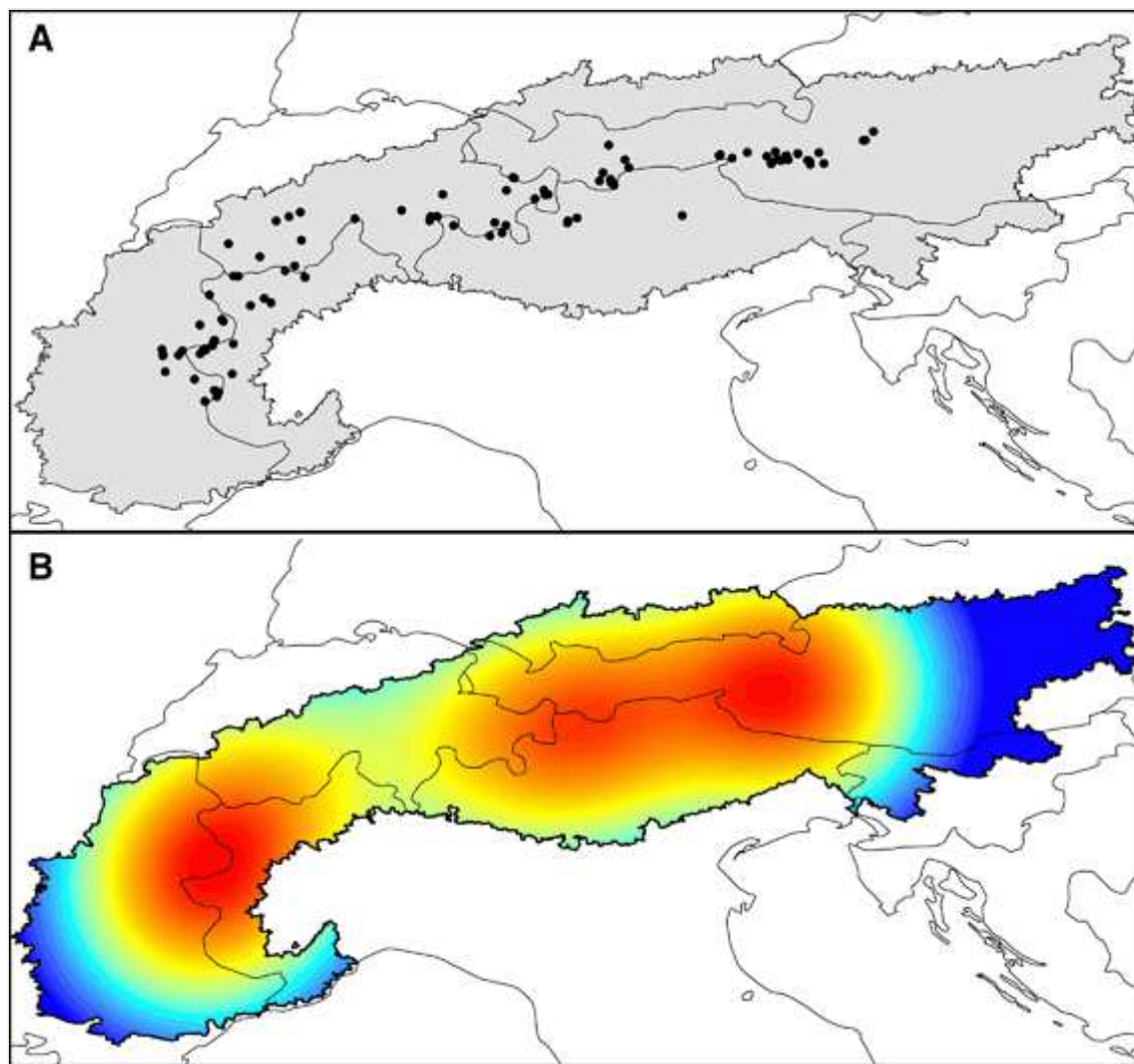
Species locations and sampling effort estimation

