

POLLINATOR DECLINE

Climate change contributes to widespread declines among bumble bees across continents

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Climate change could increase species' extinction risk as temperatures and precipitation begin to exceed species' historically observed tolerances. Using long-term data for 66 bumble bee species across North America and Europe, we tested whether this mechanism altered likelihoods of bumble bee species' extinction or colonization. Increasing frequency of hotter temperatures predicts species' local extinction risk, chances of colonizing a new area, and changing species richness. Effects are independent of changing land uses. The method developed in this study permits spatially explicit predictions of climate change-related population extinction-colonization dynamics within species that explains observed patterns of geographical range loss and expansion across continents. Increasing frequencies of temperatures that exceed historically observed tolerances help explain widespread bumble bee species decline. This mechanism may also contribute to biodiversity loss more generally.

Recent climate changes have accelerated range losses among many species (1, 2). Variation in species' extinction risk or chances of colonizing a new area determine whether species' ranges expand or decline as new climatic conditions emerge. Understanding how changing climatic conditions alter species' local extinction (extirpation) or colonization probabilities has proven exceptionally challenging, particularly in the presence of other environmental changes, such as habitat loss. Furthermore, identifying which species will most likely be at risk from climate change and where those risks will be greatest is critical to the development of conservation strategies (3, 4).

Although many mechanisms could alter how species fare as climate changes, discovering processes that strongly affect species persistence remains among the foremost challenges in conservation (5). Climate change could pose risks to species in part by increasing the frequency of environmental conditions that exceed species' tolerances, causing population decline and potentially extirpation (6, 7). Conversely, climate change may render marginal areas more suitable for a species, making colonization of that locale more likely (1). Understanding and predicting spatially explicit colonization and extinction likelihood could identify which species are vulnerable to climate change and where, identify which species may benefit, and suggest interventions to mitigate conservation risks. Colonization and extinction dynamics, in combination across a regional species assemblage, determine how species richness changes. Among taxa that contribute critically to ecosystem service provision, including pollinators such as bumble bees (*Bombus*),

species richness decline could impair ecosystem services (8).

We evaluated changes in bumble bee species occupancy and regional richness across North America and Europe using a database of ~550,000 georeferenced occurrence records of 66 bumble bee species (figs. S1 and S2 and table S1) (1, 9). We estimated species' distributions in quadrats that measured 100 km by 100 km, in a baseline (1901–1974) and recent period (2000–2014) (9). Climate across Europe and North America has changed greatly between these time periods (fig. S3). Although the baseline period was substantially longer, there were 49% more records in the recent period. Non-detection bias (difficulty distinguishing among true and false absences due to imperfect detection) in opportunistic occurrence records can reduce measurement accuracy of species distributions and overall richness (10). Consequently, we used detection-corrected occupancy models to estimate probability of occurrence for each species in quadrats in each time period (9). We calculated changes in species' probabilities of occupancy and generated detection-corrected estimates of species richness change between periods (fig. S4).

We predict greater declines in bumble bee species occupancy and species richness where changing climatic conditions more frequently exceed individual species' historically observed tolerances. Conversely, we predict greater occupancy and species richness in areas where climate changes more frequently cause local weather to fall within species' historically observed tolerances. Temperature and precipitation can affect bumble bee mortality and fecundity directly [e.g., (11)] and indirectly through changes to floral resources (12). For both periods, we calculated proximity of climatic conditions within quadrats across these continents to estimated thermal and precipitation limits of all 66 species. We averaged monthly temperatures and total precipitation in local-

ities where species were observed and rescaled these measures relative to each species's historically observed climatic limits. Those limits were calculated from averages of the five highest monthly maximum and lowest monthly minimum temperatures, or five highest and lowest monthly total precipitation values, from among values for all location-year combinations where that species was observed during the baseline. Although climate limits inferred from observed distributions might not always identify actual physiological tolerances, they can suggest such limits and can prove useful in the absence of more mechanistic data (1). We calculated local changes in this new climatic position index between baseline and recent time periods and also averaged it across all species present per quadrat to calculate community-averaged climatic position index (Fig. 1 and fig. S5).

Our measurements of bumble bee species occupancy over time provide evidence of rapid and widespread declines across Europe and North America. The probability of site occupancy declined on average by 46% ($\pm 3.3\%$ SE) in North America and 17% ($\pm 4.9\%$ SE) in Europe relative to the baseline period (Fig. 2). Declines were robust to detection-correction methods (figs. S6A and S7) and consistent with reductions in detection-corrected species richness (fig. S6B) (9).

