

Climate change impacts on bumblebees converge across continents

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For many species, geographical ranges are expanding toward the poles in response to climate change, while remaining stable along range edges nearest the equator. Using long-term observations across Europe and North America over 110 years, we tested for climate change–related range shifts in bumblebee species across the full extents of their latitudinal and thermal limits and movements along elevation gradients. We found cross-continently consistent trends in failures to track warming through time at species' northern range limits, range losses from southern range limits, and shifts to higher elevations among southern species. These effects are independent of changing land uses or pesticide applications and underscore the need to test for climate impacts at both leading and trailing latitudinal and thermal limits for species.

Biological effects of climate change threaten many species (1), necessitating advances in techniques to assess their vulnerabilities (2). In addition to shifts in the timing of species' life cycles, warming has caused

range expansion toward the poles and higher elevations (3–6). Climate impacts could cause losses from parts of species' trailing range margins (7), but those losses are infrequently observed (4). Such responses depend on species' traits, such as

heat or cold tolerance, that reflect shared evolutionary history and climatic origins (e.g., tropical or temperate) of taxa (8, 9). Climate change can interact with other threats, like land-use intensification, to alter species' responses to emerging conditions (10). Such global changes can alter or erode ecological services provided by the affected species (11). Few species assemblages contribute more to these services than bumblebees (*Bombus*), many of which are declining (12, 13). No study has yet evaluated climate change impacts across the latitudinal and thermal limits of such a large species assemblage spanning two continents.

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We assembled a database of ~423,000 georeferenced observations for 67 European and North American bumblebee species (fig. S1 and tables S1 and S2). Species observations were gathered from the Global Biodiversity Information Facility (171,479 North American and 192,039 European records) (14), *Bumblebees of North America* (15) (153,023 records), and the Status and Trends of European Pollinators Collaborative Project (237,586 records). We measured differences in species' northern and southern range limits, the warmest or coolest temperatures occupied, and their mean elevations in three periods (1975 to 1986, 1987 to 1998, and 1999 to 2010) (figs. S2 to S4) relative to a baseline period (1901 to 1974) (16). We investigated whether land use affected these results. Finally, we used high-resolution pesticide application data available in the United States after 1991 to investigate whether total pesticide or neonicotinoid applications accounted for changes in bumblebee species' range or thermal limits (table S3). Tests used phylogenetic generalized least-squares models (PGLS), using a phylogenetic tree constructed from nuclear and mitochondrial markers (17), and accounted for differences in sampling intensity between time periods (Table 1).

If species expanded their northern range limits to track recent warming, their ranges should show positive (northward) latitudinal shifts, but cool thermal limits should be stable through time. In contrast to expectations and responses known from other taxa (4), there has been no change in

the northern limits of bumblebee distributions in North America or Europe (Fig. 1A). Despite substantial warming (~ +2.5°C), bumblebee species have also failed to track warming along their cool thermal limits on both continents (Fig. 1B and Table 1). These failures to track climate change occur in parallel in regions that differ in their intensities of human land use (e.g., Canada and northern Europe), which had no direct or interaction-based effect in any statistical model (Table 1).

If bumblebee species climate responses resemble most terrestrial ectotherm taxa (4), their southern range limits should have remained stable with increasing temperatures along species' warm thermal limits. However, bumblebee species' range losses from their historical southern limits have been pronounced in both Europe and North America, with losses growing to ~300 km in southern areas on both continents (Fig. 1C). Throughout North America, species also experienced range losses from the warmest areas they historically occupied, while European species' range losses extend across the warmest regions (where mean temperatures exceed ~15°C) (Fig. 1D). These responses showed a significant phylogenetic signal, with closely related bumblebee species showing increasingly similar range shifts from southern and warm thermal limits (Table 1). As with failures to expand northward or into cooler areas, land-use changes do not relate to range losses from bumblebee species' southern or warm thermal limits.

Table 1. PGLS models showing climate change and interactive effects on North American and European bumblebees. Changes in latitude (km north of equator), thermal (°C), or elevation (m) variables observed by 1999 to 2010 for each species (relative to the 1901 to 1974 baseline period) are regressed against predictors listed on the left. Models reported in each column were selected using AIC, which can include statistically nonsignificant

variables. Sample sizes in each time period (median *n* per species = 536) were tested but excluded using AIC. Variable coefficients are given, with SEs in parentheses. A dash indicates that this variable was not part of the AIC-selected model. Ordinary least squares (OLS) regression summary statistics (adjusted *R*²) are provided to enable comparison with PGLS results; OLS coefficients are similar.