A total of 190 locations of *B. alpinus helleri* occurrence (Fig. 1) were extracted from literature, digitalized from museum and private collections of reliable experts, including those available from the Global Biodiversity Information Facility (http://www.gbif.org/); details are available in Supplementary Material. Unlabelled, inconsistent, dubious, or duplicated data were excluded. In the remaining dataset, as in Martins et al. (2014), when coordinates were not provided, they were inferred by means of geolocation services providing aerial and satellite imagery using a conservative approach. Specifically, the coordinates of the nearest prairie above treeline were taken (Amiet 1996) within 1 km from the labeled locality. In addition to this, it may be observed that *B. alpinus* is a large and conspicuous species, and therefore unlikely to go undetected. It is thus reasonable to assume that the available records allow reconstruction of its area of occurrence with sufficient accuracy.

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Fig. 1

Bombus alpinus helleri locations in *black dots* (**a**) and sampling effort map in *red–blue* scale representing more and less intensively sampled areas, respectively (**b**)

As suggested by several authors (Elith et al. 2010; Fourcade et al. 2014; Stolar and Nielsen 2015; Milanesi et al. 2016), we accounted for spatially biased sampling efforts through Gaussian kernel density analysis based on all species locations. We estimated a kernel density probability for each cell of the resulting sampling effort map (Fig. 1), and we used the resulting values to weight bias-adjusted model estimates (Stolar and Nielsen 2015, see below). Moreover, to avoid a potential source of bias in the analysis, pseudo-absences for the SDMs were randomly selected inside the minimum convex polygon estimated around species locations (Calenge et al. 2005).

Predictor variables

To estimate the distribution of the target taxon, we considered predictor variables regarding topography, such as altitude (Table 1), downloaded from the WorldClim dataset (http://www.worldclim.org at 30 s resolution, approximately 1 km) and solar radiation (averaged between 1950 and 2000). Moreover, we obtained 19 bioclimatic variables (Table 1) derived by the WorldClim dataset for current climatic conditions (averaged between 1951 and 2000) at 30 s resolution.

Finally, we also considered the (Euclidean) distance from glacier surfaces, derived from the Randolph Glacier Inventory 5.0 (http://www.glims.org/RGI).

Table 1

Predictor variables considered in the species distribution models of *Bombus alpinus helleri* and their VIF (~~variance inflation factor~~Variance Inflation Factor)

Variable	Abbreviation	VIF
Elevation[a]	Elev	>3
Solar radiation	Solar	1.01
Distance from glaciers	Dist_Ice	1.59
Annual mean temperature[a]	Bio 1	>3
Mean diurnal range[a]	Bio 2	>3
Isothermality [(BIO2/BIO7) × 100]	Bio 3	2.32
Temperature seasonality (standard deviation)	Bio 4	2.33
Maximum temperature of the warmest month[a]	Bio 5	>3
Minimum temperature of the coldest month[a]	Bio 6	>3
Temperature annual range (BIO5–BIO6)[a]	Bio 7	>3
Mean temperature of the wettest quarter[a]	Bio 8	>3
Mean temperature of the driest quarter	Bio 9	2.89
Mean temperature of the warmest quarter[a]	Bio 10	>3
Mean temperature of the coldest quarter[a]	Bio 11	>3
Annual precipitation[a]	Bio 12	>3
Precipitation of the wettest month	Bio 13	1.98
Precipitation of the driest month[a]	Bio 14	>3
Precipitation seasonality (coefficient of variation)	Bio 15	1.77
Precipitation of the wettest quarter[a]	Bio 16	>3
Precipitation of the driest quarter[a]	Bio 17	>3
Precipitation of the warmest quarter[a]	Bio 18	>3
Precipitation of the coldest quarter[a]	Bio 19	>3
Variables which VIF values >3 were removed ([a]) due multicollinearity among predictors		

