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Climatic niche breadth determines the response of bumblebees (*Bombus* spp.) to climate warming in mountain areas of the Northern Iberian Peninsula

José M. Herrera^{1,3} · Emilie F. Ploquin^{1,4} · Pierre Rasmont² · José R. Obeso¹

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Abstract

Studies examining species range shifts in the face of climate change have consistently found that response patterns are complex and varied, suggesting that ecological traits might be affecting species response. However, knowledge of how the traits of a species determine its response to climate change is still poorly understood. Here we investigate the role of species-specific climate niche breadth in forecasting bumblebee (*Bombus* spp.) responses to regional climate warming in the Cantabrian Range (north-western Iberian Peninsula). Climate niche breadth was defined using known data for occurrences of specific species at their continental (i.e., European) scale of distribution. For each bumblebee species, climate niche breadth was found to be related to (1) the elevational range shifts of species between their historical (1988–1989) and recent (2007–2009) distribution and (2) the variation in the climatic conditions of the localities they inhabited (i.e., the local climate space) between both study periods. Our results show a strong relationship between climate niche breadth, particularly thermal niche breadth, and the response of bumblebee species to climate warming, but only when this response was determined as variations in local climate space. The main conclusions of our work are thus twofold. First, variations in the climatic conditions underlying range shifts are useful in making accurate assessments of the impact of climate change on species distributions. Second, climate niche breadth is a particularly informative ecological trait for forecasting variations in species responses to climate change.

Keywords Climate niche · Climate-driven shifts · Elevation · Species traits · Species distribution · Specialist · Warming

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✉ José M. Herrera
 herreramirlo@gmail.com

¹ Departamento de Biología de Organismos y Sistemas, Unidad Mixta de Investigación en Biodiversidad (CSIC-UOPA), Universidad de Oviedo, 33071 Oviedo, Spain

² Institut des Biosciences, Laboratoire de Zoologie, Université de Mons, Place du Parc 23, 7000 Mons, Belgium

³ Present Address: Research Center in Biodiversity and Genetic Resources, University of Évora, Casa Cordovil 2a Andar, Rua Dom Augusto Eduardo Nunes, 7000-651 Évora, Portugal

⁴ Present Address: NERC Centre for Ecology and Hydrology, Biological Records Centre, Maclean Building, Benson Lane, Crowmarsh Gifford OX10 8BB, Oxfordshire, UK

Introduction

Widespread alterations in species distributions in the face of climate change have been documented (Scheffers et al. 2016). To a large extent, this is because species need to track their climatic envelopes in order to continue to live within suitable environmental conditions (Sunday et al. 2011, 2012) and changes in the range boundaries of different species have consistently found that movement responses within a community are species-specific. This has resulted in the interesting finding that while (as would be expected) most species are shifting toward cooler environments (e.g. Konvicka et al. 2003; Hickling et al. 2006; La Sorte and Thompson 2007; Chen et al. 2011a, b), others are not shifting at all, or are performing counter-intuitive range shifts (Crimmins et al. 2011; Tingley et al. 2012; Ploquin et al. 2013; Hiddink et al. 2015). This variability has been widely attributed to individual species attributes, such as dispersal ability and environmental tolerance, which ultimately determine each species' capacity

(and need) to track suitable climatic conditions via range shifts (Angert et al. 2011; Estrada et al. 2016).

Like many other pollinating insects, bumblebees (*Bombus* Latreille, 1802) are experiencing a worldwide decline which has been attributed, among other drivers of global environmental change, to climate change (Cameron et al. 2011; Goulson et al. 2015). Wide-scale reductions in range and abundance of these insects have indeed raised global concern about their impact on pollination services, especially in cool environments such as mountainous ecosystems where most other pollinating insects are less active or even absent (Hegland et al. 2009). In the Cantabrian Range (north-western Iberian Peninsula), for instance, a previous study reported significant alterations in the elevational range between the historical (1988–1989) and recent (2007–2009) distributions of a bumblebee community (Ploquin et al. 2013). Moreover, the same work reported that while most bumblebee species performed uphill shifts, others showed very little or no shift in their range, suggesting that species-specific traits might underlie variations in the responses of each species to regional climate warming (Herrera et al. 2014). However, no direct test of this hypothesis was undertaken at that time.

In this work we investigated the role that climatic niche breadth plays in determining the species-specific response of bumblebees to the regional warming that has occurred over the past 2 decades (Álvarez et al. 2009). Climatic niche breadth is assumed to play a pivotal role in modulating the response of species since species distribution is widely recognized to be greatly influenced by climatic variables (Chejanovski and Wiens 2014; Kühnel and Blüthgen 2015; Ralston et al. 2016), especially temperature (Soberón 2007). Species-specific climatic niche breadth was ascertained based on the range of climatic conditions that each species is able to tolerate and was therefore defined by their species-specific known occurrences at the continental (i.e., European) scale of their distribution (see Kamilar and Muldoon 2010 for a similar procedure).

