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Climate change vulnerability higher in arctic than alpine bumblebees

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14 **Title:** Climate change vulnerability higher in arctic than alpine bumblebees

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34

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

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

55 **Highlights:**

- 56 • Arctic bumblebees show higher vulnerability to climate change compared to  
57 alpine species.
- 58 • Arctic species will be required to disperse across larger distances than alpine  
59 species in order to track suitable climates, increasing extinction vulnerability.
- 60 • Climate change exacerbates both positive and negative changes in species  
61 distributions.
- 62 • Species living in climate extremes have increased chance of being driven to  
63 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

94 vegetated areas shifting to different physiognomic classes and contractions predicted  
95 for classes that do not have more northerly landmasses to disperse to (Pearson et al.  
96 2013).

97 In this study, we used species distribution models to predict current and future (2040-  
98 2060) species distributions of alpine and arctic specialists under multiple climate change  
99 and dispersal scenarios. Specifically, we test whether the predicted change between  
100 these two groups are significantly different as a result of arctic species needing to  
101 disperse latitudinally while alpine species needing to disperse altitudinally to track their  
102 suitable climates. We also investigate how dispersal ability may affect how these  
103 species are able to adjust to climate change.

## 104 **Materials and Methods**

### 105 *Species occurrence data*

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

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

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

### 135 *Environmental variables*

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

153 For future climate scenarios, we included data from two out of the four Representative  
154 Concentration Pathways (RCPs) adopted by the Intergovernmental Panel on Climate  
155 Change Fifth Assessment Report (IPCC, 2013). These were RCP4.5 and RCP 8.5,  
156 which represent the second-best and the worst-case-scenario in terms of future  
157 radiative forcing values, with a higher RCP corresponding to a higher degree of  
158 warming. We downloaded the relevant climate variables for these two scenarios for  
159 2041-2060 projected using four different General Circulation Models (GCMs) under the  
160 Coupled Model Intercomparison Project Phase 5 (CCSM4, GFDL-CM3, HadGEM2-ES,  
161 and MPI-ESM-LR), which have been shown to generate suitable predictions for the  
162 Northern Hemisphere (McSweeney et al. 2014, Miao et al. 2014). We then combined  
163 these projected climate variables by calculating the mean value of each pixel for each  
164 variable and used these as our future climate inputs (Miao et al. 2014). Finally, we used  
165 MODIS land cover data (MCD12Q1) to mask out any tiles which were classified as  
166 water, urban and built up, and snow and ice (Friedl et al. 2010), as these areas are  
167 unlikely to support bumblebee populations under current or future conditions within our  
168 timeframe.

### 169 *Ensemble Species Distribution Modelling (SDM)*

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

183 To create training and evaluation data for our models, occurrence and PA points for  
184 each species were split randomly, with 70% of data used for training and the remaining  
185 30% set aside and used to evaluate the performance of the trained models. We  
186 generated a different set of training data for each set of PAs, resulting in three different  
187 inputs for each species, which were each used to build individual models using each of  
188 the algorithms outlined above. This modelling pipeline results in twelve different models  
189 for each species, which we then evaluated using the Area Under the receiver operating  
190 characteristic Curve (AUC). We then used a random permutation procedure (as  
191 implemented in biomod2; Thuiller et al. 2009) to estimate variable importance for each  
192 model built.

193 We used an ensemble method to incorporate the multiple models together into a single  
194 output per species per projection (Thuiller et al. 2009). Only models that performed well  
195 (AUC > 0.75) and had high spatial congruence (IStat > 0.9) across the replicates when  
196 using the same algorithm were included (Warren et al. 2008, Aguirre-Gutiérrez et al.  
197 2013). Finally, we calculated the ensemble projections using a weighted mean method,  
198 weighing each model based on their individuals AUC scores.

