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Title: Climate change vulnerability higher in arctic than alpine bumblebees

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Abstract. Arctic and alpine species are expected to be particularly vulnerable to climate change as they inhabit areas of extreme climates. To understand how such species may respond, we compared two groups of bumblebees that specialise in arctic (*Alpinobombus*) and alpine (*Mendacibombus*) biomes. These bumblebee species are all extreme cold specialists with similar ecological niches, making them good candidate species for comparison of how groups inhabiting different biomes may respond to climate change. Using an ensemble of species distribution models for eighteen bumblebee species (ten *Mendacibombus*; eight *Alpinobombus*), we estimated their current distributions using selected climate variables. The models were used to predict future distributions based on two future climate change scenarios for 2040-2060 and three dispersal scenarios. We found significant differences between the predicted relative area changes of the two groups under all combinations of climate change and dispersal scenarios. *Alpinobombus* species were consistently projected to have larger distribution declines, while the responses of *Mendacibombus* species were much more varied, with some *Mendacibombus* species projected to have distribution expansions provided that they are able to disperse to occupy new territory. From these results, we show that arctic species would be much more likely than alpine species to experience distribution declines under climate change.

Keywords: alpine; *Alpinobombus*; arctic; bumblebees; climate change; climate extremes; *Mendacibombus*; species distribution model

Highlights:

- Arctic bumblebees show higher vulnerability to climate change compared to alpine species.
- Arctic species will be required to disperse across larger distances than alpine species in order to track suitable climates, increasing extinction vulnerability.
- Climate change exacerbates both positive and negative changes in species distributions.
- Species living in climate extremes have increased chance of being driven to extinction as suitable habitats disappear.

64 **Introduction**

65 Anthropogenic greenhouse gas emissions have altered our planet's climate (IPCC,
66 2013), and this is having substantial ecological impacts across the globe (Hughes,
67 2000, Walther et al. 2002, Bellard et al. 2012), including increased species' vulnerability
68 to extinction (Thuiller et al. 2005). To ensure effective conservation actions, we must
69 first understand how species may be differentially impacted and how they subsequently
70 respond to these changes. One way species may respond is to disperse to track the
71 changing climate (Araújo and Pearson, 2005), and a general trend of poleward or
72 upward elevational movement has been observed in response to climate warming in
73 recent years (Parmesan and Yohe, 2003, Lenoir et al. 2008). Within this context,
74 species' vulnerability can be affected by the geographic location of its current range, as
75 the intensity of warming experienced will have a direct effect on the geographical
76 distance a species will have to disperse to track this change (Chen et al. 2011).
77 Furthermore, species occupying habitats constrained by hard geographic boundaries,
78 such as the top of mountains or at coastal edges, could be most vulnerable to
79 population decline and extinction as they are restricted in the amount of suitable habitat
80 they can disperse to (Parmesan 2006, Williams et al. 2007, Loarie et al. 2009, Dirnböck
81 et al. 2011).

82 Alpine biomes have been described as having the lowest "velocity of climate change",
83 owing to topographic effects (Loarie et al. 2009), which in turn means alpine species
84 can potentially track suitable climates by dispersing relatively short distances, either
85 further up mountains or around the mountains to areas with a different aspect. Despite
86 this, there is also evidence that plants restricted to mountainous regions are
87 disproportionately sensitive to the effects of climate change compared to other species
88 (Thuiller et al. 2005, Lenoir et al. 2008), with species at higher elevations having
89 greatest risks of extinction (Guisan and Theurillat, 2000). Arctic biomes, on the other
90 hand, have a relatively higher climate change velocity (Loarie et al. 2009) due to often
91 lower topographic relief. Additionally, the Arctic has been shown to be warming more
92 rapidly than the global mean since the mid-20th century (IPCC, 2013). Substantial
93 change to arctic vegetation has been predicted as a result, with at least half of the

vegetated areas shifting to different physiognomic classes and contractions predicted for classes that do not have more northerly landmasses to disperse to (Pearson et al. 2013).

In this study, we used species distribution models to predict current and future (2040-2060) species distributions of alpine and arctic specialists under multiple climate change and dispersal scenarios. Specifically, we test whether the predicted change between these two groups are significantly different as a result of arctic species needing to disperse latitudinally while alpine species needing to disperse altitudinally to track their suitable climates. We also investigate how dispersal ability may affect how these species are able to adjust to climate change.