Species-specific climatic niche breadth was first related to the extent of range shifts exhibited by each bumblebee species between the historical and recent study period (data from Ploquin et al. 2013). Specifically, we focused on changes in mean elevation as well as the upper and lower elevational range limits. Second, climatic niche breadth was related to the variation in the climatic conditions of the localities they inhabited (i.e., the local climate space) between both study periods. We incorporate the change in local climate space as response variable because exclusively focusing on the extent of range shifts might neglect (or at least underestimate) the fact that environmental variables may or may not covary with elevation or latitude, something that might ultimately lessen the predictive power of range shifts. Indeed, the potential mismatch between range

and environmental shifts could be particularly important in mountainous systems where the orography typically modifies the spatial patterning of temperature and humidity, even at fine spatial scales. Within this context, we expected that elevational shifts would be higher, and changes in local climate space lower as the climatic niche breadth of a species narrows since this would imply higher dependence on, and need to stay within, its climate envelope.

Materials and methods

Spatial and temporal framework

We used bumblebee distribution data from the Cantabrian Range (north-western Iberian Peninsula) in two study periods: 1988–1989 (Obeso 1992) and 2007–2009 (Ploquin et al. 2013). Regional temperature rose by ca. 0.9 °C over the two decades encompassed by these studies, resulting in an upward shift of isotherms of ca. 160 m based on a regional elevational temperature lapse rate of $-0.5\text{ }^{\circ}\text{C } 100\text{ m}^{-1}$ (Álvarez et al. 2009). For all analyses data regarding bumblebee species presence and abundance from 78 sites in the first study period (1988–1989) and 51 in the second (2007–2009), which were used, with a total of 29 of the sites having been sampled in both study periods (Table S1). Sampling localities ranged from sites located at sea level, to those at approximately 2200 m a.s.l., thus the range of elevation represented virtually all the climatic conditions and suitable habitats for the regional pool of bumblebee species in the study region (Herrera et al. 2014).

In both study periods, similar time-constrained samplings (1-h per sampling locality) were made within a 100 m radius circular area during the spring and summer seasons (mid May through late August) in order to avoid bias in the sampling effort between sampling periods (see Obeso 1992 for a detailed description of sampling procedure). Based on the researchers' knowledge of the study region and using visual estimations, surveys were carried out during maximum flower blooming to avoid differences in the composition of the bumblebee assemblage between localities as a result of variations in food-resource availability. Each site was sampled once. A total of 24 and 21 bumblebee species were identified in the first and second period, respectively (Ploquin et al. 2013). However, in this work we restricted our analysis to those bumblebee species occurring in at least ten localities in each study period. This was because very low prevalence (i.e., proportion of presences and absences for each species) is likely to reduce the discriminatory power of distinguishing between suitable and unsuitable sites (see Gutiérrez-Illán et al. 2010 for a similar approach). Accordingly, 12 bumblebee species were used in all subsequent analyses.

Determining climatic niche breadth for bumblebee species

Climatic conditions at local scales might represent only a sub-sample of the set of climatic conditions at which species can occur at broader spatial scales (Quintero and Wiens 2013). For this reason we determined the species-specific climatic niche breadth of bumblebees by estimating the range of climatic conditions where each species also occurs outside of their local distribution (Soberón 2007) using the continental-scale distribution dataset for West-Palearctic bumblebees (Rasmont et al. 2015). We overlapped these distribution maps with data from the WorldClim interpolated climate surface maps (Hijmans et al. 2005) onto a GIS platform, assuming that the observed climatic space for each species would reflect the full range of climatic conditions under which it can exist, at least in terms of its West-Palearctic distribution (Feeley and Silman 2010). We used principal components analysis (PCA) in order to integrate variation across climate variables between the grid cells occupied by bumblebee species (Table 1; Table S1). The variables used were *annual mean temperature*, *annual temperature range* (maximum temperature of the warmest month minus minimum temperature of coldest month), *mean temperature of warmest quarter*, *mean temperature of coldest quarter*, *mean annual*. The first eigenvector (PC1) was mainly related to temperature patterns while the second eigenvector (PC2) was mainly related to rainfall patterns (Table S2; Fig. S1). We therefore used PC1 to estimate the temperature niche breadth (i.e., the range of temperature conditions a species experiences over its continental distribution; *sensu* Quintero and Wiens 2013) and PC2 to estimate the precipitation niche breadth for each bumblebee species, using the upper and lower limits (i.e., the 97.5 and 2.5%

quantiles, respectively), from the collection of eigenvectors obtained for each bumblebee species. Quantiles were used rather than absolute maximums and minimums in order to reduce the impact of outliers potentially caused by errors in species identification and/or geo-referencing (see Feeley and Silman 2010 for a similar procedure).

Determining species response to regional warming

Changes in elevation patterns

The first response variable used to determine the role of climate niche breadth in explaining the response of bumblebees to regional climate change was the species-specific variations in elevation patterns between the first and second study period, based on data extracted from Ploquin et al. (2013).