To avoid multicollinearity among predictors, we calculated the Variance Inflation Factor (VIF; Zuur et al. 2010), package CAR (Fox and Weisberg 2011) in the statistical environment R (R Core Team 2016). Predictors with VIF > 3 (highly related with other predictors; Table 1) were excluded from the predictor variables to use in SDMs. Thus we carried out the following analyses with seven uncorrelated predictors: solar radiation (unit KJ/m^2), distance from glaciers (unit Km), isothermality (the percentage of day-to-night temperature oscillations relative to summer-to-winter oscillations; unit °C × 100; bio 3), temperature seasonality (temperature variation during time based on the standard deviation of the monthly averages across time; unit %; bio 4), mean temperature of the driest quarter (mean temperatures during the driest quarter of year; unit °C; bio 9), precipitation of the wettest month (mean precipitation during the wettest quarter of year; unit mm; bio 13) and precipitation seasonality (coefficient of variation calculated as the standard deviation of the weekly precipitation estimates expressed as a percentage of the mean of those estimates; bio 15).

Species distribution models, surface availability, and validations

A total of 120 localities were included in the SDMs spanning the time interval 1950–2014 and covering the study area entirely; 23 of these localities were removed from the subsequent analyses due to autocorrelation among species locations which were closely situated (within a distance of 1 km; P < 0.001 Moran's *I* correlogram; Dormann et al. 2007).

Then we performed nine SDMs: (1) artificial neural networks (ANN; Ripley 2007), (2) boosted regression trees (BRT; Friedman 2001), (3) classification tree analyses (CTA; Breiman et al. 1984), (4) flexible discriminant analyses (FDA; Hastie et al. 1994), (5) generalized additive models (GAM; Hastie and Tibshirani 1990), (6) generalized linear models (GLM; McCullagh and Nelder 1989), (7) multivariate adaptive regression splines (MARS; Friedman 1991), (8) a maximum entropy algorithm (MAXENT; Phillips et al. 2006), and (9) random forests (RF; Breiman 2001). We included the sampling effort map (see above) in the development of SDMs as a bias grid in MAXENT and as case weights in the other eight models (Elith et al. 2010; Stolar and Nielsen 2015). We used several models, because single models are possible states of the real distributions (Marmion et al. 2009), and no single best algorithm in SDM exists (Qiao et al. 2015), and also to avoid single model uncertainty (Araújo and New 2007). Thus we also used an ensemble prediction (EP) by averaging outputs of the nine SDMs to cope with model variability (Segurado and Araújo 2004; Elith and Graham 2009) and to improve the reliability of the model predictions (Araújo and New 2007; Breiner et al. 2015). SDMs, including their EP, were performed

using the 'biomod2' package (Thuiller et al. 2016) in R. Moreover, Moran's *I* correlogram was calculated to verify residual spatial autocorrelation of all the SDMs (1—SDMs predicted values for each location; De Marco et al. 2008). Finally, we also estimated variable importance with 10,000 permutations (values close to 0 assume no influence of that variable on the model; Thuiller et al. 2009).

By using a random subsample of 75% of locations to calibrate the models and 25% to validate them (Thuiller et al. 2009), we carried out ten *k-fold cross-validations*. We calculated three indices to evaluate model predictive accuracy, namely the area under the receiver operating characteristic curve (AUC; Fawcett 2004; Ko et al. 2011), the true skills statistic (TSS; Allouche et al. 2006), and the Boyce index (Boyce et al. 2002). According to Swets (1988), we classified the accuracy of validation as follows: 0.90-1.00 = excellent; 0.80–0.90 = good; 0.70–0.80 = fair; 0.60–0.70 = poor; 0.50–0.60 = fail. From EP, we derived binary range maps (presence/absence) by maximizing the percentage of presence and pseudo-absence correctly predicted for the present conditions (Thuiller 2003, 2004; Seo et al. 2009).

The proportion of the available area obtained by the EP (using TSS as a threshold-setting method to estimate suitable habitat above a cut-off value; Nenzén and Araújo 2011; Fig. +2b) lying within protected areas was calculated by using shapefiles of protected areas (Nationally designated areas—CDDA; Natura 2000 data—the European network of protected sites; http://www.eea.europa.eu/data-and-maps/).