Materials and Methods

Species occurrence data

We used bumblebees within the subgenera *Alpinobombus* (Williams et al. 2019) and *Mendacibombus* (Williams et al. 2016) as our study species to compare arctic and alpine species responses to climate change. The records used were collected by the authors and other collaborators in the field to the nearest 0.01 degree or finer and sampling involved searching in regions that are potentially suitable for bumblebees, ensuring environmental representativeness of the sampling locations. The taxonomic identities of the specimens we collected were determined using both morphology and genetic analyses. Bumblebees have been found to be highly vulnerable to climate change in Europe (Rasmont et al., 2015, Biella et al., 2017). Species within *Alpinobombus* and *Mendacibombus* are specialised to extreme-cold environments and found across the arctic and alpine areas of the Northern Hemisphere. *Mendacibombus* species are found primarily in alpine and subalpine biomes, while *Alpinobombus* species are found primarily in arctic and subarctic biomes. There are a few exceptions where *B. alpinus*, *B. balteatus*, and *B. kirbiellus* of *Alpinobombus* occur in the Alps, Altai, and Rocky Mountains respectively, but these are a minority of their overall ranges, and thus we included these species within the arctic grouping. Despite belonging in two separate clades occurring in different biomes, the bumblebees used as case-studies

here are relatively similar ecologically in having generalist diets permitting them to take advantage of the different flowers available during the short seasons in their respective extreme environments. Both groups also have moderately long tongues, which is generally important for governing food-plant selection for bumblebees. Consequently these two groups of species have the merit of ecological comparability for analysis of species' vulnerability to climate change.

There are nine species within *Alpinobombus* and twelve species within *Mendacibombus*. To train our models, we included only species with at least 15 occurrence records (Pearson et al. 2006, Table 1), leaving eight *Alpinobombus* and ten *Mendacibombus* species. The records included all longitude, northwards of 35° latitude for *Alpinobombus*, and from -10° to 170° longitude, 20° to 55° latitude for *Mendacibombus*.

Environmental variables

Climate variables available from the WorldClim database at 30 arc-seconds were considered as potential explanatory variables (Hijmans et al. 2005). These layers were of a coarser resolution than our occurrence records. We chose to include five climate variables due to their importance to bumblebee physiology and survival (Austin and Van Niel 2011, Araújo et al. 2019), mirroring the methods in Williams et al. (2015, Table 2). These included isothermality, mean temperature of warmest quarter, annual precipitation, precipitation of wettest month, and precipitation of the warmest, and the proposed mechanisms for each variable on bumblebee ecology is detailed in Table 2. An additional derived variable, the ratio between precipitation of wettest month to precipitation of warmest quarter, was also calculated and added to be considered as a climate variable in subsequent models (Williams et al. 2015, Table 2). The layers containing the aforementioned six climate variables were then cropped to two different overall study regions based on the occurrence records, one for each subgenus, and a correlation matrix was built for each region (Table S1, S2). One of each pair of variables that were highly correlated ($R^2 > 0.75$) were discarded. This left five climate variables for *Alpinobombus*, and four climate variables for *Mendacibombus* to be included within our models (Table 2).

For future climate scenarios, we included data from two out of the four Representative Concentration Pathways (RCPs) adopted by the Intergovernmental Panel on Climate Change Fifth Assessment Report (IPCC, 2013). These were RCP4.5 and RCP 8.5, which represent the second-best and the worst-case-scenario in terms of future radiative forcing values, with a higher RCP corresponding to a higher degree of warming. We downloaded the relevant climate variables for these two scenarios for 2041-2060 projected using four different General Circulation Models (GCMs) under the Coupled Model Intercomparison Project Phase 5 (CCSM4, GFDL-CM3, HadGEM2-ES, and MPI-ESM-LR), which have been shown to generate suitable predictions for the Northern Hemisphere (McSweeney et al. 2014, Miao et al. 2014). We then combined these projected climate variables by calculating the mean value of each pixel for each variable and used these as our future climate inputs (Miao et al. 2014). Finally, we used MODIS land cover data (MCD12Q1) to mask out any tiles which were classified as water, urban and built up, and snow and ice (Friedl et al. 2010), as these areas are unlikely to support bumblebee populations under current or future conditions within our timeframe.

