

Title: Increasing climatic extremes contribute to declines of European and North American
bumblebees

Authors: Peter Soroye^{1*}, Tim Newbold², Jeremy Kerr¹

Affiliations:

¹ Department of Biology, University of Ottawa, Ottawa, ON, Canada, K1N6N5.

² Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and
Environment, University College London, Gower Street, London WC1E 6BT, UK.

*Correspondence to: peter.soroye@gmail.com

Abstract (125 words): Climate change could accelerate extinction risk, depending on whether
temperature and precipitation exceed species' historically-observed tolerances. Using long-term
data for 66 bumblebee species across North America and Europe, we tested whether climate
change alters likelihoods of species' extinction or colonization. Increasing frequency of hotter
temperatures predicts bumblebee species' local extinction risk, variation in colonization, and
changing species richness. Effects are independent of changing land uses. The method developed
here permits spatially explicit predictions of climate change-related population extinction-
colonization dynamics within species that reveals where species will decline or benefit due to
climate change. Increasing frequencies of temperatures that exceed historically-observed
tolerances helps explain widespread bumblebee species decline. This mechanism may contribute
to biodiversity loss more generally.

One Sentence Summary (125 characters): Warming in North America and Europe predicts
decline in bumblebee species and assemblages.

Main Text:

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).

While 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 which 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, which species may benefit from it, and suggest interventions to mitigate conservation risks. Colonization and extinction dynamics, in combination across a species assemblage, determine how species richness will change within a region. Among taxa that contribute critically to ecosystem service provision, like pollinators such as bumblebees, species richness decline could impair ecosystem services (8).

We evaluated changes in bumblebee species occupancy and regional richness across North America and Europe using a database of ~550,000 georeferenced occurrence records of 66

bumblebee species (Figure S1 and S2, Table S1; (1, 9)). We estimated species' distributions in 100 km by 100 km quadrats across the study area in a baseline (1901-1974) and recent period (2000-2014) (9). Climate across Europe and North America has changed significantly between these time periods (Figure 1). While the baseline period was substantially longer, there were 49% more records in the recent period. Non-detection bias (i.e. an inability to distinguish between true absences and false-absences because of imperfect detection) in opportunistic occurrence records can reduce the accuracy of measurements of species richness and observed distribution (10). Consequently, we used occupancy models to estimate probability of occurrence for each species in quadrats within each time period (9). We calculated the change in species' probabilities of occupancy across the study area and generated detection-corrected estimates of species richness change between periods (Figure S3).

We predict greater declines in bumblebee 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 bumblebee mortality and fecundity directly (e.g. (11)) and indirectly through changes to floral resources (12). For both periods, we calculate the 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 localities where species were observed, and rescaled these measures relative to each species' 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 (Figures S4 and S5).

Our measurements of bumblebee species occupancy over time indicate that these species have declined rapidly and broadly across Europe and North America. 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 (Figure 2). Declines were robust to detection-correction methods used (Figures S6A and S7) and consistent with reductions in detection-corrected species richness (Figure S6B) (9).

Widespread declines in bumblebee species' probability of occupancy across both North America and Europe relate to the increasing magnitude and frequency of climatic conditions that approach or exceed species' observed climatic limits, particularly for temperature. We modelled 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 (Figures 3A, S8A; Table S2), while 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 (Figures 3B, S8B; Table S2). Our model's capacity to predict change in occupancy (marginal $R^2 = 0.11$) was comparable to the predictive ability of other macroecological models of the biological impacts of climate change (2), but models predicted extirpation and colonization more capably (marginal $R^2 = 0.53-0.87$ (9)). While there was weak evidence for a phylogenetic signal in the response of occupancy (Pagel's $\lambda = 0.12$), modelling extirpation and colonization separately yields a stronger signal (9). Results were robust to detection correction method for measuring species' presences within quadrats, across spatial scales of analysis, and through a range of thresholds for inferring absences from occurrence data (9).

Bumblebee species richness declined in areas where there are increasing frequencies of climatic conditions that exceed species' historically-observed tolerances in both Europe and North America. An analysis of covariance modelling 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 in those quadrats 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).

Projections suggest that recent climate change has driven stronger and more widespread bumblebee declines than have previously been reported, especially in Europe (Figure 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 (Figures S6B, S9, S10). These findings contrast with those for other taxa that predict widespread range expansions toward warming environments in the north and resulting higher species richness in such areas (13, 14).

Changes in climatic position index predict biologically significant changes in bumblebee presence, colonization, extirpation, and richness across two continents. Species-specific changes in climatic position predict bumblebee diversity change as well as or better than using 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 = 98.7-241.9; (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 of analyses, effects of climate change on bumblebees 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 bumblebees (15–17). It is expected that interactions between these factors will accelerate biodiversity loss for this taxon, and potentially others, over large 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 bumblebee extirpation rise in areas where local temperatures more frequently exceed species' historical tolerances, while colonization of other areas is more likely in regions that more frequently fall within species thermal limits. Nevertheless, the rate of climate change-related extirpation greatly exceeds colonization rates, contributing to pronounced bumblebee species declines across both

Europe and North America with unknown consequences for the provision of ecosystem services. Mitigating climate change-driven extinction risk among bumblebees requires efforts to manage habitats to reduce exposure to growing frequency of temperatures that are extreme relative to species' historical tolerances.

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306 through figshare (DOI: 10.6084/m9.figshare.9956471).

307

308 **Supplementary Materials**

309 Materials and Methods

310 Supplementary Text

311 Supplementary Acknowledgements

312 Figures S1-S13

313 Tables S1-S8

314 References (21 - 58)

315

Figure Legends

Figure 1. Change in mean annual mean temperature (A) and mean total precipitation (B) from the baseline (1901-1974) to the recent period (2000-2015) across North America and Europe.

Figure 2. Percent change in site occupancy since a baseline period (1901-1974) for 35 North American and 36 European bumblebee species.

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

Thermal and precipitation position ranges from 0 to 1, with 1 indicating conditions at a site are at a species' hot or wet limit for the entire year, and zero meaning conditions are at a species' 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 1st and 3rd quantile to show sites that were historically close to species' hot limits (red; n=969), cold limits (blue; n=2,244), and middle of their observed climatic limits (purple; n=11,793). Rug plot shows the distribution of observations. Confidence intervals ($\pm 95\%$) are shown around linear trendlines.

Figure 4. Climate change-related change in bumblebee species richness from a baseline (1901-1974) to a recent period (2000-2014). Predictions from a model predicting percent

337 change in detection-corrected bumblebee species richness as a function of mean community-
338 averaged thermal and precipitation position.