Altitudinal shift

Using 172 dated records from 1876 to 2014, the altitudinal occurrences in time were analyzed with LOESS (or LOWES, LOcally Weighted Scatterplot Smoothing) to look for possible trends, which suggested the presence of just 1 breakpoint as the slope of the graph changed abruptly after the year 1980. Therefore, we applied a segmented (or broken-line) regression model using Altitude as a response and Year as a predictor (normalized by square root and centered by subtracting the mean value). In this kind of regression, the relationship between the response and the explanatory variables are made piecewise linear; namely straight lines change slopes at given points (Bogliani and Brangi 1990; Muggeo 2003). Since we knew the number of breakpoints (namely 1), we used the best-fit breakpoint value obtained with the *davies.test* function of the 'segmented' library in R (Muggeo 2003). As implemented in Bogliani and Brangi (1990), linear regressions were performed on the two obtained intervals (namely to the left and to the right of the breakpoint value), a *t*

test was applied to compare the two regression slopes. Subsequently, additional breakpoints were investigated by applying the *davies.test* function on each of the previously detected intervals until non-significant breakpoints were found.

Results

The suitable area was 21,484 km^2 derived by EP above the resulting cut-off value of 463 (Fig. 2) which encompasses the highest altitudes of the Alps; 50.54% of this is included in protected areas.

Fig. 2

Bombus alpinus helleri ensemble prediction map in *green–red* scale representing less and more suitable areas, respectively (**a**); binary map resulting from the cut-off value 463, *grey*, absence; *red*, presence (**b**)
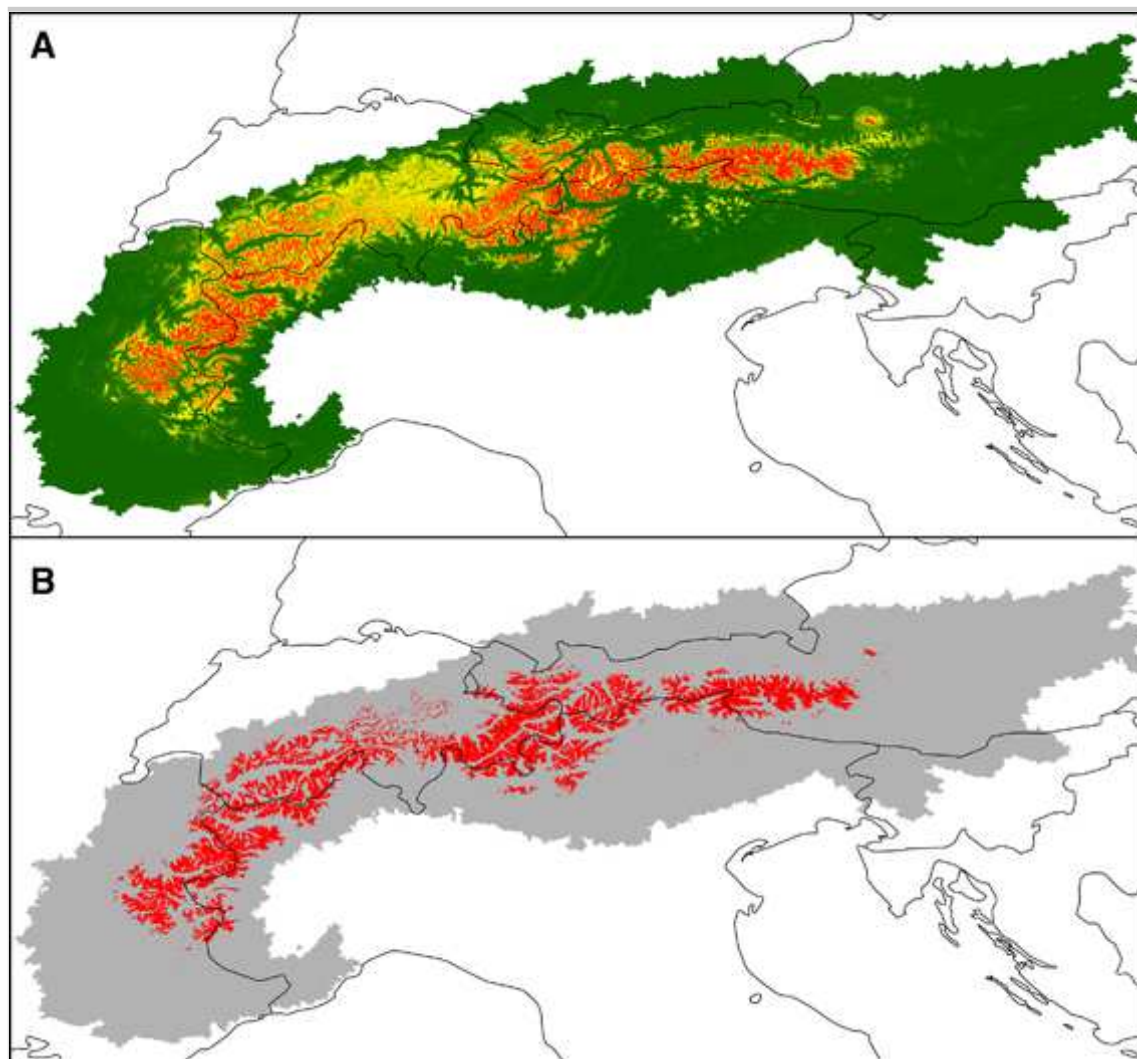
All the evaluation methods for all the SDMs showed a high predictive accuracy derived by the K-fold cross-validations carried out by sub-sampling the original data (Table 2). Specifically, EP showed the highest predictive power considering the AUC statistic, RF did when considering TSS, and MAXENT did when