Ensemble Species Distribution Modelling (SDM)

We used SDMs to estimate both current and future potential species distributions for each species (Elith and Leathwick, 2009). We included four commonly used algorithms, including two machine-learning methods, Generalised Boosted Models (GBM) and Random Forest (RF); one regression method, Generalised Additive Model (GAM); and one classification method, Classification Tree Analysis (CTA). We used the R package 'biomod2' for the pre-processing, SDM, and ensembling pipeline (Thuiller et al. 2012). We randomly generated pseudo-absences (PAs) for each species within windows of extent half a degree longitude and latitude wider than the occurrence points of the species, and the number of PAs drawn was equal to the number of presence records for the species. This was done as it has been shown than randomly generated PAs consistently yielded predictions with higher specificity (Barbet-Massin et al. 2012). We repeated this process three times for each species to create three replicate datasets for each species.

To create training and evaluation data for our models, occurrence and PA points for each species were split randomly, with 70% of data used for training and the remaining 30% set aside and used to evaluate the performance of the trained models. We generated a different set of training data for each set of PAs, resulting in three different inputs for each species, which were each used to build individual models using each of the algorithms outlined above. This modelling pipeline results in twelve different models for each species, which we then evaluated using the Area Under the receiver operating characteristic Curve (AUC). We then used a random permutation procedure (as implemented in biomod2; Thuiller et al. 2009) to estimate variable importance for each model built.

We used an ensemble method to incorporate the multiple models together into a single output per species per projection (Thuiller et al. 2009). Only models that performed well ($AUC > 0.75$) and had high spatial congruence ($IStat > 0.9$) across the replicates when using the same algorithm were included (Warren et al. 2008, Aguirre-Gutiérrez et al. 2013). Finally, we calculated the ensemble projections using a weighted mean method, weighing each model based on their individuals AUC scores.

Final estimated distributions and dispersal scenarios

To create binary maps of presence/absence for each species, we used the probability threshold that minimises the difference between sensitivity and specificity (Nenzén and Araújo, 2011). These initial maps provided us with estimated current distributions, as well as predicted future distributions with no dispersal restrictions except the window of extent used in the projection process. This represented a long-distance dispersal scenario, assuming the bumblebees are able to cross any distance to suitable habitat based on the modelled results, although this is unlikely (Williams et al. 2018). A second dispersal scenario involved no-dispersal, where only areas that are already currently part of the distribution are counted in any future projections. Finally, a third dispersal scenario included short-distance dispersal, where future distributions were counted if it is part of or connected (in the cardinal directions) to the current distribution in the future projection. This third scenario represents the most realistic possibility, as it gives the

bumblebees a chance to disperse, but only when there is a corridor of suitable habitat (Williams et al. 2018). To compare whether *Alpinobombus* and *Mendacibombus* respond differently to climate change, we used Mann-Whitney U-tests to compare relative area changes. Specifically, we compared the two subgenera under the three dispersal and two emission scenarios, resulting in six separate U-tests, one for each possible pair of scenarios. A Wilcoxon signed-rank test was also used to test whether the two emission scenarios had significant effects on the results at the 95% level. As we expected RCP8.5 to always lead to an exaggerated response when compared to RCP4.5 rather than a unidirectional change, we converted all values to their absolute values for this test.

Results

All of the ensemble models had strong AUCs, with 16 out of the 18 outputs >0.9 (Table S3).

Figure 1 shows that *Alpinobombus* species have larger distribution declines than the *Mendacibombus* species, and this was confirmed by the Mann-Whitney U-tests used ($p < 0.05$ for all six possible scenarios; Table S4). Under a no-dispersal scenario, three out of ten *Mendacibombus* species lose more than 50% of their current distribution under both emission scenarios, while all eight *Alpinobombus* species included in the analysis have greater than 50% loss. Under the short-distance dispersal scenario, four species were able to expand their range under both climate change scenarios. These were *B. convexus*, *B. himalayanus*, *B. marussinus*, and *B. turkestanicus*, all of which are within *Mendacibombus*. Out of these, *B. convexus*, *B. himalayanus*, and *B. marussiunus* also have the smallest decline observed, even with no dispersal.