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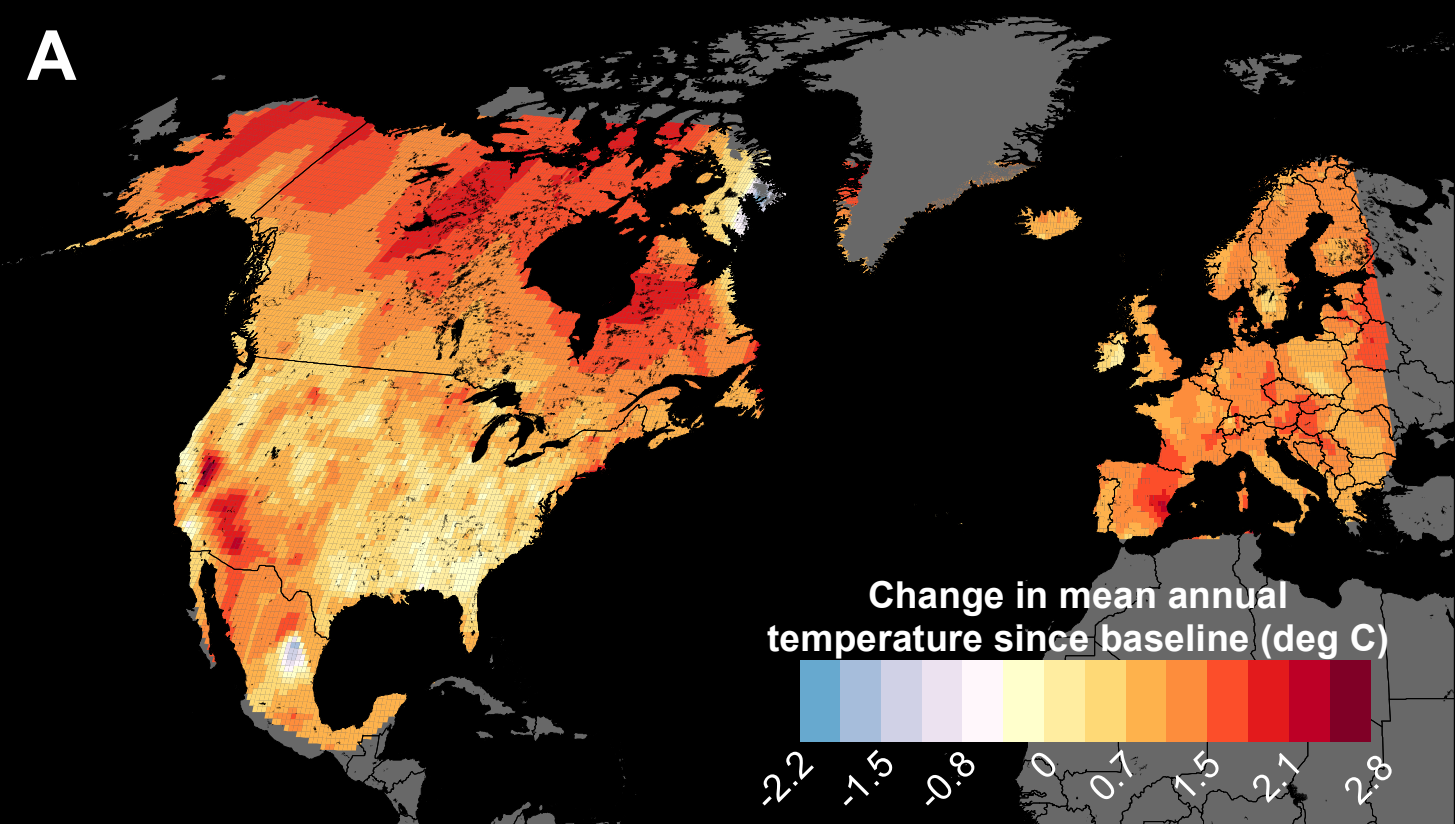
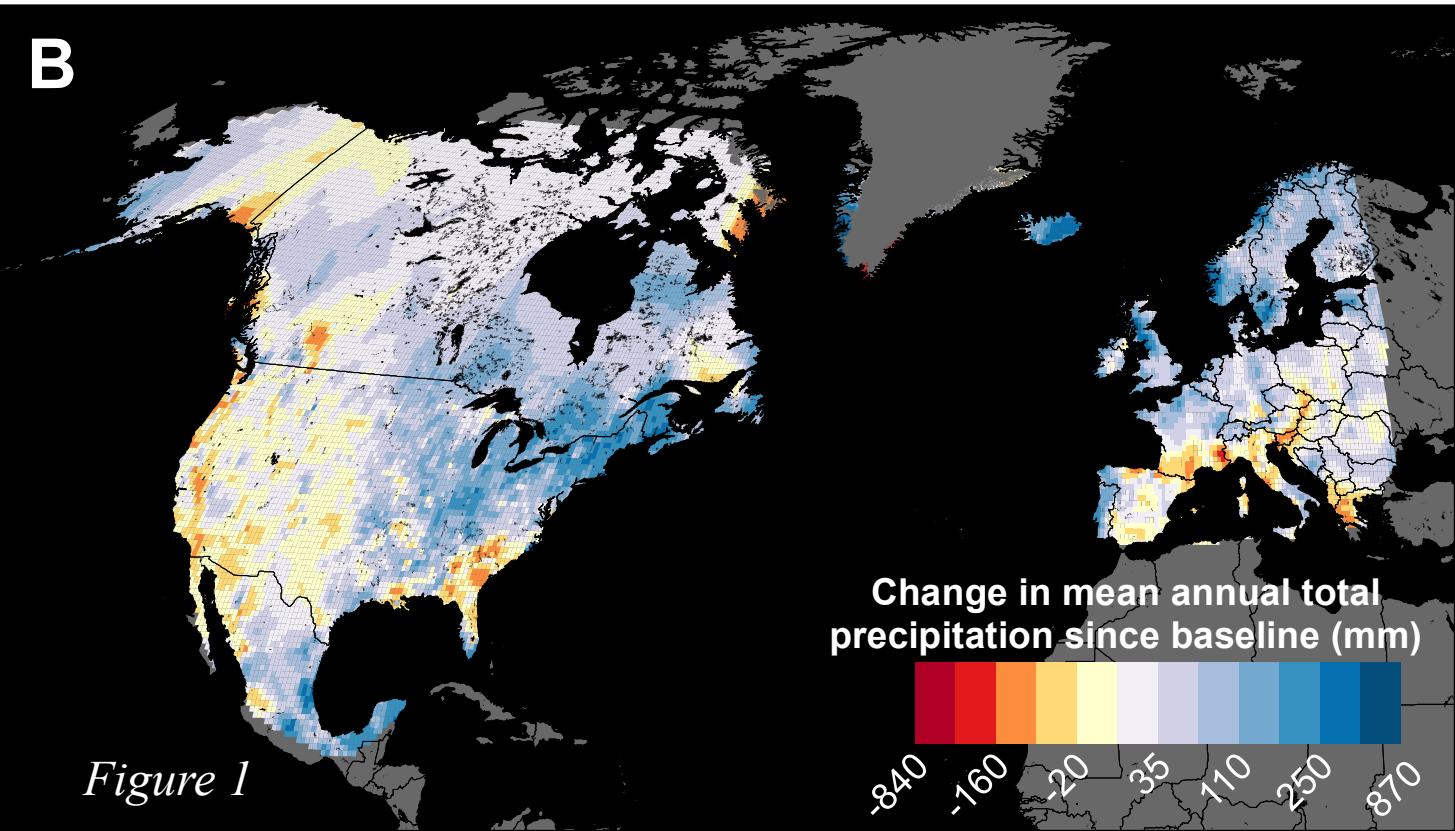
A**B**