considering BI (Table 2). Conversely, ANN showed the lowest predictive power when considering both AUC and TSS, while it was lowest for RF with BI (Table 3).

Table 2

Variable importance (%) in the nine species distribution models and in their ensemble predic

Variable	MAXENT	GLM	GBM	GAM	CTA	ANN	FDA	MARS	R
Distance from glaciers	27	64.3	44.8	52.5	64.1	76.9	49.4	43.5	4
Temperature seasonality	11.7	48.6	22.8	39.4	21.6	51.4	7.5	20.6	4
Precipitation of the wettest month	20.3	0.1	25	28.7	34	21.2	6.2	29.4	2
Precipitation seasonality	17.2	4.9	10.5	11	16.7	29.4	0	13.8	1
Mean temperature of the driest quarter	22.5	1.1	4.6	43.3	0	9.8	22.7	32.6	4
Isothermality	1.8	3.2	0	26.1	0	18.7	4.8	0	4.
Solar radiation	1.8	0	0.9	2.1	0	14.3	0	0	8.

Table 3

Model evaluation of nine species distribution models and their ensemble prediction; the closer the values to 1, the higher the agreement between the predictions and original data

Model	AUC	TSS	BI
EP	0.986	0.884	0.968
RF	0.981	0.931	0.777
BRT	0.971	0.893	0.872
MAXENT	0.958	0.819	0.991
GAM	0.954	0.873	0.921
FDA	0.936	0.802	0.961
MARS	0.932	0.807	0.945

Model	AUC	TSS	BI
CTA	0.901	0.804	0.989
GLM	0.899	0.809	0.873
ANN	0.883	0.801	0.809
For abbreviations, see "Methods"			

Distance from glaciers was the most important variable related to the species' occurrence in all SDMs and EP (Table 32). In detail, in EP the variables with an importance >10% included distance from glaciers (32.4% in EP), temperature seasonality (23.5% in EP), and precipitation of the wettest month (11.2% in EP).

We plotted the probability of occurrence derived from EP in relation to each used variable (Fig. 3). For the distance from glaciers, the probability of occurrence was highest at low distances, and there was a strong decrease onwards. Temperature seasonality showed a unimodal distribution with narrow hump peaking at approximately 5500. Precipitation of the wettest month peaked at 160 mm; at values higher than the peak, the probability decreased less steeply than it increased at values lower than the peak. Increases in probability distribution were also detected with less informative variables, such as high solar radiation (0.7% in EP) and low isothermality and precipitation seasonality (1.8 and 7% in EP respectively); the minimum probability was associated with mean temperatures of the driest quarter close to 0 °C (6.3% in EP).