Changes in local climate space

The second response variable used in the determination of the role of climate niche breadth was the species-specific variations in the local climate space between the first and second study period (Kamilar and Muldoon 2010). For each species, we thus calculated the proportional change in local temperature (hereafter CTC) and precipitation (CPC) conditions as $[(P_2/P_1 - 1) \times 100]$, where P_1 and P_2 are the mean values of the climate variable concerned (i.e., either temperature or precipitation) in the localities where the species was recorded in the first and second period, respectively. Local climate data for each locality came from the Climate Atlas of the Iberian Peninsula (Ninyerola et al. 2005), a database based on rainfall and temperature data, at c. 200-m resolution, from 1950 onwards collected from more than 3000 weather stations across the Iberian Peninsula. We focused on

Table 1 Thermal and precipitation niche breadth for each bumblebee (*Bombus* spp.) species

Species	Thermal niche breadth	Precipitation niche breadth
<i>B. hortorum</i> (L., 1761)	6.2 [−3.5, 3.5] (1059)	5.5 [−2.7, 2.8] (1059)
<i>B. jonellus</i> (Kirby, 1802)	5.4 [−3.9, 1.5] (908)	6.9 [−3.9, 3.8] (908)
<i>B. lapidarius</i> (L., 1758)	6.4 [−3.0, 3.3] (976)	4.8 [−1.6, 3.2] (976)
<i>B. lucorum</i> (L., 1761)	6.8 [−4.2, 2.6] (1186)	7.0 [−2.9, 4.1] (1186)
<i>B. mesomelas</i> Gerstaecker, 1869	7.7 [−4.5, 3.1] (151)	3.1 [−0.6, 2.5] (151)
<i>B. muscorum</i> (L., 1758)	6.0 [−2.8, 3.1] (510)	4.6 [−1.3, 3.2] (510)
<i>B. pratorum</i> (L., 1761)	7.7 [−4.0, 3.6] (1204)	6.9 [−2.8, 4.1] (1204)
<i>B. ruderarius</i> (Müller, 1776)	5.7 [−2.9, 2.7] (673)	4.3 [−1.5, 2.8] (673)
<i>B. sichelii</i> Radoszkowski, 1859	5.6 [−3.9, 2.0] (42)	4.5 [−2.9, 2.7] (42)
<i>B. soroeensis</i> (Fabricius, 1793)	6.9 [−4.3, 2.6] (959)	6.9 [−2.6, 4.3] (959)
<i>B. terrestris</i> (L., 1758)	6.5 [−2.4, 4.0] (949)	4.2 [−1.3, 2.8] (949)
<i>B. wurflenii</i> Radoszkowski, 1859	7.2 [−4.9, 2.3] (444)	7.5 [−2.1, 5.3] (444)

Thermal and precipitation niche breadth were estimated using the difference between the 97.5% and 2.5% quantiles from the collection of eigenvectors resulting from the PCA used to summarize the climatic niche of each bumblebee species (see Table S1 and the main text for details). Minimum and maximum values are shown in brackets and number of distributional records (known locations) are shown in parentheses

average temperature and rainfall because these variables play a key role in species distribution in mountain systems, where there are strong thermal and humidity gradients linked to elevation (e.g. Gutiérrez-Illán et al. 2010; Stefanescu et al. 2011; Herrera et al. 2014).

In order to obtain means (and deviation) in CTC and CPC measurements, we drew 500 bootstrap re-samples for each species using a random sample of individuals from the first and second datasets. Individual-based sub-sampling (i.e., extracting a random number of individuals from survey data irrespective of the total catches at each locality) rather than locality based (i.e., extracting a fixed number of specimens for each locality, e.g. Chen et al. 2011a) was applied because of the low number of individuals of particular species in some localities. Both CTC and CPC values for each species were calculated by one-sample *t*-test, using sequential Bonferroni corrections (Table S3; see Ploquin et al. 2013 for a similar procedure). All statistical analyses related to CTC and CPC shown hereinafter were based on this sub-sampling procedure.

Relationships between climate niche breadth and local climate

The relationships between climate niche breadth and both response variables (i.e., change in local climate space and elevational range shifts between study periods were tested using simple linear and quadratic regressions). Statistical analysis for both the two regressions and for Principal Component Analysis (PCA) were performed using, respectively, the *lm* and *stats* packages of the statistical software R (R Development Core Team 2016). All normality requirements were fulfilled and the presence of spatial autocorrelation in the data was also checked with Moran's *I* tests using the library *ade4* (Dray and Dufour 2007). No spatial structure

was found in the residuals, thus indicating it to be a suitable spatial framework with which to test temporal changes in bumblebee distribution irrespective of spatial constraints. Means \pm SE are used throughout the text, unless otherwise stated.

Results

Climate niche breadth and species responses

Table 1 shows the range, as well as the minimum and maximum values, of the eigenvectors resulting from the PCA used to summarize the climatic niche of each bumblebee species. We found variations in climate niche breadth between individual species, the lowest temperature niche breadth, 5.4, being for *B. jonellus* and the highest, 7.7, for both *B. mesomelas* and *B. pratorum*, while precipitation niche breadth ranged from 3.1 for *B. mesomelas* to 7.5 for *B. wurflenii*.