Predictors	Latitude		Thermal		Elevation
	Northern	Southern	Cool	Warm	
Intercept	−268.3 (614.7)	657.8 (150.4)	2.436 (0.5)	657.8 (150.4)	1075 (340.7)
Latitudinal or thermal limit (1901–1974)	0.04 (0.08)	−0.12 (0.04)	−0.009 (0.05)	0.19 (0.1)	–
Mean latitude (1999–2010)	–	–	–	–	−0.21 (0.07)
Covariates					
Continent	1158 (1039)	–	–	10.59 (2.24)	384.5 (504.1)
Δ Crop land (1999–2010)	−4.25 (7.68)	–	–	–	–
Δ Pasture (1999–2010)	−43.1 (60.71)	–	–	–	–
Interactions with continent					
Thermal or latitudinal limits (1901–1974)	−0.12 (0.14)	–	–	−0.47 (0.12)	–
Δ Crop land (1999–2010)	−9.38 (41.73)	–	–	–	–
Δ Pasture (1999–2010)	74.95 (74.35)	–	–	–	–
Mean latitude (1999–2010)	–	–	–	–	−0.03 (0.1)
Models of trait evolution					
AIC (Independent)	915.5	863.2	291.3	274.5	863.6
AIC (Brownian motion)	962.4	897.4	339.3	293.9	916.4
AIC (Ornstein-Uhlenbeck)	917.5	861.8	293.3	264.9	865.4
AIC (Pagel)	915.3	862.2	293.1	273	860.8
Pagel's λ	−0.15	0.49	0.04	0.64	−0.1
Equivalent OLS regression summary statistics					
Adjusted <i>R</i> ²	0.15	0.14	−0.01	0.30	0.28

Species with southern geographical ranges retreated to higher elevations across Europe and North America (Table 1 and Fig. 2), consistent with observations of range losses from their southern range limits. Elevation shifts are larger in Europe [i.e., Akaike's information criterion (AIC)-based model selection includes a small continental effect; intercept for Europe, 1459 m (366 SE); North America, 1074 m (340 SE) (Fig. 2)]. Europe's mountainous areas are oriented predominantly east-west, potentially inducing more pronounced upslope shifts. Mean elevations of observations for southern species have risen ~300 m since 1974. Observed shifts along elevation gradients vary considerably among species (3) but follow a coherent geographical pattern. Mean elevations among northern species in Europe and North America shifted lower. Over recent decades, alpine tree lines have advanced upslope in response to human activities, geomorphological factors, and warming (18), potentially overtaking nesting, overwintering, and forage habitats in historically open areas. High-elevation hab-

itat changes could contribute to generalist pollinator declines in mountainous areas (19), particularly among bumblebee species whose ranges have not expanded from their cold thermal limits.

In addition to land-use changes, we investigated whether pesticide use affected shifts in thermal and latitudinal range limits among bumblebees. Spatially detailed, annual pesticide measurements, including neonicotinoid insecticides, were available for the United States after 1991. Neither total pesticide nor neonicotinoid applications there relate to observed shifts in bumblebee species' historical ranges or thermal limits (table S1). Neonicotinoid effects known from individual and colony levels certainly contribute to pollinator declines and could degrade local pollination services. Neonicotinoid effects on bumblebees have been demonstrated experimentally using field-realistic treatments (20). These locally important effects do not "scale up" to explain cross-continental shifts along bumblebee species' thermal or latitudinal limits. The timing of climate change-related shifts

among bumblebee species underscores this observation: Range losses from species' southern limits and failures to track warming conditions began before widespread use of neonicotinoid pesticides (figs. S2 and S3).

Regional analyses suggest that latitudinal range shifts toward the poles are accelerating in most species groups (3), while their trailing range margins remain relatively stable (4). Assemblages showing pronounced northward range expansions and limited southern-range losses, like butterflies, originated and diversified in tropical climates and retain ancestral tolerances to warmer conditions (21). Those species' warming-related extinction risks in temperate environments are low (8) but increase toward warmer areas where climatic conditions resemble those under which they evolved (7, 22). Drawing on comprehensive range data, bumblebee species show opposite range responses across continents relative to most terrestrial assemblages (4): rapid losses from the south and lagging range expansions in the north. Mechanisms leading to observed lags in range responses at species' northern or cool thermal limits require urgent evaluation. Colonization of previously unoccupied areas and maintenance of new populations strongly affect whether species track shifting climatic conditions (23), capacities that appear insufficient among bumblebees. Observed losses from species' southern or warm boundaries in Europe and North America, and associated phylogenetic signals, are consistent with ancestral limitations of bumblebees' warm thermal tolerances and evolutionary origins in cool Palearctic conditions (24). Warming-related extreme events cause bumblebee population losses (25) by imposing demands for energetically costly behavioral thermoregulation, even at high latitudes and elevations (26). Such effects are not yet observed for European bumblebees in cooler regions, where species generally experience temperatures exceeding those observed historically within their ranges (Fig. 1D) (10). Range losses there will likely accelerate without mitigation from climatic refugia (27).