Declines among bumble bee species relate to the frequency and extent to which climatic conditions approach or exceed species' historically observed climatic limits, particularly for temperature. We modeled change in probability of site occupancy with phylogenetic generalized linear mixed models using thermal position variables (baseline, change since baseline, and the interaction between these), precipitation position variables (baseline, change since baseline, and the interaction between these), the interaction between baseline thermal and precipitation position terms, and the interaction between change in thermal position and change in precipitation position. We controlled for continent (9). The models support our predictions: Probability of occupancy decreases when temperatures rise above species' upper thermal limits (Fig. 3A, fig. S8A, and table S2), whereas warming in regions that were previously near species' cold limits is associated with increasing occupancy. Evidence for precipitation influencing site occupancy was mixed, but declines were more likely in sites that became drier (Fig. 3B, fig. S8B, and table S2). Our model's capacity to predict change in occupancy [marginal coefficient of determination (R^2) = 0.11] was comparable to the predictive ability of other macroecological models of the biological impacts of climate change (2), but our models predicted extirpation and colonization more capably [marginal R^2 = 0.53 to 0.87 (9)]. Whereas there was weak evidence for a phylogenetic signal in the response of occupancy (Pagel's λ = 0.12), modeling extirpation

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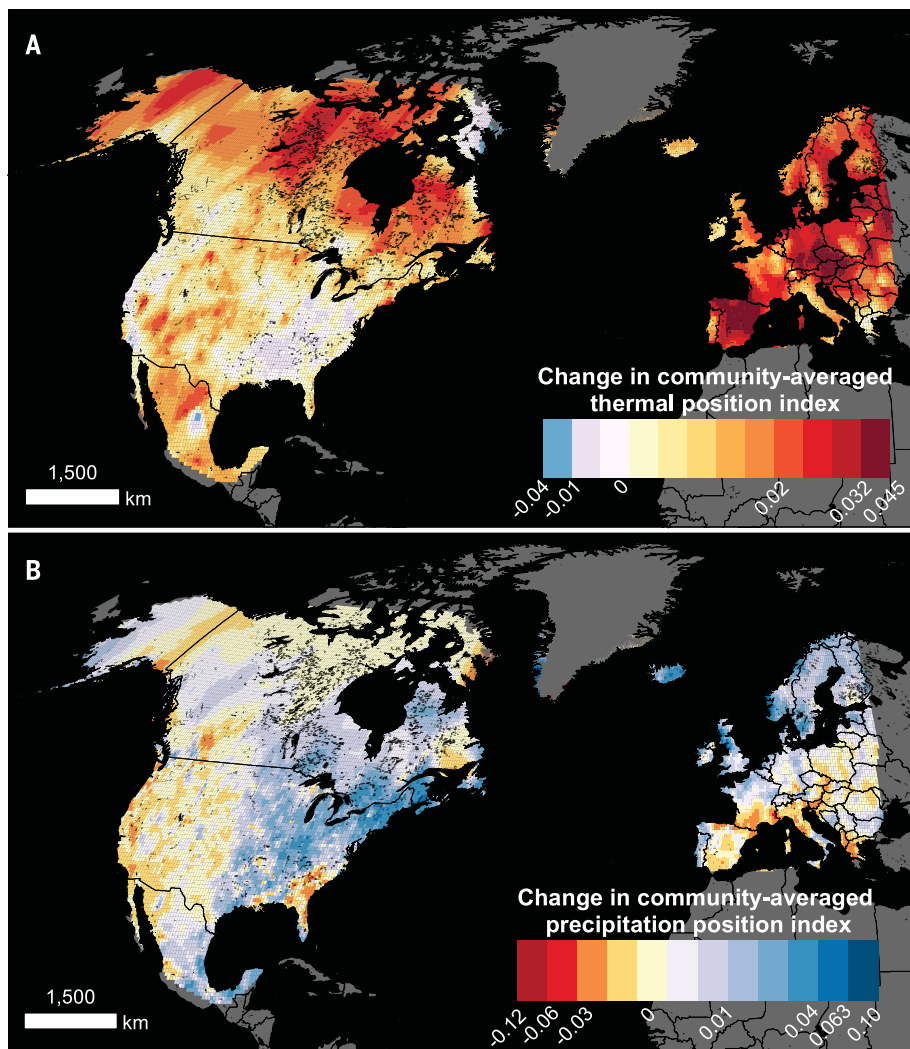


Fig. 1. Change in community-averaged measures from the baseline (1901–1974) to the recent period (2000–2015). Local changes in (A) thermal and (B) precipitation position indices are shown. Increases indicate warmer or wetter regions and that, on average, species in a given assemblage are closer to their hot or wet limits than they have been historically. Declines indicate cooling or drying regions and that, on average, species in a given assemblage are closer to their cold or wet limits than they have been historically.