Shifts in both mean elevation and the lower and upper boundaries were found between the historical and recent distribution of bumblebee species and are shown in Table 2, where the strong variations in the responses of bumblebees to regional climate warming are evident.

Table 3 provides data on changes in the local climate space of inhabited localities between sampling periods, specifically, the proportional change in temperature (CTC) and precipitation (CPC) conditions (see also Table S3). CTC values were higher than CPC values in all bumblebee species, but there was also variation between species: CTC ranged from 4.2 ± 2.2 in *B. jonellus* to 23.4 ± 2.4 in *B. wurflenii*, and CPC ranged from 0.3 ± 2.6 in *B. muscorum* to 9.2 ± 2.3 in *B. ruderarius*.

Table 2 Shifts of mean elevation, and both upper and lower boundaries between 1988 and 1989 and 2007–2009 (m). Data extracted from Ploquin et al. (2013)

Species	Mean elevation	Lower boundary	Upper boundary
<i>B. hortorum</i> (L., 1761)	– 522.7 (134.8)	– 8.0 (31.8)	– 7.1 (159.0)
<i>B. jonellus</i> (Kirby, 1802)	+ 88.3 (97.6)	– 615.3 (186.2)	+ 203.9 (19.8)
<i>B. lapidarius</i> (L., 1758)	+ 291.5 (100.6)	570.2 (421.4)	+ 61.7 (271.8)
<i>B. lucorum</i> (L., 1761)	+ 395.3 (120.1)	+ 252.2 (389.4)	+ 273.4 (213.6)
<i>B. mesomelas</i> Gerstaecker, 1869	+ 67.1 (93.9)	+ 642.9 (177.3)	– 1.0 (14.4)
<i>B. muscorum</i> (L., 1758)	+ 717.8 (121.4)	+ 61.5 (53.8)	+ 258.1 (148.5)
<i>B. pratorum</i> (L., 1761)	+ 396.6 (159.9)	+ 42.5 (67.5)	+ 216.6 (99.8)
<i>B. ruderarius</i> (Müller, 1776)	+ 108.0 (74.8)	+ 429.0 (553.7)	+ 22.9 (179.7)
<i>B. sichelii</i> Radoszkowski, 1859	– 145.4 (107.6)	– 34.3 (132.3)	– 75.3 (121.5)
<i>B. soroeensis</i> (Fabricius, 1793)	– 99.8 (124.6)	+ 226.7 (166.1)	– 116.2 (233.0)
<i>B. terrestris</i> (L., 1758)	– 73.6 (167.4)	+ 9.1 (10.2)	– 1.4 (280.8)
<i>B. wurflenii</i> Radoszkowski, 1859	+ 315.1 (66.1)	+ 1151.5 (245.8)	– 69.7 (149.1)

Means (\pm SE) are shown. Positive values indicate uphill shifts while negative values indicate downhill shifts

Table 3 Number of individuals (NoI) per bumblebee (*Bombus*) species and number of inhabited localities (NoL) in their historical (P_1 ; 1988–1989) and recent (P_2 ; 2007–2009) distribution across the Cantabrian Range (Northern Iberian Peninsula)