Figure 1

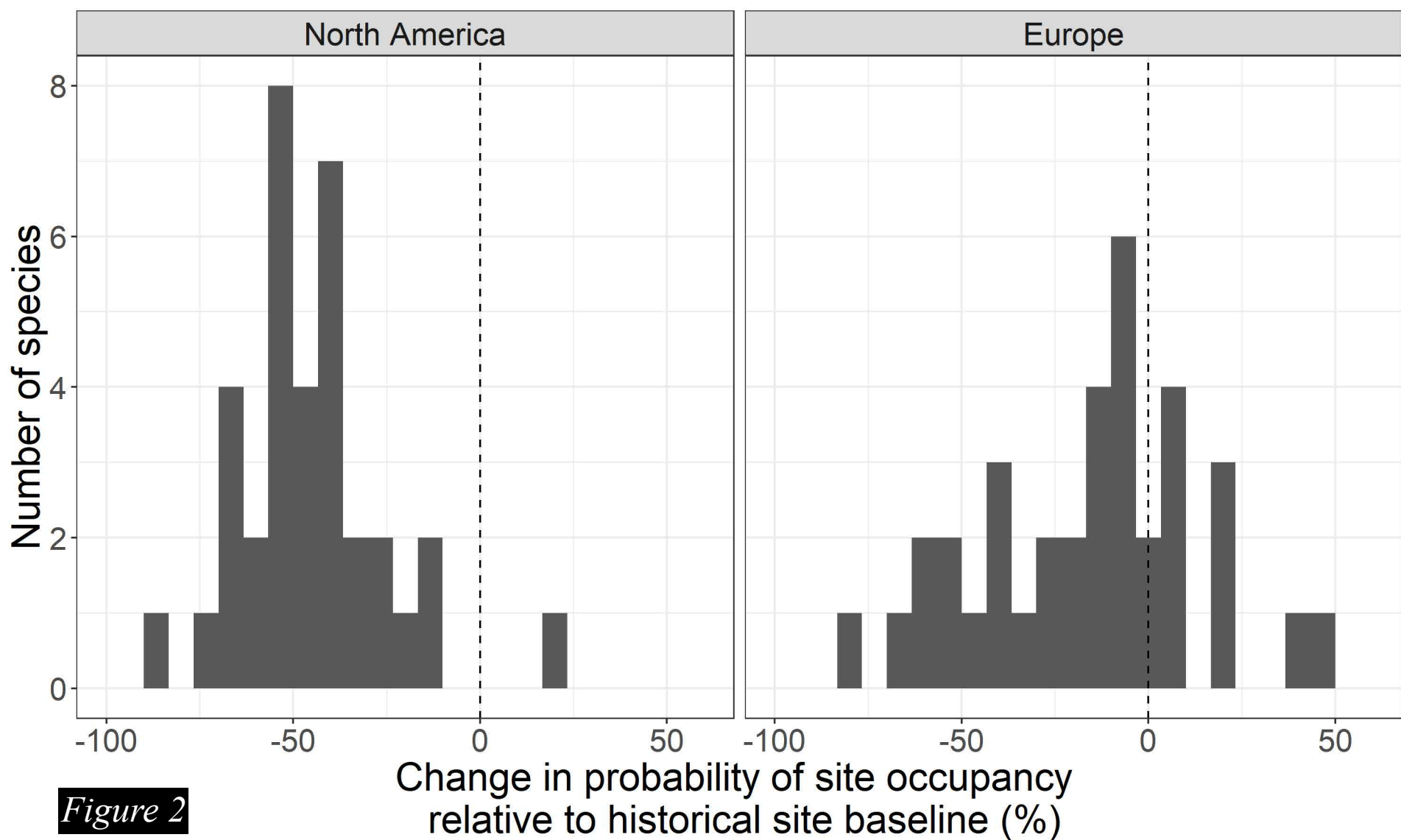
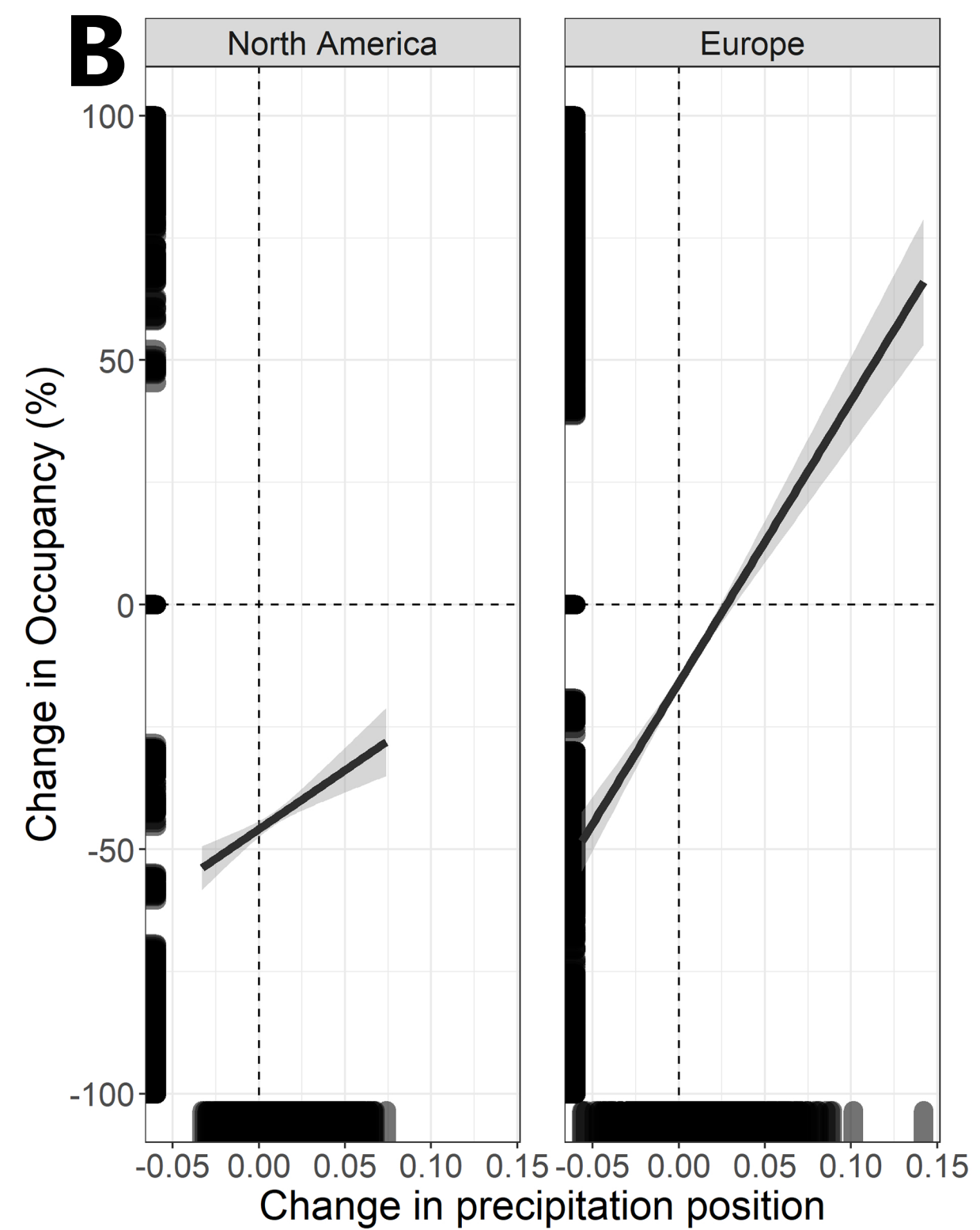
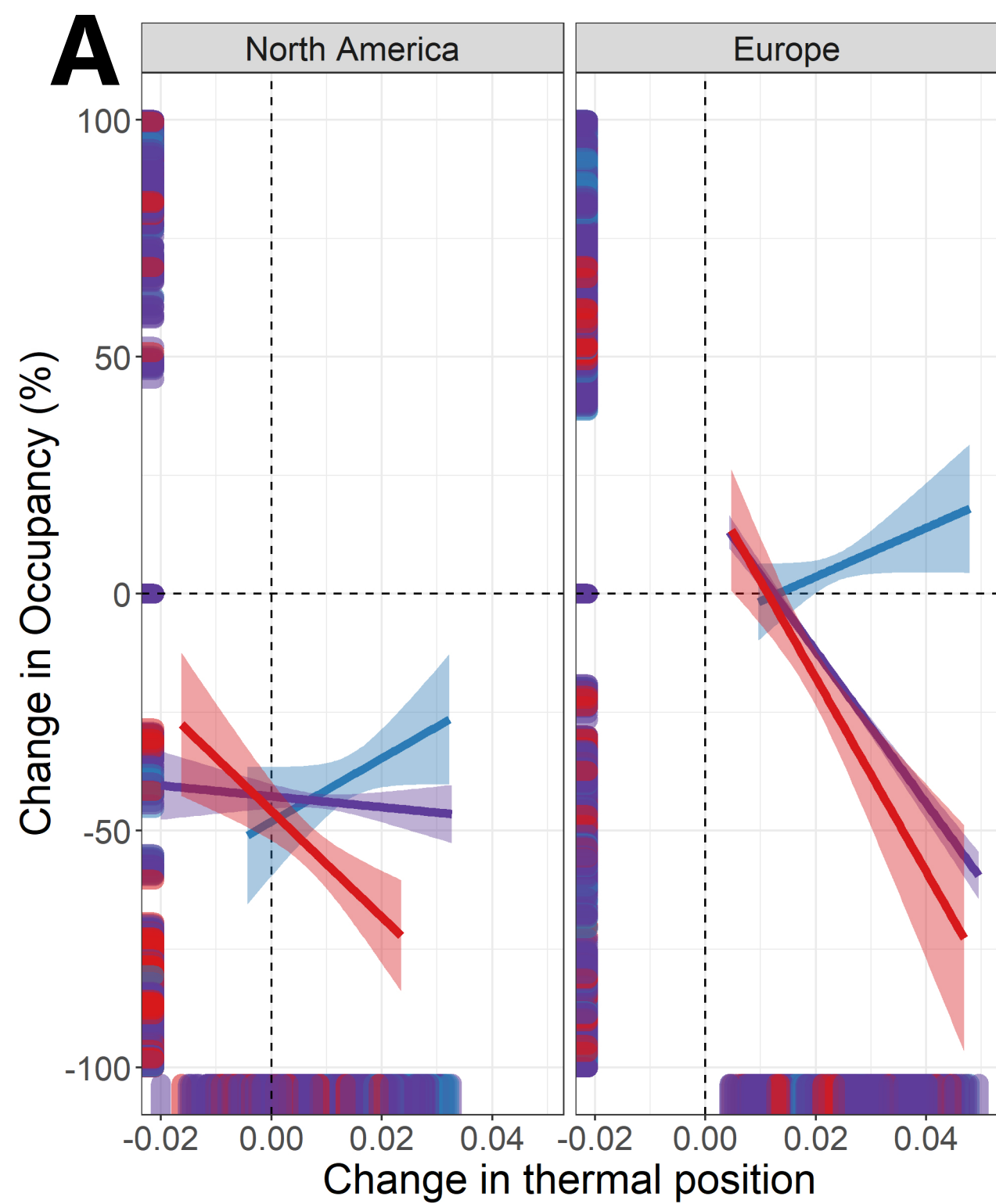
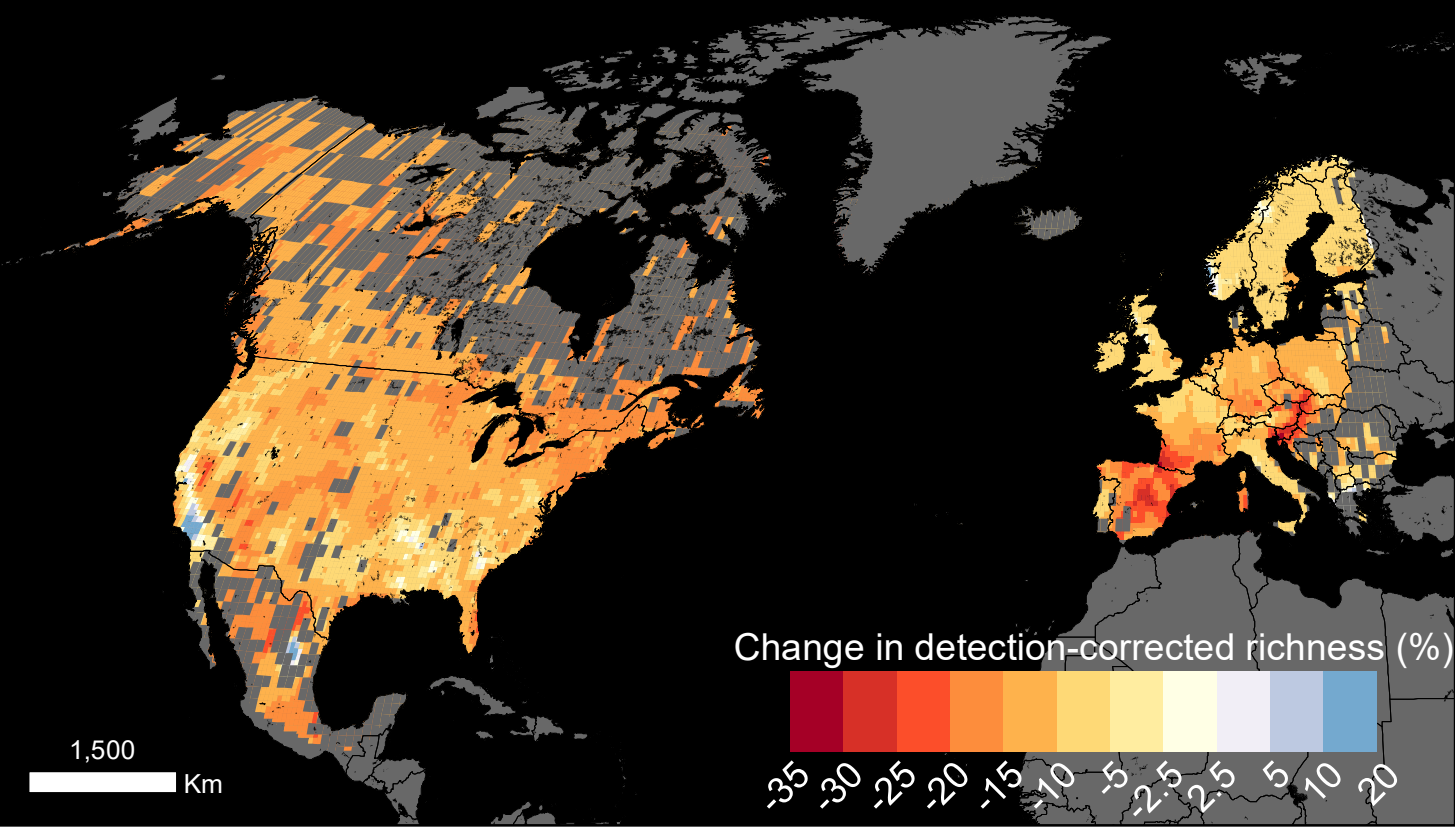


Figure 2





Change in detection-corrected richness (%)



.35 .30 .25 .20 .15 .10 .5 .25 .25 5 10 20

1,500

Km



Supplementary Materials for
Increasing climatic extremes contribute to declines of European and North American
bumblebees

Peter Soroye*, Tim Newbold, Jeremy Kerr.