The comparison between the two emission scenarios show that RCP8.5 will lead to significantly exaggerated relative change in area ($p = 1.871\text{e-}10$, RCP4.5 median = 0.544; RCP8.5 median = 0.675). The only exception to this was seen in *B. avinoviellus*

under the long-dispersal scenario, where there was a distribution decline under RCP4.5 and a distribution expansion under RCP8.5 (Fig. 1).

The dispersal scenarios had varied effects on the bumblebees' future distributions. Some species may be heavily affected under the no-dispersal scenario, but the capacity to disperse reverses this trend. This can be seen for *B. convexus*, *B. himalayanus*, *B. marussinus*, *B. turkestanicus*, all of which are in *Mendacibombus*, where there is a projected distribution expansion under both short-distance dispersal and long-distance dispersal scenarios. In other species (*B. avinoviellus*, *B. waltoni*, *B. defector*, *B. margreiteri*, *B. polaris*, *B. kirbiellus*, *B. balteatus*, *B. neoboreus*), dispersal can ameliorate the effects of climate change, though there is still an overall distribution decline for these species. These species are split more evenly between the two subgenera, with four species from each subgenus. Finally, there are six species where the dispersal scenario does not affect their predicted distribution at all. These are *B. handlirschianus*, *B. mendax*, *B. natvigi*, *B. pyrrhopygus*, *B. alpinus*, and *B. hyperboreus*, and includes the two *Mendacibombus* species and four *Alpinobombus* species. Figure 2 shows the relative mean predicted area change in distribution area under the short-distance dispersal scenarios and RCP 8.5 for all species by 2050 geographically. This specific scenario is chosen as it is the most realistic and likely to happen under current policies.

Discussion

Our results suggest that the topography of the region within which a species is resident plays an important role in its vulnerability to climate change. Under all dispersal scenarios, *Alpinobombus* species are projected to experience significantly larger proportional distribution declines, while there is greater variation in responses observed among *Mendacibombus* species. This suggests that arctic species will consistently be more vulnerable to the effects of climate change, with larger distribution declines as a result of more extensive warming in the area and greater distances that arctic species must disperse cross-latitude to track suitable climates (Loarie et al. 2009, IPCC 2013).

In contrast, the more complex topography found in alpine habitats potentially allows much more varied responses by alpine species. This could be further enhanced by more complex climatic effects due to mountain topography, including aspect and shading (Elsen and Tingley 2015).

For some species, if they were able to disperse longer distances, we found that climate change may not necessarily be severely detrimental, and they may in some cases thrive and expand their distributions under climate change (Fig. 1). These included *B. convexus*, *B. himalayanus*, *B. marussinus*, and *B. turkestanicus*, all of which are found around the mountain ranges surrounding the Tibetan plateau, with *B. convexus* being found on the south-eastern side and the other three in the western side of the plateau (Fig. 2). On the other hand, not all alpine species are necessarily less vulnerable to climate change. These include *Bombus margreiteri*, *B. mendax*, and *B. handlirschianus*, the three species with the highest distribution losses predicted in *Mendacibombus*, with losses comparable to those seen in *Alpinobombus* species. Interestingly, these are also some of the species found outside of the Tibetan plateau: instead they are found across parts of Mongolia, Kamchatka, the Alps, and the Caucasus-Turkey-Elborz mountain ranges, respectively. This suggests that for alpine species, the mountain ranges around the Tibetan plateau may be able to offer higher refugia for species under climate change while the species in other alpine areas may lack this option.

For most species, dispersal could potentially ameliorate the expected negative effects of climate change, even if long-distance dispersal is unlikely for bumblebees (Williams et al. 2018), leading to a failure to track warming habitats (Kerr et al., 2015). However, this is not always the case, as six species (*B. handlirschianus*, *B. mendax*, *B. natvigi*, *B. pyrrhopygus*, *B. alpinus*, and *B. hyperboreus*) seem to have very similar projected distribution declines, regardless of dispersal scenarios (Fig. 1). These are the species which are likely to be already at their climate extremes and hence, for such species, land availability becomes the dominant factor determining whether a species can track suitable habitat. In Fig. 2b, we see that the highest loss of area occurs at the edge of any available land. In these areas, dispersal ability no longer matters and species currently distributed here have no potential to disperse at all under climate change, and

thus are likely to be the most vulnerable to the effects of climate change (Pearson et al. 2014).