Species	NoI		NoL		Local mean temperature				Local mean precipitation				CTC \pm SE		CPC \pm SE	
	P_1	P_2	P_1	P_2	P_1	P_2	P_1	P_2	P_1	P_2	P_1	P_2				
<i>B. hortorum</i> (L., 1761)	147	74	37	17	10.3 \pm 0.04	[5.7, 14.1]	10.9 \pm 0.06	[5.7, 14.0]	1058.5 \pm 26.4	[771.1, 1320.0]	1069.2 \pm 35.4	[834.0, 1230.1]	5.5 \pm 2.8		0.8 \pm 2.6	
<i>B. jonellus</i> (Kirby, 1802)	30	48	11	12	7.1 \pm 0.05	[8.7, 5.5]	6.8 \pm 0.04	[4.9, 11.8]	997 \pm 31.0	[730.2, 1346.0]	1028.2 \pm 43.1	[768.0, 1346.2]	3.0 \pm 2.2		1.3 \pm 3.0	
<i>B. lapidarius</i> (L., 1758)	86	154	16	22	8.9 \pm 0.07	[3.7, 14.0]	6.9 \pm 0.05	[3.7, 11.8]	1018.8 \pm 43.3	[817.0, 1282.0]	992.4 \pm 29.7	[824.0, 1230.1]	28.9 \pm 2.3		2.5 \pm 1.5	
<i>B. lucorum</i> (L., 1761)	94	222	30	34	8.9 \pm 0.05	[3.7, 14.0]	7.0 \pm 0.04	[3.4, 13.9]	1036.0 \pm 28.0	[771.1, 1288.0]	1049.1 \pm 31.1	[730.0, 1346.2]	26.4 \pm 3.4		9.2 \pm 2.1	
<i>B. mesomelas</i> Gerstaecker, 1869	99	81	26	15	7.3 \pm 0.03	[0.3, 10.6]	5.6 \pm 0.05	[3.7, 7.8]	981.5 \pm 33.1	[797.2, 1318.0]	961.0 \pm 48.2	[768.0, 1346.2]	30.3 \pm 2.8		7.0 \pm 3.9	
<i>B. muscorum</i> (L., 1758)	65	22	30	10	11.8 \pm 0.03	[7.2, 14.1]	10.1 \pm 0.05	[6.5, 14.0]	1043.8 \pm 31.4	[771.1, 1319.0]	1039.4 \pm 47.2	[844.0, 1230.1]	16.8 \pm 2.4		3.6 \pm 3.7	
<i>B. pratorum</i> (L., 1761)	57	20	28	14	10.4 \pm 0.05	[0.5, 14.0]	8.3 \pm 0.04	[5.4, 14.0]	1066.1 \pm 30.4	[792.0, 1319.0]	1119.3 \pm 37.6	[788.0, 1322.0]	25.3 \pm 2.6		2.5 \pm 3.4	
<i>B. ruderarius</i> (Müller, 1776)	34	104	14	19	7.5 \pm 0.05	[4.9, 13.1]	6.7 \pm 0.05	[3.7, 10.4]	966.7 \pm 46.7	[797.2, 1288.0]	1055.2 \pm 44.4	[768.0, 1334.0]	11.9 \pm 2.1		3.8 \pm 4.3	
<i>B. sichelii</i> Radoszkowski, 1859	59	131	12	21	6.4 \pm 0.05	[3.6, 8.0]	6.1 \pm 0.04	[3.7, 7.9]	965.0 \pm 29.0	[771.1, 1288.0]	997.1 \pm 55.6	[768.0, 1437.0]	3.7 \pm 2.1		1.2 \pm 0.0	
<i>B. sonoeensis</i> (Fabricius, 1793)	105	368	19	27	7.8 \pm 0.04	[3.7, 10.7]	6.4 \pm 0.05	[3.4, 8.8]	1067.1 \pm 34.4	[622.3, 1318.0]	1012.6 \pm 33.2	[730.0, 1322.0]	18.0 \pm 2.3		3.2 \pm 2.3	
<i>B. terrestris</i> (L., 1758)	192	278	35	29	11.1 \pm 0.05	[0.3, 14.1]	9.0 \pm 0.05	[3.7, 14.0]	1051.0 \pm 26.7	[771.1, 1319.0]	1026.8 \pm 31.7	[768.0, 1334.0]	23.3 \pm 2.5		4.6 \pm 2.1	
<i>B. wuflfenii</i> Radoszkowski, 1859	56	41	18	10	8.1 \pm 0.05	[0.3, 14.1]	6.2 \pm 0.04	[3.7, 7.3]	986.7 \pm 34.6	[771.1, 1221.0]	945.2 \pm 57.1	[731.0, 1231.0]	30.6 \pm 2.4		10.3 \pm 2.3	

Mean annual temperature ($^{\circ}$ C) and precipitation (mm³) of inhabited localities for each study period as well as proportional change in local temperature conditions (CTC) and precipitation (CPC) are also shown. Minimum and maximum values are shown in brackets

Climate niche breadth on species responses

No relationship between climatic niche breadth (i.e., thermal niche breadth or precipitation niche breadth) and any of the observed elevational shifts (i.e., mean elevation or lower and upper elevation boundary) was found ($r^2 < 0.1$ and $P > 0.05$ in all pairwise combinations; Fig. 1). Climate niche breadth, however, was strongly correlated with changes in local climate space. Specifically, thermal niche breadth was significantly related to CTC (quadratic polynomial regression: $r^2 > 0.75$; $P < 0.001$) such that the greater the change in temperature conditions between the two study periods the broader the thermal niche breadth (Fig. 2). This was primarily accounted for by the strong relationship between CTC and changes in the lower elevational boundary of distribution of bumblebee species between their historical and recent distribution, rather than with other elevational changes (Fig. 3). On the other hand, precipitation niche breadth significantly related to CPC (polynomial regression: $r^2 > 0.50$; $P < 0.05$). Thus, species showing extreme values of rainfall tolerance were those showing higher variations between both sampling periods in the precipitation patterns of inhabited localities. Furthermore, a significant relationship between CTC and CPC was also found (linear regression: $r^2 = 0.50$; $F_{1,11} = 10.08$; $P = 0.009$).

Discussion

The importance of ecological traits in determining the impact of climate change on species distributions has mainly been analyzed using the extent of range shifts as response variable. Our work, however, demonstrates that climate niche breadth (especially thermal niche breadth) can explain the response of bumblebee species to regional climate change in mountain areas of the Northern Iberian Peninsula, but only when this response is quantified in terms of variations in local climate space. Our work thus suggests that the exclusive use of range shifts may lessen the predictive power of such species traits in determining the impact of climate change on species distribution (Classen et al. 2015). It should be noted that we are not suggesting that using range shifts should in all cases be replaced by consideration of only the variations in climatic conditions underlying such shifts, but rather that using variations in local climatic conditions instead of range shifts themselves can be particularly informative in mountainous systems where the orography typically modifies the spatial patterns of climatic variables even at fine spatial scales (Rangwala and Miller 2012).