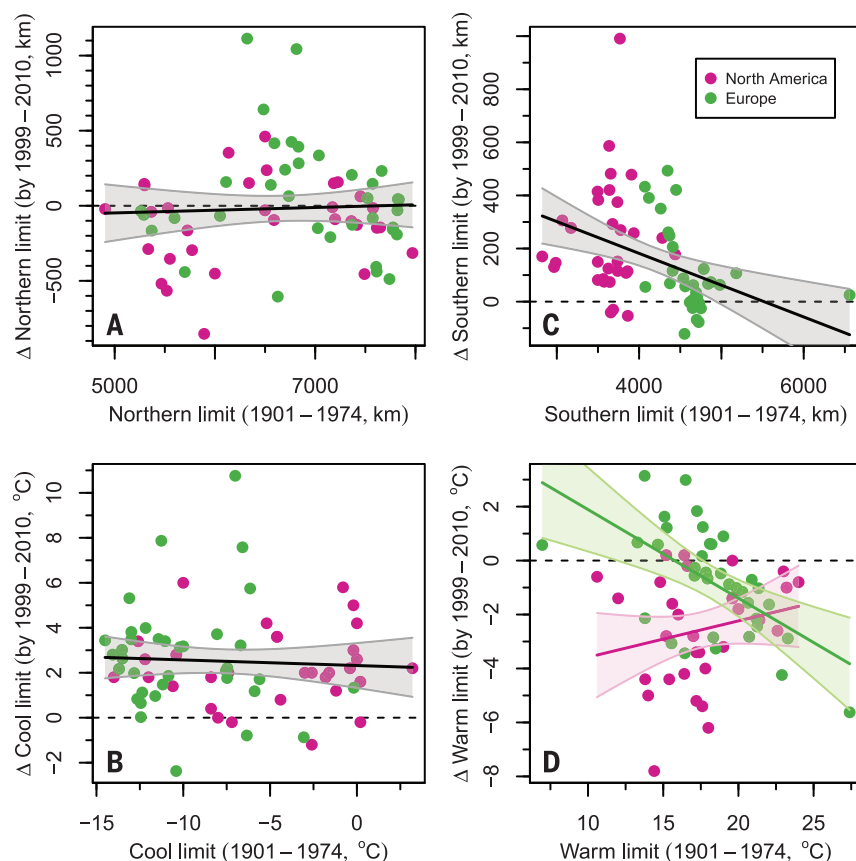


Fig. 1. Climate change responses of 67 bumblebee species across full latitudinal and thermal limits in Europe and North America. For each measurement, the y axis shows differences in the latitude of species' range limits [(A) Northern, (C) Southern] or thermal limits [(B) Cool; (D) Warm], respectively, by 1999 to 2010 relative to baseline conditions for 1901 to 1974. Each point represents the mean of five observations at the latitudinal or thermal limits for one bumblebee species (green circles for Europe and pink for North America). Null expectations (dashed lines) are for no temporal change in latitudinal or thermal limits. Range expansions from species' historical northern limits (A) are indicated by positive values, and positive values indicate range losses from species' southern limits (B). Temperature changes show whether bumblebee species are tracking differences along their thermal limits through time (no change), falling behind (positive values), or retreating more rapidly than mean conditions detect (negative values). Confidence bands (95%) for regression models (i.e., with and without continent + interaction against latitudinal or thermal change terms) with the lowest AIC are shown.

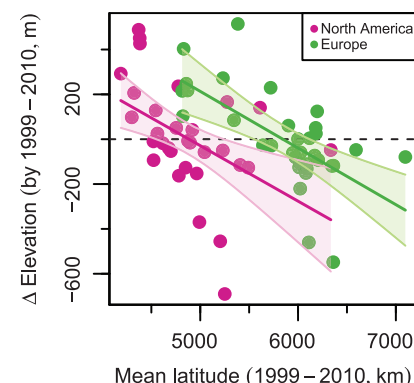


Fig. 2. Change in elevation of 67 bumblebee species by 1999 to 2010 relative to their mean latitude. Elevations are calculated using mean elevations across species observations. The slopes are similar between continents (according to regression and PGLS analyses). The confidence bands (95%) of regression slopes are shown.

Climate change appears to contribute distinctively, and consistently, to accumulating range compression among bumblebee species across continents. Experimental relocation of bumblebee colonies into new areas could mitigate these range losses. Assessments of climate change on species' ranges need to account for observations across the full extent of species' latitudinal and thermal limits and explicitly test for interactions with other global change drivers.

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SUPPLEMENTARY MATERIALS

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Materials and Methods

Supplementary Text

Supplementary Acknowledgments

Figs. S1 to S4

Tables S1 to S3

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