Using SDMs for our analysis, we modelled the suitable habitats for each species individually using their current distribution and the climatic variables within this area. We were able to achieve high model accuracy with AUCs > 0.9 for 16 (out of 18) species' models. Mean temperature of the warmest quarter was consistently an important explanatory variable for all species, which may reflect its importance in influencing colony foraging and reproductive success. The other variables had varying importance for each species (Table S5, S6).

An assumption made when predicting bumblebee distribution under climate change is that increasing frequency and severity of extreme climatic events will be related to increasing climatic means. We have taken steps to minimise modelling uncertainty by using an ensemble modelling approach, including only models with high AUCs and high spatial congruence, and considering a range of possible dispersal abilities of the species. However, there remain substantial uncertainties in estimating how these species will respond to climate change, as these models include dispersal as the only means by which species respond to climate change. This approach disregards other potentially important factors, such as possible evolutionary change (though unlikely in the timeframe considered) as vulnerable species adapt to climate change (Thomas et al. 2001), or biotic interactions between species (Staniczenko et al. 2017). For example, bumblebee dispersal will also rely heavily on the dispersal of their food plants, which will also be limited by the time required for suitable soils to develop and may not be captured by the climate variables used in our models. We have attempted to take these variations into account by including three very different possible dispersal scenarios, including two extreme and an intermediate scenario. We believe short-distance dispersal is the most likely scenario, as this captures circumstances where there is a corridor of suitable habitat for the bumblebees to disperse through into the predicted future distributions (Williams et al. 2018).

Model uncertainty may also arise due to potential spatial mismatch between species occurrence records and WorldClim data. This is likely to have a larger impact on alpine species, as environmental heterogeneity is much higher in alpine regions when compared with arctic regions. This could potentially affect the resulting absolute distribution sizes, overestimating species extent, with alpine species being more affected. However, the final conclusions drawn are unlikely to be greatly affected as we were comparing the relative distribution changes of the species, and any overestimation will be consistent in both current and future distributions. Moreover, data available from WorldClim allows us to apply our data to the entire Northern Hemisphere at a spatial resolution of 30 arc-second, although it is possible that these data fail to capture finer scale nuances needed to detect possible microclimates (Suggitt et al., 2011). This will also likely have a greater impact on the alpine species due to higher environmental heterogeneity in the alpine regions. In this case, declines for the alpine species may be overestimated for the SDD and LDD scenarios, further widening the difference in species response between the alpine and arctic species observed from our results.

With careful consideration of their limitations, we believe SDMs remain useful in providing insight into species' potential future distribution under climate change (Guisan et al. 2013, Araújo et al. 2019), and our results show that arctic species more vulnerable to the effects of climate change than alpine species.

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Author contributions: All authors conceived the study. PHW collected and analysed the species occurrence data with collaborators. CKFL wrote the paper. All authors participated in discussing and editing the manuscript.

Data accessibility

The occurrence points used to generate the species distribution models used in the study are currently not deposited publically as they are part of a larger project and will be arranged shortly in the future. In the interim, please contact the authors directly for more information.

Supplementary Materials

The following materials are available as part of the online article from <https://escholarship.org/uc/fb>

Table S1. Correlation matrix for the chosen BIOCLIM variables within the *Alpinobombus* study region.

Table S2. Correlation matrix for the chosen BIOCLIM variables within the *Mendacibombus* study region.

Table S3. AUCs of the ensemble models built for each species.

Table S4. Results of the multiple pairwise Mann-Whitney U-tests comparing the relative area change of *Mendacibombus* to *Alpinobombus* under the three dispersal and two emission scenarios.

Table S5. Average variable importance of the ensemble models built for *Alpinobombus* species.

Table S6. Average variable importance of the ensemble models built for *Mendacibombus* species.