Despite climate being widely recognized as critical in determining the distribution patterns of bumblebees at fine spatial scales (e.g. Iserbyt and Rasmont 2012; Rasmont and Iserbyt 2012; Herrera et al. 2014) as well as broad (Williams et al. 2007, 2009; Kerr et al. 2015; this study), the role

of climatic niche breadth in forecasting variations in their species-specific responses to climate change has been surprisingly neglected (e.g. Deutsch et al. 2008; Tingley et al. 2009; Sinervo et al. 2010). To a large extent, this might be related to the lack of broad-scale distribution maps which are necessary to take into account the complete range of climatic conditions at which a species occurs. However, with the burgeoning availability of fine-grained, broad scale datasets

such as those used in this study (Rasmont et al. 2015), determining climatic niche breadth for individual species has become feasible, not only for bumblebees, but for an increasing number of species belonging to very distinct taxonomic groups (e.g. Kamilar and Muldoon 2010). Indeed, accurate information regarding species distribution patterns coupled with high-resolution climatic data sets is widely considered as being one of the most promising ecological approaches to

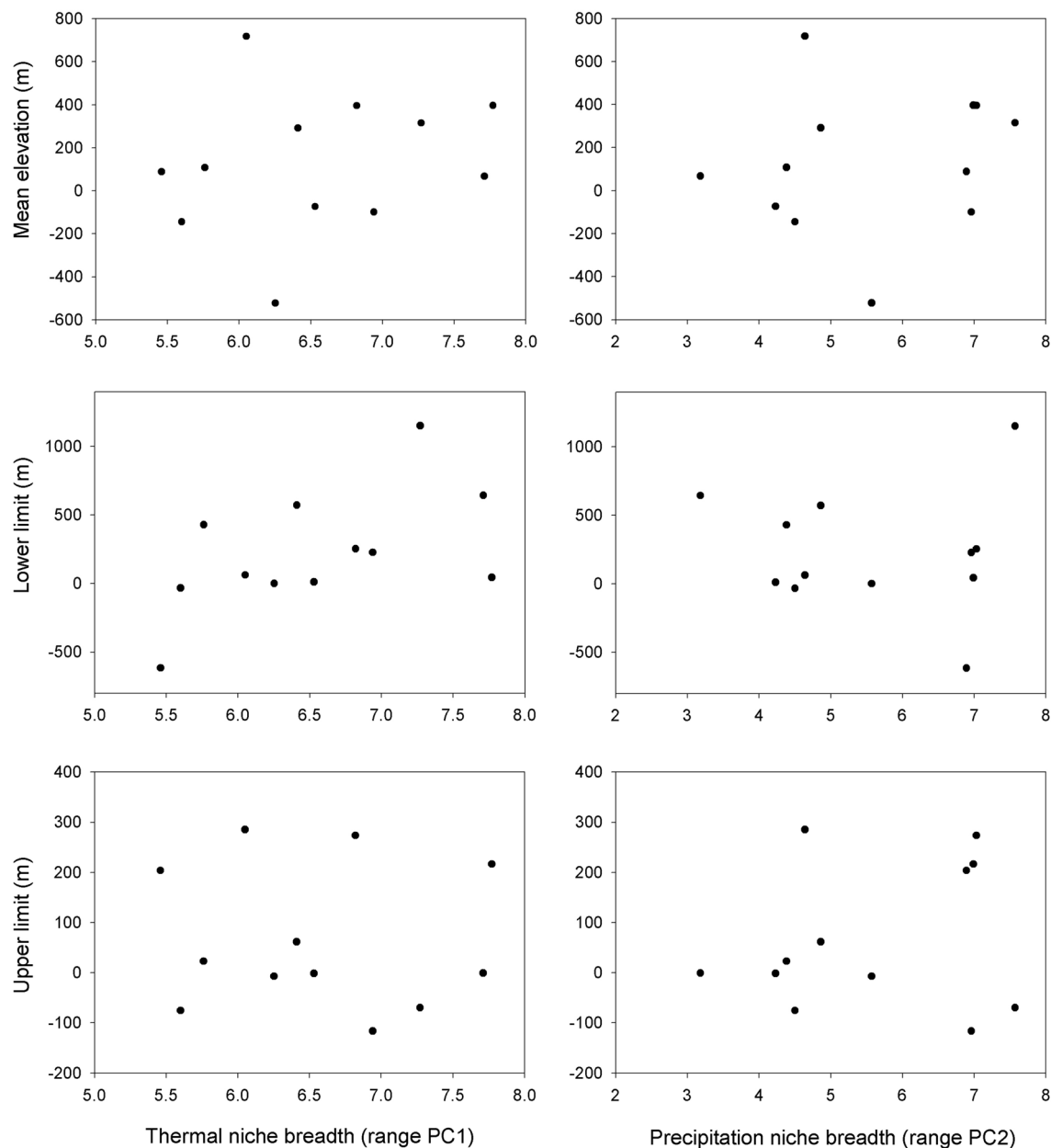


Fig. 1 Relationships between thermal niche breadth (TNB; left panels) and precipitation niche breadth (PNB; right panels) and changes in mean elevation (ME; upper panels), lower limit (LL; middle panels) and upper limit (UL; lower panels) between the historical (1988–1989) and recent (2007–2009) distribution of bumblebees in the Cantabrian Range. PC1 and PC2 on the y axes correspond to,