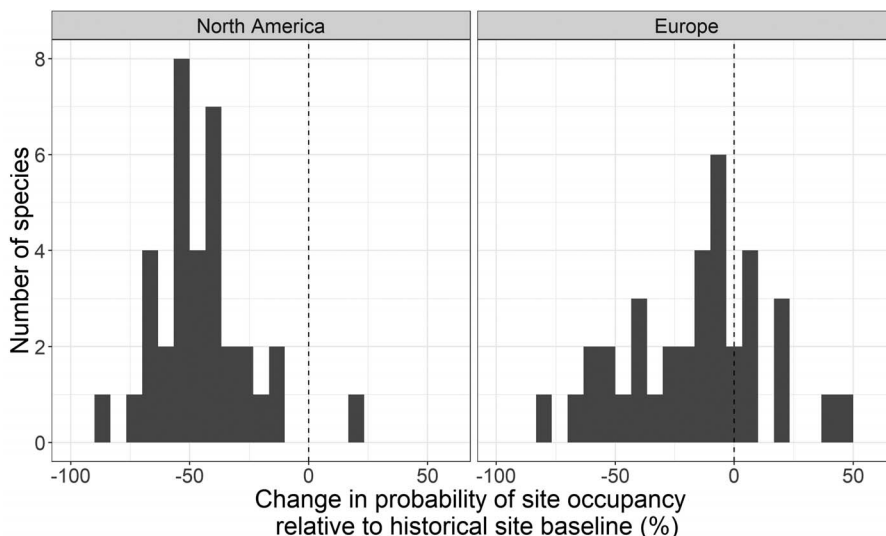


Fig. 2. Percent change in site occupancy since a baseline period (1901–1974) for 35 North American and 36 European bumble bee species.

and colonization separately yields a stronger signal (9). Results were robust to detection-correction method for measuring species' presences in quadrats, across spatial scales of analysis, and through a range of thresholds for inferring absences from occurrence data (9).

Bumble bee species richness declined in areas where increasing frequencies of climatic conditions exceed species' historically observed tolerances in both Europe and North America. An analysis of covariance that modeled the response of detection-corrected richness to community-averaged measures of climatic position revealed that, consistent with observed trends in species-specific occupancy change, richness was more likely to decline in regions experiencing warming, especially when species present were in the warmest parts of their historical ranges (table S2). These models accounted for potential spatial autocorrelation, and results were consistent regardless of method to correct for differences in species detection probabilities (9).

Fig. 3. Change in probability of occupancy in response to change in thermal and precipitation position from the baseline (1901–1974) to the recent period (2000–2014).

Thermal (A) and precipitation (B) positions range from 0 to 1, with 1 indicating that conditions at a site are at a species's hot or wet limit for the entire year and 0 meaning that conditions are at a species's cold or dry limit for the entire year during the historic period. For ease of visualizing the significant interaction between baseline thermal position and change in thermal position, the continuous baseline thermal position variable has been split at the first and third quantile to show sites that were historically close to species' hot limits (red; $n = 969$ sites), cold limits (blue; $n = 2244$ sites), and the middle of their observed climatic limits (purple; $n = 11,793$ sites). Rug plots show the distribution of observations. Confidence intervals ($\pm 95\%$) are shown around linear trendlines.