#### 199 *Final estimated distributions and dispersal scenarios*

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

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

222

## 223 **Results**

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

226 Figure 1 shows that *Alpinobombus* species have larger distribution declines than the  
227 *Mendacibombus* species, and this was confirmed by the Mann-Whitney U-tests used ( $p$   
228 < 0.05 for all six possible scenarios; Table S4). Under a no-dispersal scenario, three out  
229 of ten *Mendacibombus* species lose more than 50% of their current distribution under  
230 both emission scenarios, while all eight *Alpinobombus* species included in the analysis  
231 have greater than 50% loss. Under the short-distance dispersal scenario, four species  
232 were able to expand their range under both climate change scenarios. These were *B.*  
233 *convexus*, *B. himalayanus*, *B. marussinus*, and *B. turkestanicus*, all of which are within  
234 *Mendacibombus*. Out of these, *B. convexus*, *B. himalayanus*, and *B. marussiunus* also  
235 have the smallest decline observed, even with no dispersal.

236 The comparison between the two emission scenarios show that RCP8.5 will lead to  
237 significantly exaggerated relative change in area ( $p = 1.871e-10$ , RCP4.5 median =  
238 0.544; RCP8.5 median = 0.675). The only exception to this was seen in *B. avinoviellus*

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

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

258

## 259 **Discussion**

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

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

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

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

298 thus are likely to be the most vulnerable to the effects of climate change (Pearson et al.  
299 2014).