respectively, Principal Components 1 and 2 used to estimate thermal and precipitation niche breadth. Statistics (using quadratic regressions): TNB-ME: $r^2=0.04$, $F_{1,11}=0.45$, $P=0.51$; TNB-LL: $r^2=0.29$, $F_{1,11}=4.19$, $P=0.07$; TNB-UL: $r^2=0.00$, $F_{1,11}=0.03$, $P=0.84$ and PNB-ME: $r^2=0.05$, $F_{1,11}=0.26$, $P=0.77$; PNB-LL: $r^2=0.26$, $F_{1,11}=1.65$, $P=0.24$; PNB-UL: $r^2=0.06$, $F_{1,11}=0.32$; $P=0.73$

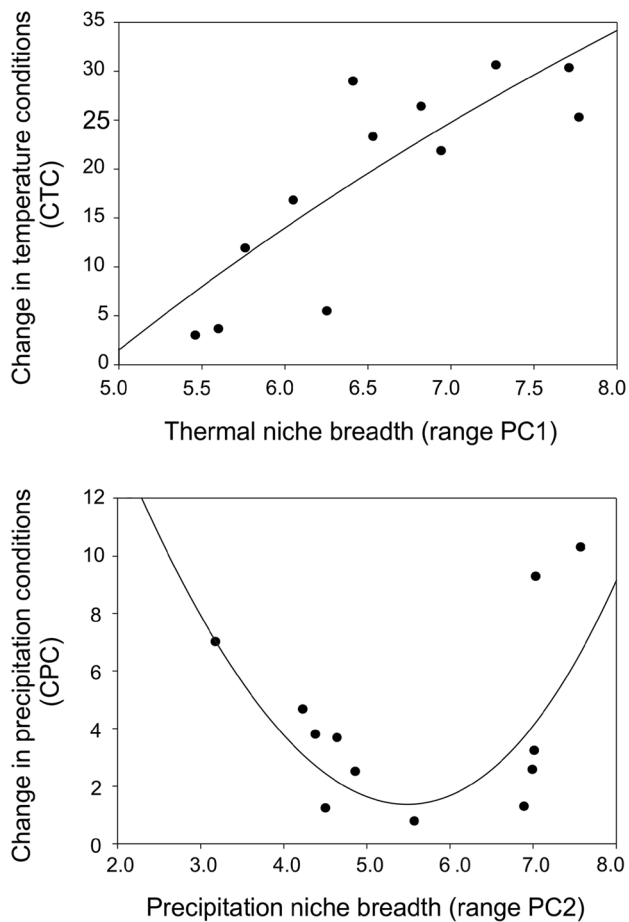


Fig. 2 Relationships between thermal niche breadth (TNB) of bumblebees and the proportional change in temperature conditions of inhabited localities (CTC) between their historical (1988–1989) and recent (2007–2009) distribution (upper panel), and between precipitation niche breadth (PNB) and the proportional change in precipitation conditions of inhabited localities (CPC). PC1 and PC2 in y axes correspond, respectively, to Principal Components 1 and 2 used to estimate thermal and precipitation niche breadth. Statistics (using quadratic regressions): TNB-CTC: $r^2=0.76$, $F_{1,11}=14.27$, $P=0.001$ and PNB-CPC: $r^2=0.53$, $F_{1,11}=5.10$, $P=0.03$

describing, analyzing and predicting the impact of climate change on the spatial patterns of a species' distribution.

Specifically, we found that the wider the thermal niche breadth of bumblebees, the stronger the change in the temperature conditions (CTC) of their species-specific inhabited localities between study periods. This response pattern is to be expected as thermal specialists (i.e., those species showing narrower thermal niches) necessarily need to track their preferred thermal conditions in order to remain within their climate envelopes (Bellard et al. 2012). In contrast, thermal generalists are assumed to be resilient to changing climatic conditions, enabling them to be present in a wider range of thermal conditions in a climatic change scenario. These same response patterns for specialist and generalist