Correspondence to: peter.soroye@gmail.com

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Materials and Methods

Bumblebee observations, observed distribution, and species richness

We used a dataset comprising 557,622 observations of 66 bumblebee species from 1901-2015, from across North America and Europe. The dataset has been previously used in (1), and contains data assembled from a variety of sources including (21–24), and other sources acknowledged in the Supplementary Acknowledgements. To produce this database from the assembled set of records, potentially unreliable records (including incomplete species, locality, and sampling year information, or disagreement between record georeferencing and stated country of origin) were flagged and removed. We assumed that records in the ocean less than 2500m from a high-resolution coastline were coastal observations with spatially-imprecise georeferences and reassigned these to the nearest point on land. Approximately 6% of the records obtained from GBIF lacked latitude-longitude coordinates for collection localities. For these records, we obtained georeferencing data from a digital gazetteer, GeoNames (<http://geonames.org>; Creative Commons Attribution 3.0 License). Among these records, we retained those located near populated places for which reliable geographic coordinates were available.

Of the 119 species present in the originally assembled data within our study area, we retained 66, which had at least 100 spatially unique records in the baseline period (1901-1974; inclusively) and at least 30 in the recent period (2000-2014; inclusively). These 66 species appeared well sampled across their ranges, including at range margins. The dataset included 264,494 observations of 36 North American species and 293,128 observations of 36 European species, spread across 116,254 unique location-years (i.e. spatiotemporally unique observations; Figure S1). The mean and median species-period sample size was 1887 and 848 unique location-

year observations, respectively (Table S1). While the baseline period was longer, there were comparable numbers of unique location-year observation in each period (54,446 in the baseline and 61,809 in the recent). We examined the georeferencing for every observation and removed all instances of a bee observations that could not be reconciled with lists of countries they inhabit and comparison with range maps from IUCN Red List reports (<http://www.iucnredlist.org/>; accessed Nov 16, 2017). We merged observations of *Bombus moderatus* with *B. cryptarum*, per IUCN Red List documentation and (23), which considers these species to be synonymous. All records included georeferencing and date information. Duplicate collection records of a species for a given location-year were removed to reflect species occurrence rather than sampling or population density.

We mapped presence and absence for each species within 100km by 100km equal-area quadrats across the study area in the baseline and recent periods. We inferred absence when there was no observation of the focal species in the cell in a period but at least one other species recorded. We tested the robustness of our results to this definition of absence by repeating all analyses after defining absence as no observation of the focal species but at least i) three and ii) five other species. For each species, we estimated the observed distribution as the number of cells in the study area where each species was present, and we compared recent and baseline maps of observed distribution to determine extirpation and colonization. We determined mean rates of extirpation or colonization for a species as the proportion of regional extinction or colonization events relative to the total number of cells a species occupied in the baseline. We measured the change in observed distribution for each species. In baseline and recent periods, respectively, species occupied ranges of 17 to 561 and 12 to 338 cells (mean = 195.3 and 117.2), respectively. We measured observed distribution uniquely by continent for species that are

present in both Europe and North America and did not calculate North American observed distributional change for one species which was only recorded there in the current period (*B. distinguendus*). Differences in sampling effort between periods of different lengths can bias detection of presence and subsequent estimates of change and occupancy, so we accounted for sampling effort in all our subsequent analyses. While the baseline period was substantially longer, the recent period had 49% more records, and 13% more unique location-year-species observations (Figure S2, Table S1). Extirpation and colonization likelihoods showed significant negative relationships with sampling effort, while sampling effort was not significantly related to observed species richness change. This was not surprising as non-detection-corrected richness analyses were restricted to a subset of well-sampled cells.

We combined the presence maps of the 66 species to build a map of regional species richness for each period (Figure S10). Variation in sampling effort can bias the estimation of observed biodiversity trends (25, 26), so we excluded quadrats without a minimum of 50 unique location-year observations in the baseline and most recent period. This resulted in 40 North American and 124 European sites, within which we calculated the percent change in species richness from the baseline to the most recent period. While the strict selection protocol limits the number of quadrats in our species richness analysis, a less strict selection (e.g. including quadrats without a minimum of 50 unique location-years observations) fails to account for sampling bias and removes our ability to attribute changes in richness to any climatic variables. All data were organized in R 3.4.1 (27) using packages *tidyverse* (28) and *raster* (29).

The scale of analysis (100km by 100km) is relatively coarse compared to local ecological studies, but these quadrats are large enough to enable reasonable sampling intensity across North America and Europe in both periods without sacrificing relevance for conservation and policy

planning. To test the effect of spatial scale on our results, we repeated analyses at a i) 50km by 50km scale and ii) 200km by 200km scale.

Occupancy models

To correct for imperfect detection in our dataset of bumblebee observations, we used single-species occupancy models to estimate occupancy for the 66 species in each period. These models account for the possibility of false-absences within detection/non-detection data by explicitly estimating detection probability (p) separately from probability of occurrence (30–34). Estimating detection probability for a species during a period requires multiple “survey units” or “visits” to sites within that period. We split each of our time periods into three “survey units” (baseline: 1901-1924, 1925-1949, and 1950-1974; recent: 2000-2004, 2005-2009, and 2010-2014). We used observations of a species during a survey unit to inform detection, and absence of a species when others were seen as a non-detection. It is possible that there are biases in the species sampled within our dataset. Bumblebees are a charismatic insect species that have been collected by researchers and independent naturalists for hundreds of years, but, as with any taxon, it is possible that agriculturally important species (e.g. *B. terrestris* and *B. impatiens*), common species, and larger or more recognizable species have greater likelihoods of detection. We used total number of records to help inform species-specific detection probabilities in our occupancy models to account for sampling bias. Unfortunately, reliable inter- and intra-specific data on other traits that may influence detection probability, such as body size, are not available for all species to include in our models. A necessary assumption of occupancy modelling is that there is no change in occupancy (or species turnover) within a survey period or between survey units within the same period: the closure assumption (35). Estimates of site occupancy rely on this assumption to calculate a probability of detection from the pattern of detection/non-

detections during a period (31). Aggregation of occurrence data into periods to estimate species' presence or absence makes a similar assumption that presence/absence remains static within those periods. Violations of the closure assumption during occupancy modelling are likely to be frequent throughout the literature and within-period colonization or extinction tends to result in overestimates of occupancy probabilities (31, 35). Since this study focuses on relative change in occupancy probabilities instead of the absolute values themselves, potential violations of the closure assumption are not likely to alter our results or conclusions. Probability of occupancy for a species was only calculated across the continent(s) it is known to inhabit. Detection-corrected species richness, calculated as the summed probability of species occurrence in a region, was estimated across the study area for each period (this measure is similar to detection-corrected estimates of taxonomic diversity used in (36)). Using estimates of species-specific site occupancy and detection-corrected species richness for each period, we calculated the percent change in these values between the baseline and recent periods. All data were organized and transformed in R v3.4.1 (27) using packages *raster* (29) and *rgdal* (37).

Occupancy models were fit using the Bayesian general-purpose modelling software JAGS (38), with R v3.4.1 (27) and package *R2jags* (39). Each species- and season-specific model computed season- and site-specific occupancy, using season-specific sampling effort (i.e. the total number of unique location-year observations of any species in a cell) as a covariate for the underlying detection process. We used noninformative Bayesian priors for all parameters and each model ran three Markov chains for 100k iterations, discarding the first 50k as a burn-in and thinning by 10, resulting in 5000 samples from the joint posterior distribution. We ran models until values of the Brooks-Gelman-Rubin statistic suggested convergence had been reached (<1.1) for all parameters (40). The JAGS code specifying our model, including the priors used, is

available with the rest of the data and materials (available on figshare DOI:
10.6084/m9.figshare.9956471).

Climatic position variables

For each of the 66 bumblebee species, we extracted the average of the five highest monthly maximum and five lowest monthly minimum temperatures from among the values for all location and year combinations within the species' geographic range in the baseline period (1901-1975). These maximum and minimum temperatures were assumed to represent the thermal limits for the species, and previous studies have found that this measure is robust to both variation in the number of records used to calculate it and variation in species sampling effort (1). Maximum and minimum precipitation limits were extracted from the five highest and five lowest monthly total precipitation values from among all location and year combinations within the species' geographic range in the baseline period. Climatic limits were rescaled for each species to equal 0 for the lower climatic (i.e. cold/dry) limit and 1 for the upper climatic (i.e. warm/wet) limit. While these derived environmental limits may not represent the actual critical limits that a species can tolerate, they offer an indication of the species' environmental tolerances and measuring the change in the environment relative to these derived limits enables tests of our main hypotheses.