Fig. 3

Response curves (in *black*) and 95% confidence intervals (in *grey*) of the probability of *B. alpinus helleri* occurrence derived by the ensemble prediction of the nine species distribution models in relation to predictor variables value
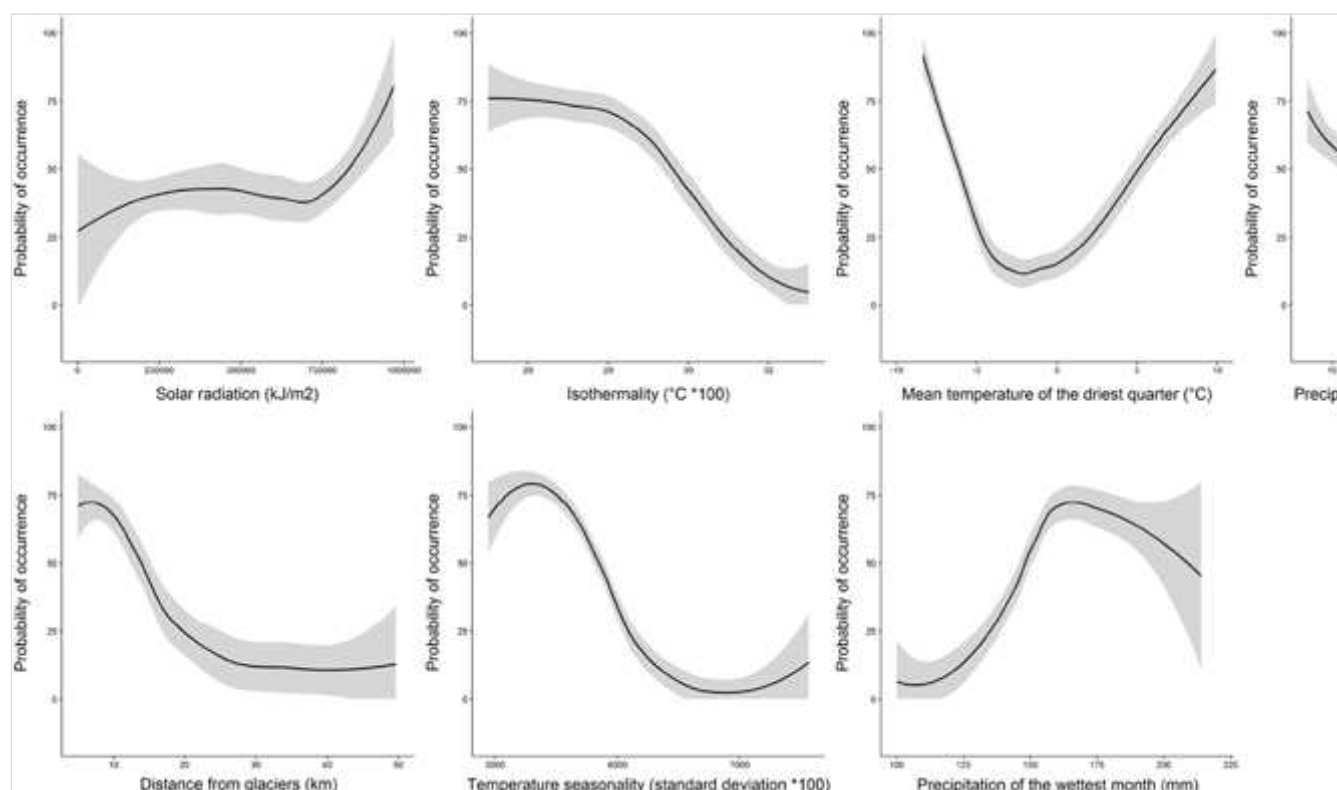
The best-fit approach identified 1984 as the year with changing slopes for breakpoint regressions (Fig. 4). Year was not significant in the left (older) time interval (from year 1876 to 1984, intercept = 2346.77 $p < 0.001$; year = 0.141 $p = 0.903$, $R^2 - \text{adj} = -0.01$), but it was strongly significant in the second (more recent) interval (from 1984 to 2014, intercept = 2098.921 $p < 0.001$; year = 11.834 $p < 0.01$, $R^2 - \text{adj} = 0.120$). The two slopes were significantly different ($p < 0.001$). Additional breakpoints within each interval were not significant.