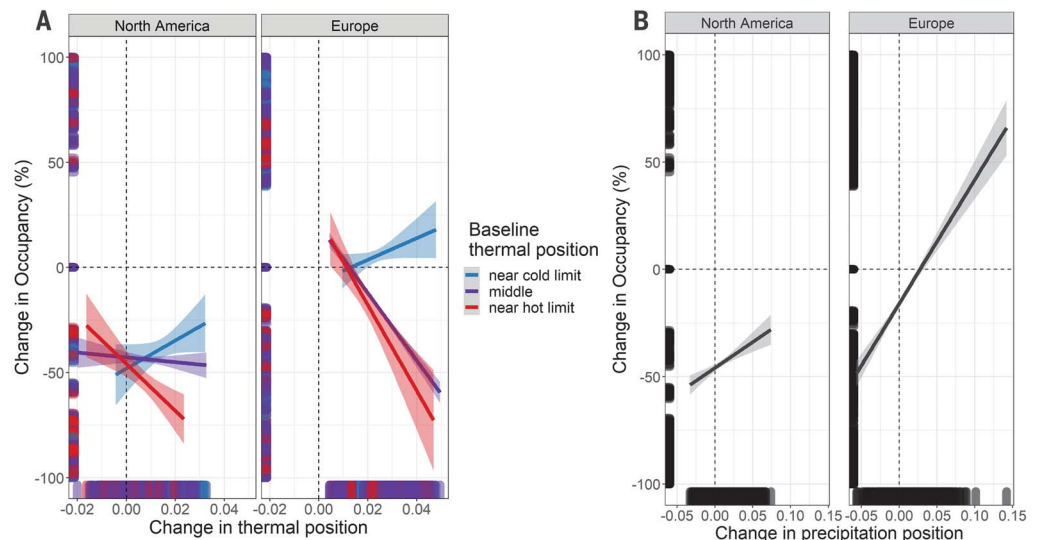
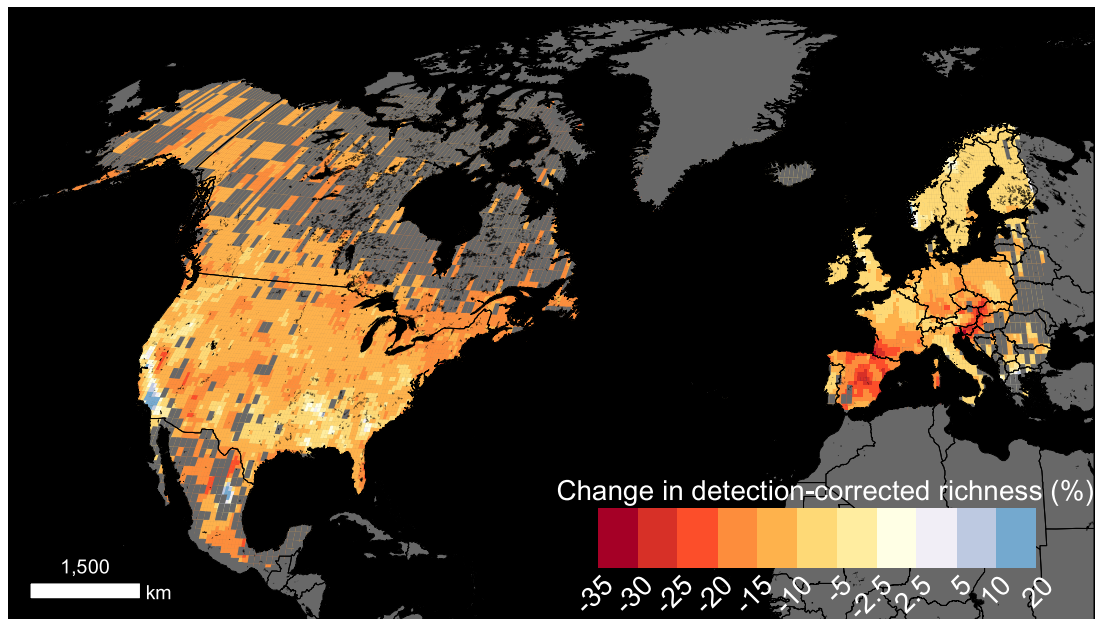


Fig. 4. Climate change–related change in bumble bee species richness from a baseline (1901–1974) to a recent period (2000–2014).

Predictions are from a model projecting percent change in detection-corrected bumble bee species richness as a function of mean community-averaged thermal and precipitation position.



Projections suggest that recent climate change has driven stronger and more widespread bumble bee declines than have been reported previously, especially in Europe (Fig. 4). European estimates of observed richness rely particularly on observations from well-sampled regions that were cooler in the baseline period and that have experienced less warming subsequently (9), which may have contributed to underestimation of recent species richness decline across that continent (figs. S6B, S9, and S10). These findings contrast with those for other taxa that predict widespread range expansions and increasing species richness toward warming environments in the north (13, 14).

Changes in climatic position index predict biologically important changes in bumble bee

presence, colonization, extirpation, and richness across two continents. Species-specific changes in climatic position predict bumble bee diversity change as well as or better than mean, maximum, or minimum temperature or precipitation measures [models using climatic position index: marginal R^2 2.6% lower to 23% higher; change in deviance information criterion = 98.7 to 241.9 (9)]. Including land-use change in the models revealed a significant negative effect but did not influence results for climatic position variables (table S4) (9). At this scale, effects of climate change on bumble bees appear distinct from effects of land use. Other anthropogenic changes, such as agricultural intensification, pesticide use, and pathogens, can also affect occupancy and extirpation risk of bumble bees

(15–17). Interactions between these factors are expected to accelerate biodiversity loss for bumble bees and other taxa over broad areas (18, 19). Understanding how interactions between climate and land-use changes alter extinction risk is vital to conservation of pollinator species.

Climate is expected to warm rapidly in the future (20). Using a spatially explicit method of measuring climatic position and its change over time, we show that risks of bumble bee extirpation rise in areas where local temperatures more frequently exceed species' historical tolerances, whereas colonization probabilities in other areas rise as climate changes cause conditions to more frequently fall within species' thermal limits. Nevertheless, overall rates of climate change–related extirpation among species

greatly exceed those of colonization, contributing to pronounced bumble bee species declines across both Europe and North America with unknown consequences for the provision of ecosystem services. Mitigating climate change-driven extinction risk among bumble bees requires efforts to manage habitats to reduce exposure to the growing frequency of temperatures that are extreme relative to species' historical tolerances.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Supplementary Text
Supplementary Acknowledgments
Figs. S1 to S13
Tables S1 to S8
References (22–59)

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