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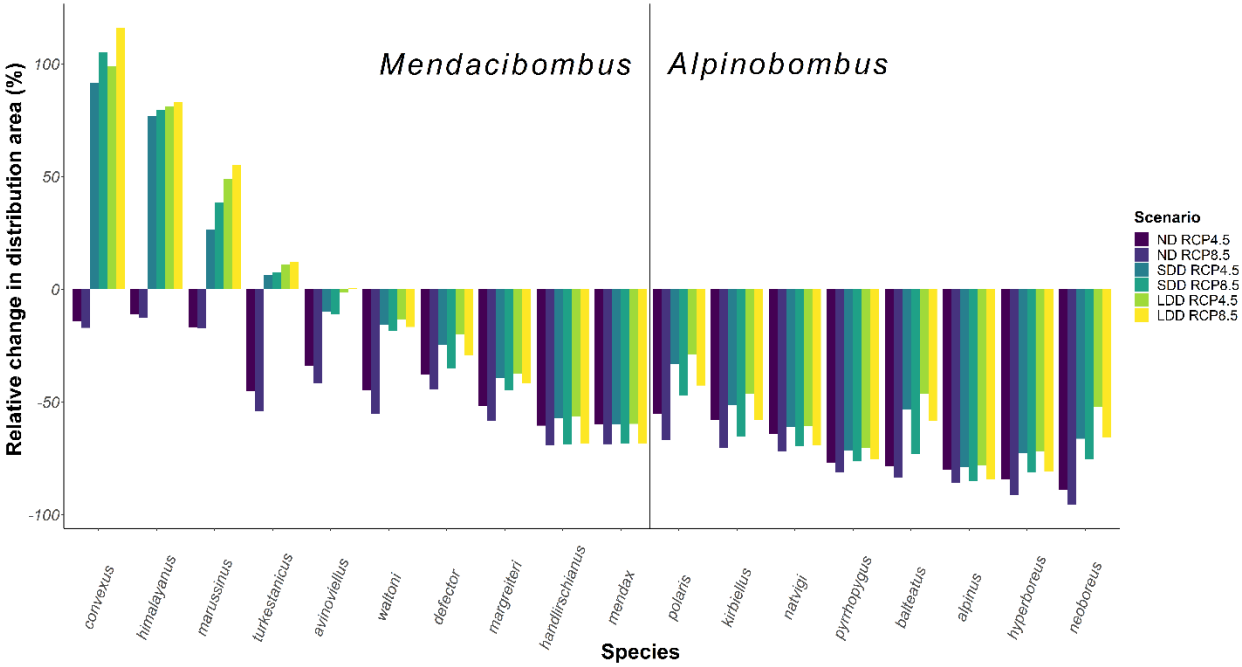
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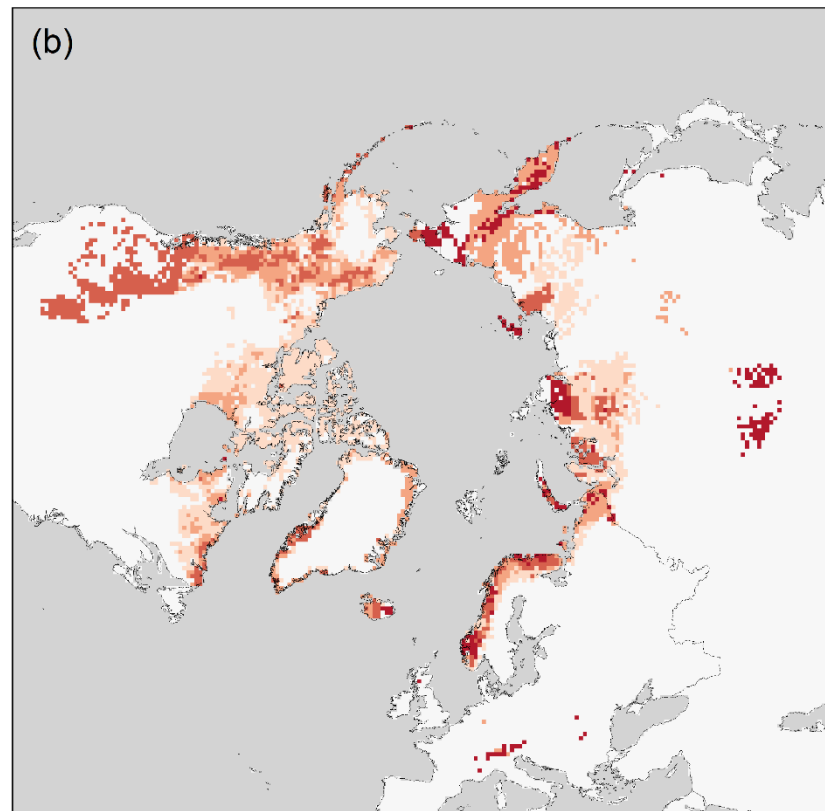
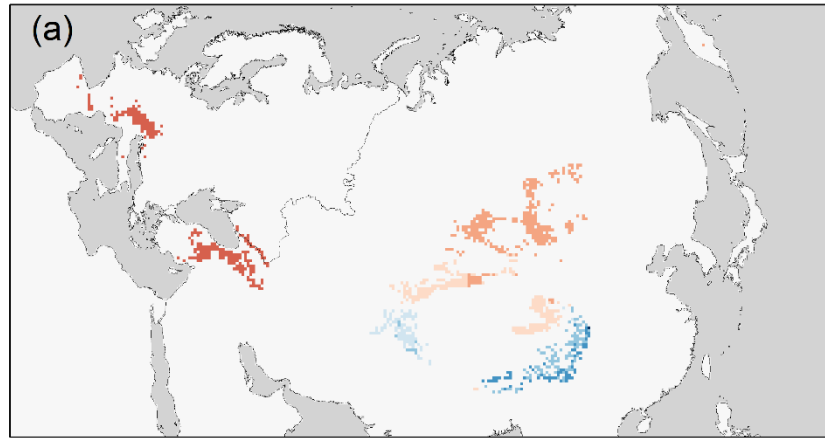
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509 **Figure 1.** Relative percentage change in distribution area between current and six projected
510 distributions for each bumblebee species based on an ensemble of species distribution models.
511 Includes two emissions scenarios: Representative Concentration Pathway (RCP) 4.5 and 8.5;
512 and three dispersal scenarios: No Dispersal (ND), Short Distance Dispersal (SDD), and Long
513 Distance Dispersal (LDD).
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Relative distribution change