Fig. 4

Long-term altitudinal records of *Bombus alpinus helleri*. Linear regressions (*black lines*), 95% confidence intervals (in *grey*). The *dotted line* shows the breakpoint year of changing slope, at the year 1984
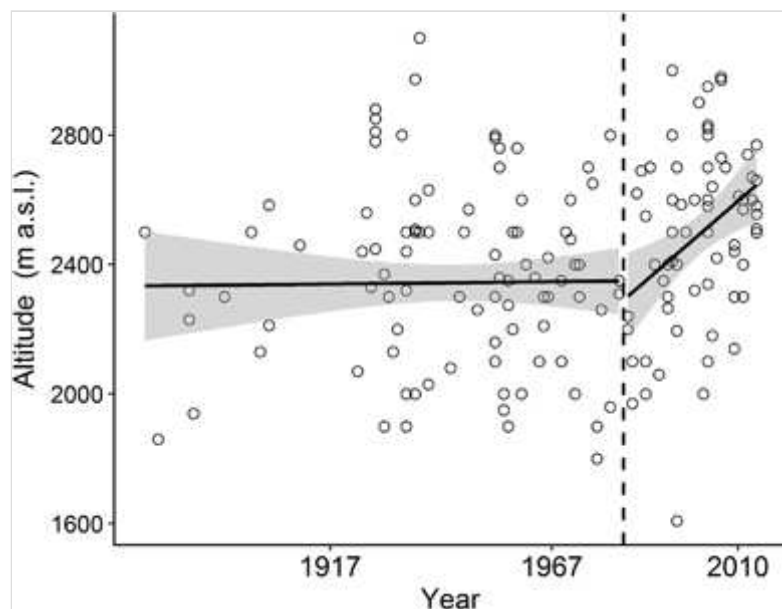
We detected a loss in altitudinal range equal to 479 m a.s.l. calculated as follows. When considering the 25% quantile values of 20-records-wise groups, it is the difference between the most recent group within the right interval (more recent) and the group with the minimum value within the left interval (older), namely 2479–2000 m a.s.l.. In these 2 groups, the highest altitudes were similar (2980 and 2972 m a.s.l., respectively).

Discussion

Bombus alpinus helleri and its role in the alpine ecosystem

Bumblebees are important flower visitors and are among the most efficient pollen vectors (Park et al. 2015). *B. alpinus helleri* is most likely playing a key role in the pollination of a wide range of plants within its altitudinal range. Few research studies have investigated the foraging preferences of the target taxon (Pittioni 1942; De Beaumont 1958; Schedl 1982), but by merging published and our unpublished observations, 39 plant species are listed (Online Resource). In turn, bumblebees are directly dependent on the quality of their foraging habitat; the fitness of their colonies needs a relatively high amount of resources for direct use as food for the workers and as storage for the larvae to feed on (Francis et al. 2016).

The variables included in our models efficiently described the distribution patterns of the model-taxon. Differences in variable importance among SDMs are mainly due to different algorithms, different assumptions, and different complexities of statistical models that combine predictor variables in different ways (Segurado and Araújo 2004). Our analyses suggest that *B. alpinus helleri* is a stenoecious species, because a higher probability of occurrence was associated with narrow ranges of several variables (response curves of SDMs, Fig. 3).

The shape of the response curves could provide some details on the patterns of distribution of this taxon, as follows. In Fig. 3, higher probability of presence is associated with lowest winter temperatures (the "driest quarter" in the Alps). This could suggest that *B. alpinus helleri* avoids areas with hotter winters (from −5 to 5 °C, e.g. at lower altitudes). Moreover, high probability is also associated with temperatures higher than 5 °C, which could hint for overwintering queens starting to forage relatively early after winter with cool weather. In addition, low temperature variation across the year ("temperature seasonality") is related to the presence of the species. The responses to winter temperatures and temperature variation could suggest that the taxon requires cool temperatures. This interpretation is also corroborated by specific physiological tests on *B. alpinus*, that showed lower tolerance to high temperatures than other species (Martinet et al. 2015). For precipitation, a specific range during summertime (when the "wettest month" is in the Alps) determines the presence of the species. However, the response curve is steeper at low than at high precipitation. This could be interpreted as avoidance of drier areas. Glaciers also play a conspicuous role in defining suitable habitat for the presence of *B. alpinus helleri*, which explains why the taxon occurs at such high altitudes. Given the contraction faced by glaciated surfaces lately (Zemp et al. 2015) and the strong dependency of glacial-habitat fauna on them (Rossaro et al. 2016), serious concerns arise for the fate of the highest-altitude ecosystems.