For each species, in each cell of the study area in both periods, we rescaled the local maximum and minimum monthly temperatures and precipitations onto the same scale as the climatic limits. These rescaled values were averaged across months to estimate the thermal position index and precipitation position index: values of 1 indicate that temperatures or precipitation across the whole year equals the warm or wet tolerance limits, and values of 0 indicate that temperatures or precipitation across the year approach or meet the cold or dry

tolerance limits for the species (values greater than 1 and less than 0 are possible where climate change has caused temperatures or precipitation to exceed species' upper thermal or precipitation limits or to fall below lower thermal or precipitation limits). The change in thermal and precipitation position was calculated by subtracting position in the baseline period from position in the recent.

To calculate the community-averaged estimates of climatic position, we clipped each species' thermal and precipitation position maps to their observed distribution in the baseline period, and then overlapped all the position maps, averaging all index values in a given cell. This shows the mean thermal or precipitation position for the entire estimated assemblage of species in that region (Figure S4). We did this for both periods, and then measured the change from the baseline to recent (Figure S5).

In addition to these species-specific and community-averaged climatic position variables, we calculated average annual mean, maximum, and minimum temperature and mean annual precipitation across the study area. These annual climate variables are commonly used to attempt to predict climate change-related effects on biodiversity, and act as a reference model against which we compare predictions of the climate position indices we developed here. As with climatic position variables, we measured mean/max/min temperature and annual precipitation in each period and then measured the change from baseline to recent (Figure 1).

Climate data were obtained from the Climate Research Unit (41) at a resolution of 0.5 X 0.5 degrees. After the calculation of the climatic position index, data were projected and resampled to Cylindrical Equal Area projection at 100 km X 100km resolution to match the bumblebee data, using R 3.4.1 (27) and packages *raster* (29) and *rgdal* (37).

523 Statistical analyses

524 *Change in local occupancy.* We tested the relationship between climatic position and change
525 in probability of local site occupancy by constructing a series of linear mixed models (LMM).
526 Change in occupancy probability was the difference in occupancy probability between the
527 baseline and recent periods and could range continuously from -100% to 100%, with negative
528 values indicating a decrease in probability of occupancy and positive values indicating an
529 increase in probability of occupancy. Models included the thermal position variables (baseline
530 period, change since the baseline, and the interaction between these), the precipitation position
531 variables (baseline period, change since the baseline, and the interaction between these), the
532 interaction between baseline thermal position and precipitation position, and the interaction
533 between change in thermal position and change in precipitation position.

534 North America and Europe have substantially different histories of land use, human
535 development, and population trends, and different approaches to species conservation, all of
536 which may contribute to differences in rates of species and assemblage change. We included
537 continent as a categorical variable to account for hypothesized differences in rates of change
538 between North America and Europe (1). Species was included as a random effect in the model to
539 account for differences in species' responses to climate. We ran identical models with separate
540 random intercepts for site and for species and noted qualitatively consistent results between these
541 models and models without site. In cases where models did not clearly converge, we re-ran
542 models using several different optimizers with $>10^7$ evaluations and found consistent results. We
543 calculated conditional and marginal R^2 using the method proposed by (42).

544 *Observed extirpation/colonization.* We ran another series of models separately testing the
545 relationship between local colonization and extinction, and climatic position variables. We used

binomial generalized linear mixed models (GLMM), again including species as a random effect. The model structure was identical to change in occupancy models (see previous section), although we included sampling effort, calculated as the total number of observations in each cell in a period (sampling effort was not included in change in occupancy models because it was already used to estimate occupancy). We calculated conditional and marginal R^2 in the same way as in the change in occupancy models. Colonization and extinction models with site included as a separate random effect produced consistent results.

Phylogenetic analyses. To account for phylogeny in our analyses, we repeated the occupancy, extinction, and colonization modelling using a phylogenetic generalized linear mixed model framework, with a comprehensive molecular and nuclear phylogeny (43). We programmed models using the *MCMCglmm* (44) and *ape* (45) packages in R, following the framework from (46). All models used uninformative univariate priors for random effects corresponding to an inverse-Gamma with shape and scale parameters equal to 0.01. Models were run with a minimum of 105k iterations with a thinning factor of 20 and discard the first 5k, resulting in a minimum of 5000 samples from the joint posterior distribution. Model parameters were visually assessed for convergence, and if all parameters did not appear to converge then were reran for more iterations and a longer burn-in. We estimated marginal and conditional R^2 , and phylogenetic signal (Pagel's λ) using code from (46). As is common with Bayesian models, we compared them using the Deviance Information Criterion (DIC). *B. magnus* was not present in the phylogeny and so was excluded from these analyses. The structure of fixed model effects tested was identical to the descriptions provided above, and we found that model parameter values using the PGLMMs were very consistent with those from models in *lme4*. We present

results from the PGLMMs here as previous work has shown significant phylogenetic signal in patterns of bumblebee declines and in their response to climate change (1, 47).

Observed species richness. We constructed an analysis of covariance model (ANCOVA) to test the relationship between change in species richness and climatic position. The model included the thermal position variables (baseline period, change since the baseline, and the interaction between these), the precipitation position variables (baseline period, change since the baseline, and the interaction between these), and continent and sampling effort as controlling variables. We used quadratic polynomials for the baseline thermal and precipitation position. To avoid overfitting due to the low sample size in this test ($n = 164$ sites) and because they were neither significant in the occupancy models nor necessary for our hypothesis testing, we did not include the interaction between baseline thermal position and precipitation position, nor the interaction between change in thermal and precipitation position. We also removed sampling effort and the 2nd order polynomial of baseline precipitation position as covariates after seeing that they were not significant and that the model was not improved by their addition ($\Delta AIC < 2$). We did not expect sampling to be significant since this analysis was restricted to well-sampled cells with at least 50 unique location-year observations in each period. Results from the model were robust to the presence of outliers, and aside from violations of spatial autocorrelation in the residuals, appeared to satisfy all other assumptions.

We checked for spatial autocorrelation in the residuals by visually inspecting a correlogram of Moran's I (Figure S11A) and found some evidence of spatial autocorrelation. We proceeded by constructing a simultaneous autoregressive (SAR) spatial error model to correct for residual autocorrelation, as suggested by (48) and (49). This reduced much of the variability in Moran's I (Figure S11B). Model results with the SAR model were qualitatively similar to the ANCOVA

results that we report here (Tables S2 and S3). We calculated the Nagelkerke Pseudo- R^2 of the model as a measure of the variance explained.

Given the number of sites where we could measure species richness change with confidence was relatively low (124 in Europe and 40 in North America), we compared the mean community-averaged climatic position of the species richness sites to the mean community-averaged climatic position of the entire continent to check that the species richness sites were representative. We used a series of Welch's two-sample t-tests to compare the means of the community-averaged thermal position variables (in the baseline and the change between periods) and the community-averaged precipitation position variables (in the baseline and the change between periods) of the species richness cells to their respective continental averages.

Detection-corrected species richness. We built an ANCOVA model to test the relationship between climatic positioning and detection-corrected species richness. The model structure here was identical to the occupancy PGLMMs but used community-averaged measures of climatic positioning and did not include the random effects of species. As with the observed species richness models, we checked for spatial autocorrelation and used the same procedure to correct for this with SAR models (Figure S12). Spatial autocorrelation was significant in the original model, but results were qualitatively similar between SAR and ANCOVA models (Tables S2 and S3).

The explained variance of the detection-corrected species richness model was substantially lower than the observed species richness model (8% vs 38%). This is likely to be a result of the occupancy modelling process. The occupancy modelling took the binary measures of species detection/non-detection and used a derived detection probability to estimate continuous probabilities of occupancy from these from 1s and 0s, across the entire continent it occupies. In

each period, the occupancy models estimate a probability of 1 (or very close) for cells where the species was detected in any one of the survey units, and they estimate some probability between 0 and 1 for cells where a species was never detected. This latter occupancy probability depends on the species-period-specific detection probability and the total sampling effort in that cell. For most species the occupancy probability of cells where they were not detected is between 0 and 0.4. As detection probability and sampling effort vary by period, the same cell can have a different occupancy estimate in the baseline and recent period, even when the species was never observed there or when it has persisted through both periods. This between-period variation reflects the uncertainty within estimates of occupancy probability during a period, and likely drives the lower adjusted R^2 values we see when comparing the detection-corrected and observed species richness models. A similar reasoning likely explains the differences between marginal R^2 of change in occupancy models (0.11) compared to extinction and colonization models (0.87 and 0.53, respectively).

Comparison with mean climate variables. For all our models, we created a model identical in structure but with mean climate variables (i.e. mean baseline annual temperature, mean baseline total annual precipitation, and the change in these to the recent period) instead of climatic position variables. We also compared using average annual maximum and minimum temperature variables. All continuous variables in both sets of models were centered and rescaled before modelling, and we used Information Criterion and R^2 to compare between climatic position and mean climate models. We tested models where baseline thermal and precipitation variables were fit as either linear, or quadratic polynomial terms, since we predicted that species would be more likely to decline in occupancy where sites were already closer to an upper or lower limit in the

baseline. With the exception of PGLMMs, all models were constructed in R v3.5.1 (27), using packages *lme4* (50) and *spdep* (51) for simultaneous autoregressive models.

Spatial projection across recent period

Using the detection-corrected species richness model (adjusted $R^2 = 0.14$) and 0.5-degree resolution climate data (41), we spatially projected the predicted change in species richness since the baseline across the entire study area (Figure 4). We also projected change using the non-detection-corrected species richness model (adjusted $R^2 = 0.44$; Figure S9). We used rescaled climatic position and climatic position change layers at 0.5×0.5 degree grid resolution and used the respective model coefficients to predict what percent climate-change-induced change in assemblage richness occurred from the baseline period (1901-1974) to the recent period (2000-2014).