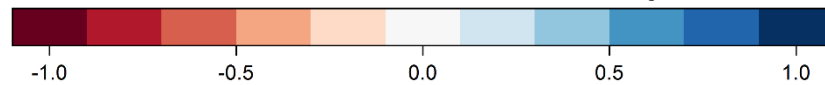


Figure 2. Relative predicted mean area change for (a) *Mendacibombus* and (b) *Alpinobombus* species under the short-distance dispersal scenario predicted in 2050 under RCP8.5.

519 **Table 1.** Bumblebee species, split into two subgenera, included in the ensemble of species
520 distribution models and the number of occurrence points for each species that were collected
521 from the field.

Subgenus	Species	Occurrence
		Points
<i>Alpinobombus</i>	<i>kirbiellus</i>	227
	<i>polaris</i>	161
	<i>balteatus</i>	119
	<i>pyrrhopygus</i>	59
	<i>natvigi</i>	56
	<i>alpinus</i>	38
	<i>hyperboreus</i>	25
	<i>neoboreus</i>	25
<i>Mendacibombus</i>	<i>waltoni</i>	77
	<i>convexus</i>	71
	<i>mendax</i>	44
	<i>defector</i>	43
	<i>turkestanicus</i>	40
	<i>margreiteri</i>	39
	<i>handlirschianus</i>	24
	<i>avinoviellus</i>	23
	<i>marussinus</i>	20
	<i>himalayanus</i>	17

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524 **Table 2.** Climate variables used in the species distribution models for each subgenera and their proposed mechanisms on
 525 bumblebee distribution.

Variable	Units	BIOCLIM		Proposed Mechanism	<i>Alpinobombus</i> model	<i>Mendacibombus</i> model
		#				
Isothermality	NA	bio3		High values represent larger daily temperature fluctuations, leading to more energy spent on thermoregulation	✓	✓
Mean temperature of warmest quarter	°C	bio10		Extreme values reduce food-plant nectar and pollen production and also profitable foraging opportunities	✓	✓
Annual precipitation	mm	bio12		Low values reduce food-plant nectar and pollen production, and high values reduce foraging opportunities	✓	
Precipitation of wettest month	mm	bio13		High values (particularly for <i>Mendacibombus</i>) reduce foraging opportunities		
Precipitation of warmest quarter	mm	bio18		Low values reduce food-plant nectar and pollen production, and high values reduce foraging opportunities	✓	✓
Ratio: Precipitation of Wettest Month to Precipitation of Warmest Quarter	NA	bio13/ bio18		High values for a relatively intense month of rainfall (particularly for <i>Mendacibombus</i>) reduce foraging opportunities	✓	✓

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