Loss in altitudinal range

Bombus alpinus helleri seems to be considerably reducing its altitudinal range. After more than a century with no substantial change in altitudinal distribution, the lower altitudinal limit has moved uphill 479 m in the last 33 years (since 1984). Altitudinal shifts are recorded in a number of other specialist species (Jiménez-Alfaro et al. 2014; Flousek et al. 2015). The root cause of this phenomena is, most probably, the rising temperature. The period from 1983 to 2012 was the warmest over the last 800 years in the Northern Hemisphere (IPCC, Intergovernmental Panel on Climate Change 2014). A warming of 0.2 °C/decade occurred worldwide in the period from 1984 to1998 (IPCC, Intergovernmental Panel on Climate Change 2014), but high-altitude areas warmed even more at a rate of 0.4 °C/decade in the period from 1979 to1998 (Pepin and Seidel 2005). The temperature timeline in the Alps shows that greater warming rates and fewer cooling events have been the rule since the 1980s (Beniston et al. 1997).

Many rare species are retracting their distribution into marginal areas where their optimum niche is assured (Casey et al. 2015), and bumblebees are among them (Manino et al. 2007; Kerr et al. 2015). From our analyses, it is clear that *B.*

alpinus helleri became restricted to the higher elevations of the Alps (upper-alpine altitudinal belt). Therefore, shrinkage in their altitudinal range raises serious concerns for the fate of the taxon when considering both the upper limit in the Alps and the reduction of land surface as altitude increases.

Conservation and management implications

Specific conservation actions have not been designed yet, despite the fact that *B. alpinus* is included in the European Red List of Bees (Nieto et al. 2014), is a Vulnerable species (Rasmont et al. 2015b), is considered extinct in some parts of its historic area of occurrence, and that it has been argued that it will disappear worldwide by 2100 (Rasmont et al. 2015a).

At a regional and local scale, short-term actions might be the following: (i) exchange of males between areas of proven occurrence inside protected areas, which would overcome the bumblebees' limited dispersal ability (Lepais et al. 2010); (ii) guaranteeing top-quality habitats in the available remnants, given the loss in altitudinal range.

The latter action could take place by limiting the activities which compete with habitat availability and quality. We propose the integral protection of areas surrounding glaciers, at least downwards to 2400 m a.s.l., in order to limit human activities that could alter the habitat. This would be feasible, as half of the suitable surface for this endemic bumblebee lies within protected areas. This is particularly urgent because, as clearly documented, the suitable areas for ski-pistes and the ones for high-altitude species are likely to overlap more as both shift to higher altitudes in response to climate change (Brambilla et al. 2016).

Other human activities to be considered concerns livestock. Conservation managers and decision-makers should carefully evaluate the real need for livestock and their density above the treeline.

Simple models on cattle impacts are feasible (Barcella et al. 2016) and recent work suggests that low densities of livestock are the best for ecosystem functioning (Lázaro et al. 2016). In alpine prairies, livestock in high density competes with the bumblebees' life cycle by removing the food sources (Lázaro et al. 2016) and even decreasing the habitat quality (Fleischner 1994). Biella (2015) presents a case in the Italian Central Alps, but this is a widespread situation.

Given that these activities are directly impacting ecosystems at high altitudes and therefore also *B. alpinus helleri,* short-term mitigation actions that would limit them are urgently needed.

Acknowledgements

Electronic supplementary material

Below is the link to the electronic supplementary material.

Supplementary material 1 (PDF 17 KB)

Supplementary material 2 (DOCX 217 KB)

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