Effects of land-use change

Using high-resolution data on historic land-use from the Global Harmonized Land-use dataset (52), we calculated the mean proportion of cropland, pasture, and urban land cover (hereafter human-dominated land-use) in each period for cells across the study area. We then measured the mean change in human-dominated land-use between periods. We built PGLMM's of change in probability of occupancy, extinction and colonization, as well as spatial autoregressive error models of detection-corrected species richness, which included the best fitting variables from previous steps of analysis and human-dominated land-use change. We compared these models with land-use to pure climate change models using information criterion values and R^2 and compared the values and estimated significance of fixed effects.

Agricultural species might be declining through increased use of certain pesticides, which could modify relative rates of decline between species. We calculated the proportion of cropland across species' geographic ranges in the baseline period, and used linear regressions to separately test the association between this and i) the number of unique location-year observations of a species, ii) the mean change in probability of occupancy of a species, and iii) the mean change in observed (non-detection-corrected) distribution of a species.

Supplemental Text

Non-detection corrected declines

Occupancy, extirpation, and colonization. Consistent with measured declines in occupancy (Figure 2), observed distributions declined on average by 54% ($\pm 3.4\%$ SE) in North America and 18% ($\pm 7.2\%$ SE) in Europe relative to the baseline period (Figure S6A).

Rates of observed extirpation and colonization were calculated for each species as the proportion of extirpation or colonization events relative to the total number of cells occupied historically. Across all species in North America and Europe there was a 72% ($\pm 2.2\%$ SE) and 49% ($\pm 2.8\%$ SE) chance, respectively, that a given bumblebee species was lost from a quadrat it occupied historically. Globally, extirpation events were 8 times (± 1.7 SE) more likely than colonization events, with ratios being higher in North America (Figure S7). Imperfect species detection and patchy sampling mean that extirpation can be overestimated in opportunistic datasets, so observed extirpation rates likely represent the upper bound of true extinction probability.

Non-detection corrected species richness. Since the baseline period, local (non-detection corrected) species richness has declined by about 18.6% ($\pm 3.2\%$ SE) in North America, while richness in Europe has stayed relatively constant (2.2% increase since the baseline $\pm 2.6\%$ SE; Figure S6B). Species richness declines do not reflect differences in sampling intensity in this subset of well-sample cells and was not informative or significant in statistical models.

Response of change in occupancy to precipitation position

While the relationship between change in occupancy and proximity to thermal limits was statistically detectable and followed our expectations, relationships with precipitation showed more mixed results. Declines in occupancy were stronger in sites that became drier since the baseline but other effects were inconsistent, and we did not see an interaction between baseline precipitation and change in precipitation as we expected if exposure to precipitation limits from climate change was a driver of declines (Figure 3, Figure S8, Table S2). While direct effects of precipitation are undoubtedly important for bumblebees at a local scale, especially in terms of moisture availability, we are unable to detect these effects with this analysis. Conflicting indirect effects of precipitation (through changes in floral resources or vegetation structure), may make these effects more difficult to measure and detect than direct effects of temperature.

Response of extirpation and colonization to climatic position

Patterns in extirpation across the 66 bumblebee species display a strong signal of climate change, especially increasing temperature. We used a phylogenetic generalized linear mixed model (PGLMM) with a similar fixed and random effect structure as the site occupancy-climate change model, but here including sampling effort as a covariate. As expected, extirpation probability related to thermal position in the baseline period, change since then, and their

interaction (Table S2). Increasing thermal position was linked to greater probability of extirpation for species in regions that were already near their upper thermal limit, and lower probability of extirpation for species in regions historically closer to their cold limits (Figure S13A). As with occupancy, precipitation position showed more ambiguous associations. While sites that became drier had higher probability of extirpation, the effect of baseline precipitation was not significant and there was no significant interaction between these two effects (Figure S13C). Our model explained most of the variation in the response of extirpation to climatic position (marginal $R^2 = 0.87$). The strong relationship between temperature warming and extirpation risk among bumblebee species is consistent with previous work demonstrating that extinction risk depends on shifts in the spatial distributions of thermal niches in other taxa (53, 54) and is of particular importance since bumblebee species are being pushed towards their upper thermal limits across most of North America and Europe (Figure S5A).

Trends in local colonization also showed a strong association with climate change, providing independent support for a separate prediction of our hypothesis. A PGLMM with similar fixed and random effects to the extirpation models shows that the three thermal position variables appear to significantly drive colonization, with precipitation position showing inconsistent effects (Table S2). Species were more likely to colonize regions which were historically near the cold limit and had warmed, and historically hot regions that cooled were more likely to be colonized than historically cool or moderate regions that became colder (Figure S13B). Regions that moved towards species' wet limits were more likely to be colonized (Figure S13D). Regions that were simultaneously hot and dry historically had higher rates of colonization, as did regions that got simultaneously hotter and drier. Models explained a large part of the variation in local colonization (marginal $R^2 = 0.53$). The difference in explained variance between the extirpation

and colonization models (marginal R^2 0.87 vs 0.53) could suggest that the process of colonization is less tied to physiological climate limits than extirpation. In regions that were historically moderate or near species' hot limits, rates of extirpation greatly exceeded rates of colonization following warming. Given that species and communities appear to have been moderately situated with respect to their climatic limits in many northern regions across North America and Europe that warmed (Figure S5A), this finding may help explain why most bumblebees are not generally expanding their ranges at poleward limits of their distributions to track climate change (1, 14).

The models revealed a significantly detectable phylogenetic signal in the response to both extirpation and colonization to climatic position, with the signal for extirpation (Pagel's λ = 0.88) being stronger than the signal for colonization (Pagel's λ = 0.70). Previous work has also detected significant phylogenetic signal in patterns of declines across bumblebees (47) and found that traits can influence the sensitivity of bumblebees to land-use and agricultural pressures (55). More data on inter- and intra-specific variation on traits should be gathered to test questions about how traits and evolutionary change may mediate responses to climate change at this scale.

Comparing climatic position models to mean climate variables

While measures of climate like mean annual temperature or mean annual precipitation are easy to gather, inter-specific variation in physiological tolerances mean that how these conditions influence species depends on proximity to species physiological limits. A regional measure of climatic position directly measures whether climatic conditions are near or outside species' tolerances to test whether changing exposure to such conditions drives persistence and colonization. Predictions from this hypothesis are consistent with recent trends in North American and European bumblebees (Figures 3 and S13) and using thermal and precipitation

position variables instead of mean climate variables produces models that better predict extinction, colonization, and change in occupancy (marginal R^2 7% lower to 12.5% higher) and are more informative ($\Delta DIC \sim 202.4$, $\Delta DIC \sim 102.8$ and $\Delta DIC \sim 164.9$ respectively). This increase in explanatory power was consistent when comparing to models using average annual maximum (marginal R^2 1.6% to 23% higher; $\Delta DIC = 98.7$ -157.5) or minimum temperatures (marginal R^2 2.6% lower to 21.3% higher; $\Delta DIC = 128.2$ -241.9). We show that accounting for inter-specific variation significantly improves detection of relatively local-scale climate impacts on bumblebees. Regardless of technique used, there is a biologically meaningful signal of climate change within patterns of bumblebee decline.

Climatic sampling across continents

We tested whether the most well-sampled quadrats in our analysis (which were used for the non-detection-corrected species richness analysis) presented a representative sample of historic climate and climatic patterns across North America and Europe, and found that well-sampled regions in Europe tended to be cooler in the baseline and experience less warming between periods (Welch's two-sample t-test results: t-statistics = 2.72 and 4.16, p-values = 7.0×10^{-3} and 4.8×10^{-5} , df = 227 and 206, respectively). Previous estimates of European bumblebee richness change extrapolating from well-sampled areas may have systematically underestimated recent richness declines. Well-sampled quadrats in North America appeared representative of the general temperature trends experienced over the continent as a whole, but tended to be historically wetter and have gotten wetter than the continental average (Welch's two-sample t-test results: t-statistics = 2.95 and 2.30, p-values = 5.1×10^{-3} and 0.03, df = 41.5 and 40.2, respectively).

Land-use change

Human land-use has also been associated with pollinator declines (8). We find that while human-dominated land-use change appears to have strong negative effects on probability of occupancy and detection-corrected species richness, this effect is distinct from those presented by climate change. Including LU in the models showed a significant negative effect of land-use but produced virtually identical results for climatic position variables, suggesting that direct effects of climate change on bumblebees are distinct from effects of land-use (Table S4).

We did not find any statistically significant relationship between percent of species' geographical range covered by cropland and unique location-year observations (t -value= -0.79, p -value= 0.43, d.f.= 64), mean change in probability of occupancy (t -value= 0.07, p -value= 0.94, d.f.= 64), or mean change in observed distribution (t -value= 1.24, p -value= 0.22, d.f.= 64). It appears that rates of species decline do not appear to strongly differ between species more associated with agricultural areas, although we note that our subset of well-sampled species is likely already biased toward species more associated with agricultural and urban areas.

Additional tests of modelling robustness

Spatial scale. Spatial scale of analysis is an important factor to consider for any study involving extirpation/colonization and range change. Where possible, spatial scale of a study should be chosen with consideration to the biologically relevant area encompassing population dynamics of the study species (56, 57), but reasonably chosen spatial scales can still reveal valuable macroecological patterns (58). Here, we selected 100km by 100km cells as the spatial scale of our analysis, which represented a balance between having adequate sampling density across our study area and a high resolution to detect “local” effects of climate and climate change. Repeating analyses in 50km by 50km cells and 200km by 200km cells produced results

that were qualitatively similar (Tables S5 and S6), suggesting our analyses were robust to the scale used.