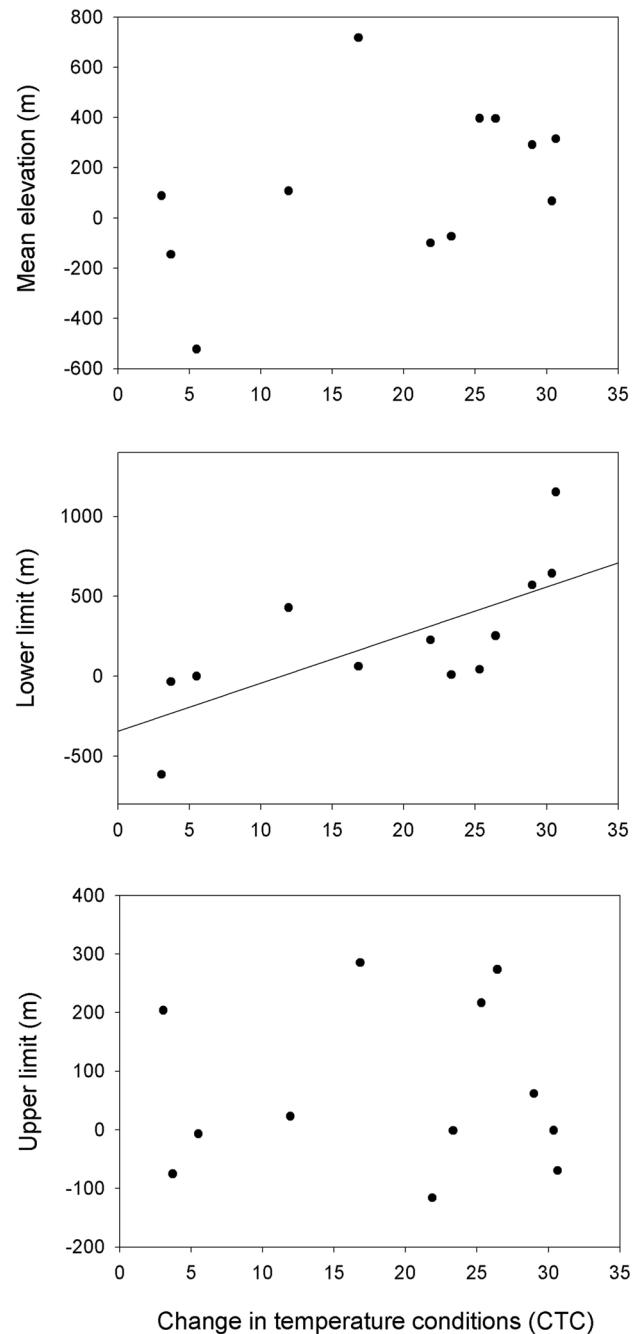


Fig. 3 Relationships between change in temperature conditions of inhabited localities (CTC) and changes in mean elevation (ME; upper panel), lower limit (LL; middle panel) and upper limit (UL; lower panel) between study periods. Statistics (using quadratic regressions): CTC-ME: $r^2=0.22$, $F_{1,11}=2.9$, $P=0.10$; CTC-LL: $r^2=0.51$, $F_{1,11}=10.64$, $P=0.008$; CTC-UL: $r^2=0.01$, $F_{1,11}=0.00$, $P=0.90$. Only statistically significant relationships are shown

species have indeed been previously shown for butterfly species in other nearby Iberian mountain areas (Stefanescu et al. 2011). In close agreement with the conclusions of Ploquin et al. (2013), we found that variations in a species' thermal

climate space were mainly driven by marked upwards shifts in its lower elevational boundaries, particularly in those species at the southern limit of their distribution in the Cantabrian Range, such as *B. mesomelas* and *B. wurflenii* (Rasmont et al. 2015). Our data thus underlines the particular sensitivity to climate change of bumblebee species on the basis of their niche position and breadth (Williams et al. 2007, 2009), and reinforces the idea that global warming poses an immediate and severe threat to cool-adapted species in mountain areas in temperate mountain areas (Warren et al. 2001; Penado et al. 2016).

We also found precipitation niche breadth to play a significant role in explaining the response of a species to regional climate change. Specifically, we found a quadratic u-shaped relationship between the species' precipitation niche breadth and the rate of change in precipitation patterns of inhabited localities between sampling periods (CPC). We suggest, however, that this response pattern could be related to the strong and positive relationship between CTC and CPC since the spatial distribution of bumblebee species was principally driven by temperature and only to a lesser extent by precipitation patterns. This means that each species' need to track suitable thermal conditions in response to climate change could be so strong as to be the determining factor in CPC. Indeed, this idea is supported by the fact that the species showing higher values of CPC (left side of Fig. 2) were among those showing the highest values of CTC (e.g. *B. mesomelas* and *B. terrestris*).

Conclusions

The main conclusions of this work are twofold. On the one hand, it suggests that variations in the climatic conditions underlying range shifts (rather than range shifts themselves) are useful for making an accurate assessment of the impact of climate change on a species' distribution, as well as the role of the species-specific traits at explaining such an impact. This finding is by no means trivial as the importance of ecological traits in determining the impact of climate change on species distributions has, to date, mainly been analyzed using range shifts as response variable. In this context, and in the absence of a significant relationship between a given ecological trait and the strength and direction of range shifts, most previous studies have concluded that such species-specific ecological traits have poor predictive power.

On the other hand, our work highlights climatic niche breadth as a particularly informative ecological trait for forecasting variations in bumblebee responses to climate change. Our findings are thus in line with previous works suggesting that differences in climatic tolerance might be key to determining the ability of different bumblebee species to cope with climate change. What is more, the current

study expands on previous works by showing not only how sensitive bumblebees are to different climatic factors, but also how this information can be used to understand the mechanisms underlying climate-driven shifts.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval The authors declare that they have complied with ethical standards.

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