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

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

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

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

345

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

#### 353 **Data accessibility**

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

358

### 359 **Supplementary Materials**

360

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

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

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

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

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

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

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

374

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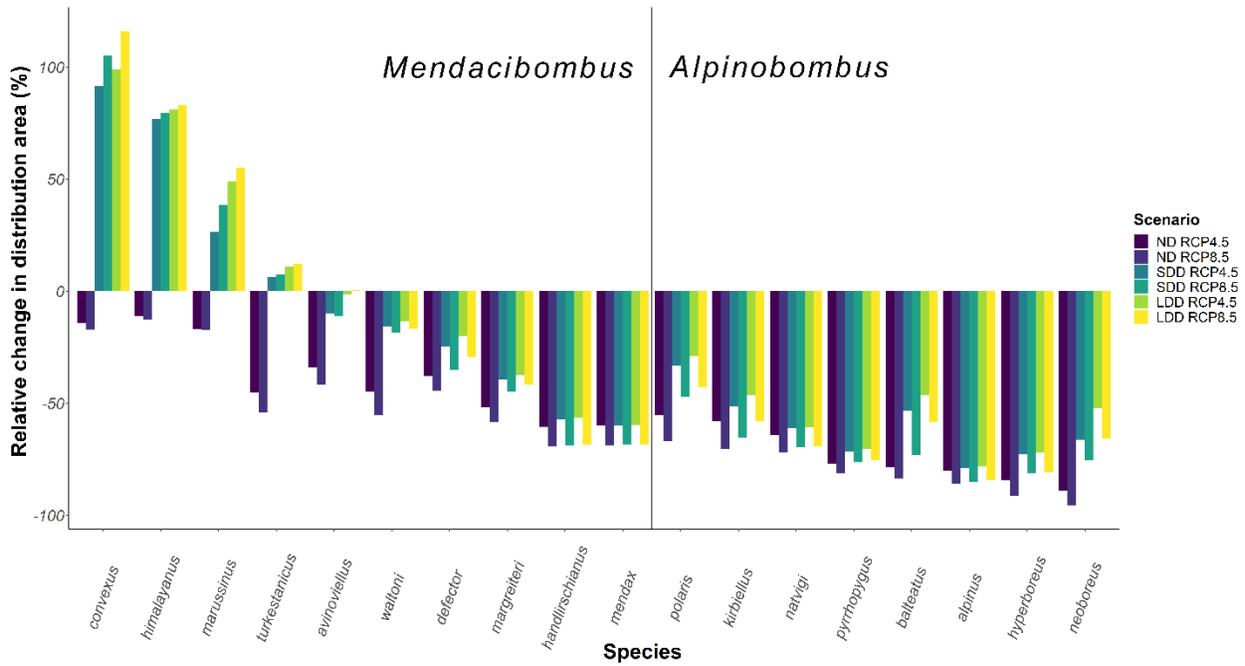
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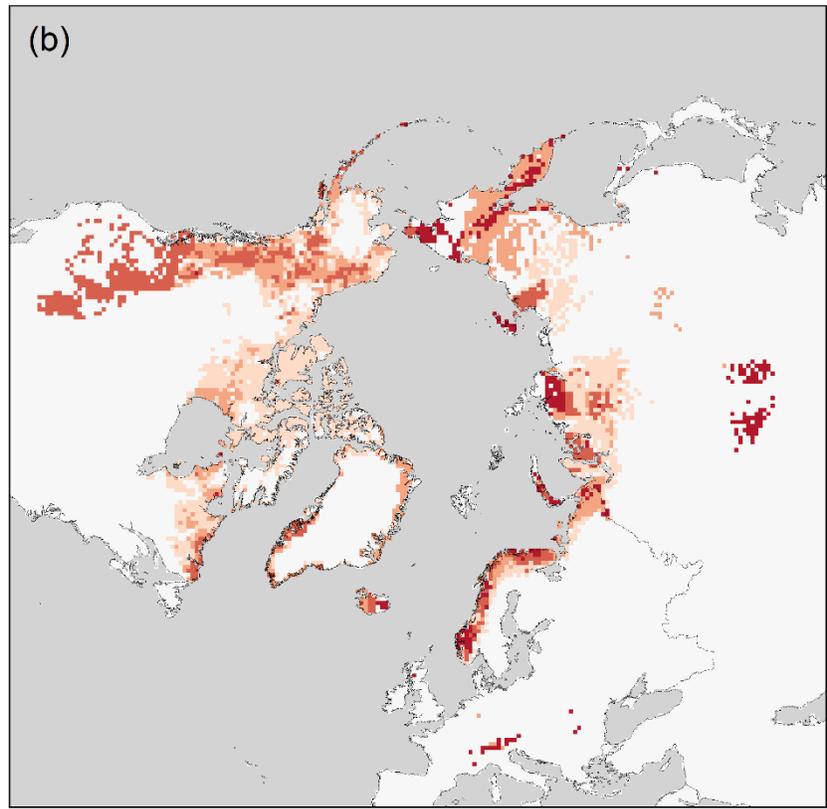
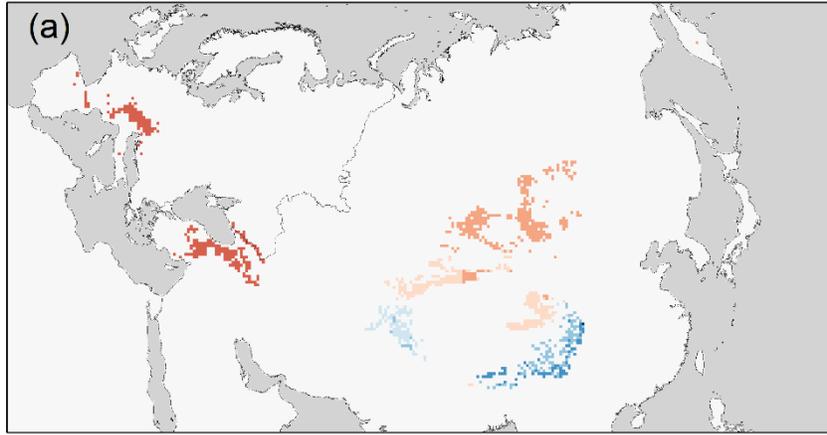
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506



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).  
514



Relative distribution change



515

516 **Figure 2.** Relative predicted mean area change for (a) *Mendacibombus* and (b) *Alpinobombus*

517 species under the short-distance dispersal scenario predicted in 2050 under RCP8.5.

518

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

522

523

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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527