Absence threshold. When converting our occurrence records into presence absence data, we inferred absence of a species when the focal species was not seen but at least one other species was (absence threshold of one). A liberal absence threshold could result in overestimating absences (and ultimately detection ability), which could lead to overestimates of extirpation and local colonization. We tested the sensitivity of our results to our definition of absence by repeating analyses using an absence threshold of three and five, and found that all results were qualitatively similar (Tables S7 and S8).

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820 Pawlikowski); NBDC (Eire, U. FitzPatrick); FMNH (Finland, J. Paukkunen); Czech Republic (J.
821 Straka, L. Dvorak); France (G. Mahé); NSIC (Norway, F. Odegaard); UK (S.P.M. Roberts); Italy
822 (A. Manino); Spain (L. Castro) Global Biodiversity Information Facility (GBIF), <http://gbif.org>
823 for records from North America and Europe. P.S. would also like to thank A. Abdelgadir and J-
824 Y. Maba for support.

825

Supplemental Figures

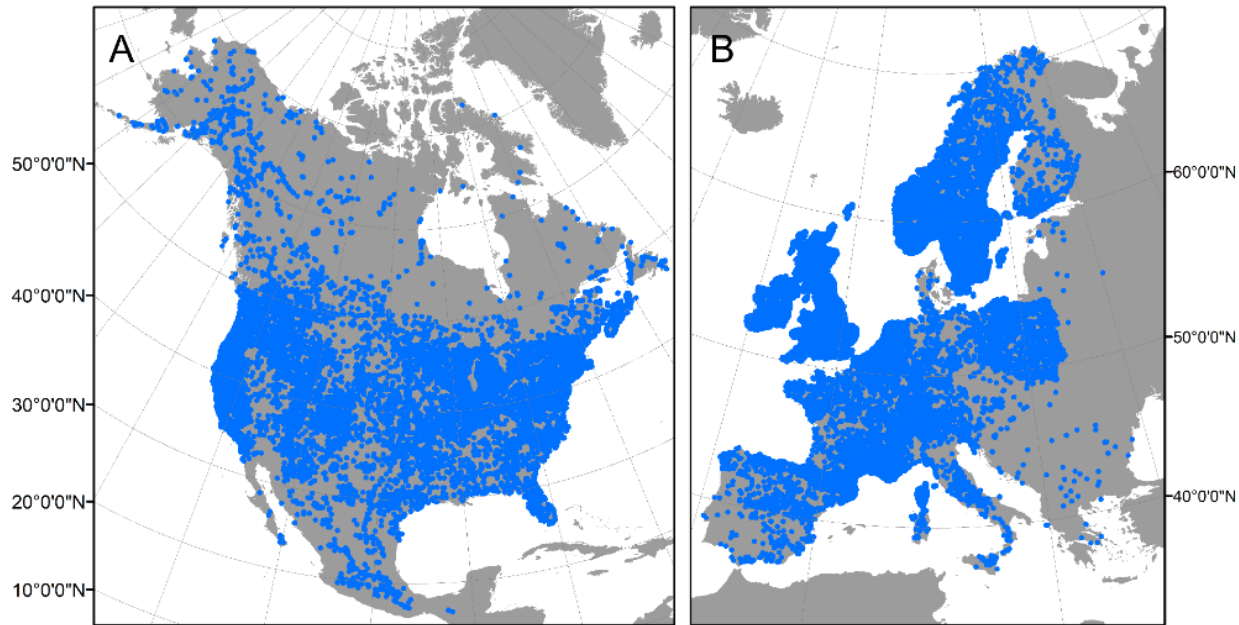


Figure S1. Distribution of unique species-location-year sampling locations from North America (A) and Europe (B).

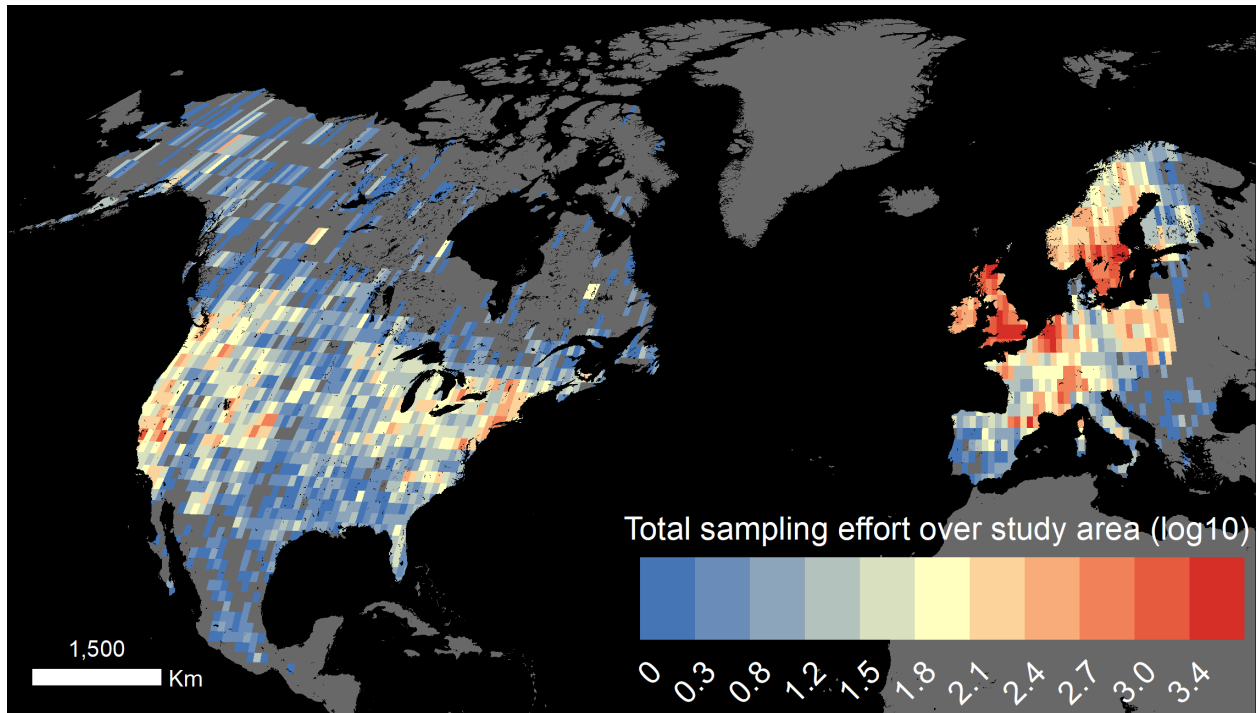


Figure S2. Density of unique location-year observations per 100km by 100km grid cell across North America and Europe.

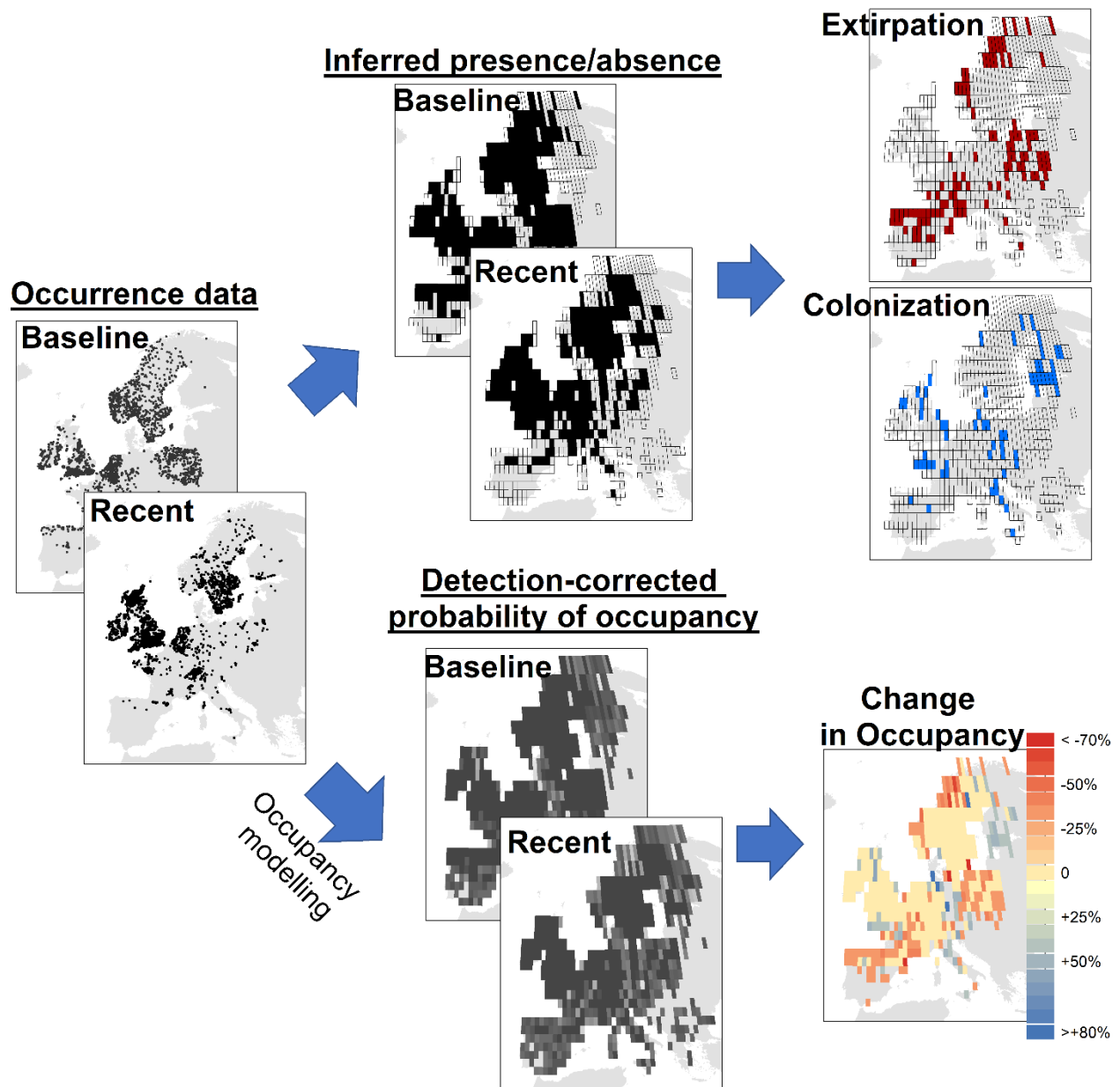


Figure S3. Graphical description of methods visualizing relation between occurrence records and eventual measures of detection-corrected change in occupancy, extirpation, and colonization for *Bombus hortorum*.

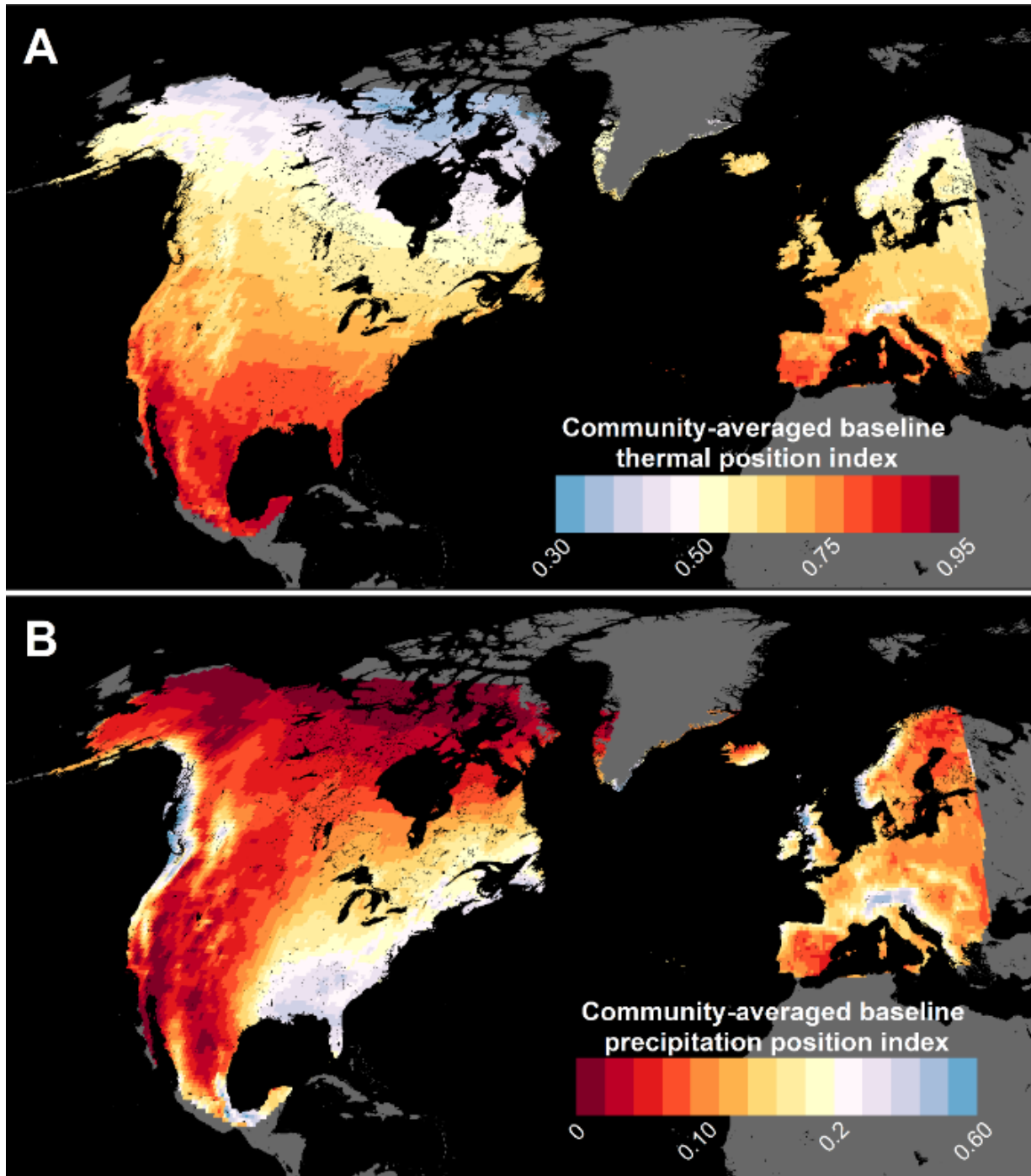
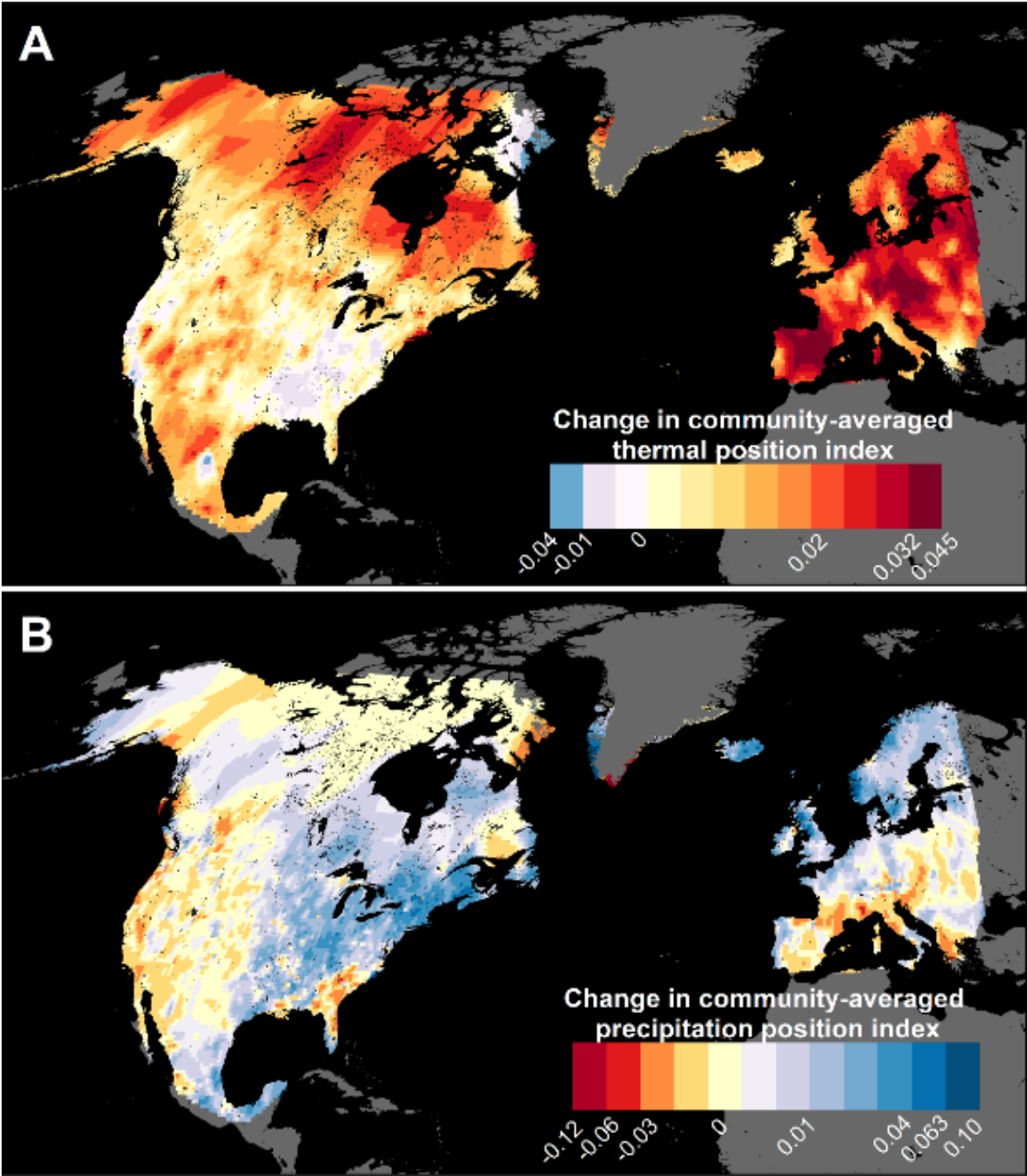


Figure S4. Community-averaged thermal (A) and precipitation position (B) in the baseline period (1901-1974) across North America and Europe. Both thermal and precipitation position indices have a potential range of 0 to 1. Zero indicates that species in the assemblage are on average at their cold/dry tolerance limit for the entirety of the year in the period. One

848 indicates that species in the assemblage are on average at their hot/wet tolerance limit for the
849 entirety of the year in the period.

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Figure S5. Change in community-averaged thermal (A) and precipitation position (B) from the baseline (1901-1974) to the recent period (2000-2015) across North America and Europe. Positive change indicates that regions have warmed or become wetter and that on average, species in the assemblage are closer to their hot/wet limits than historically. Negative change indicates that regions have cooled or dried and that on average, species in the assemblage are closer to their cold/wet limits than in the past.

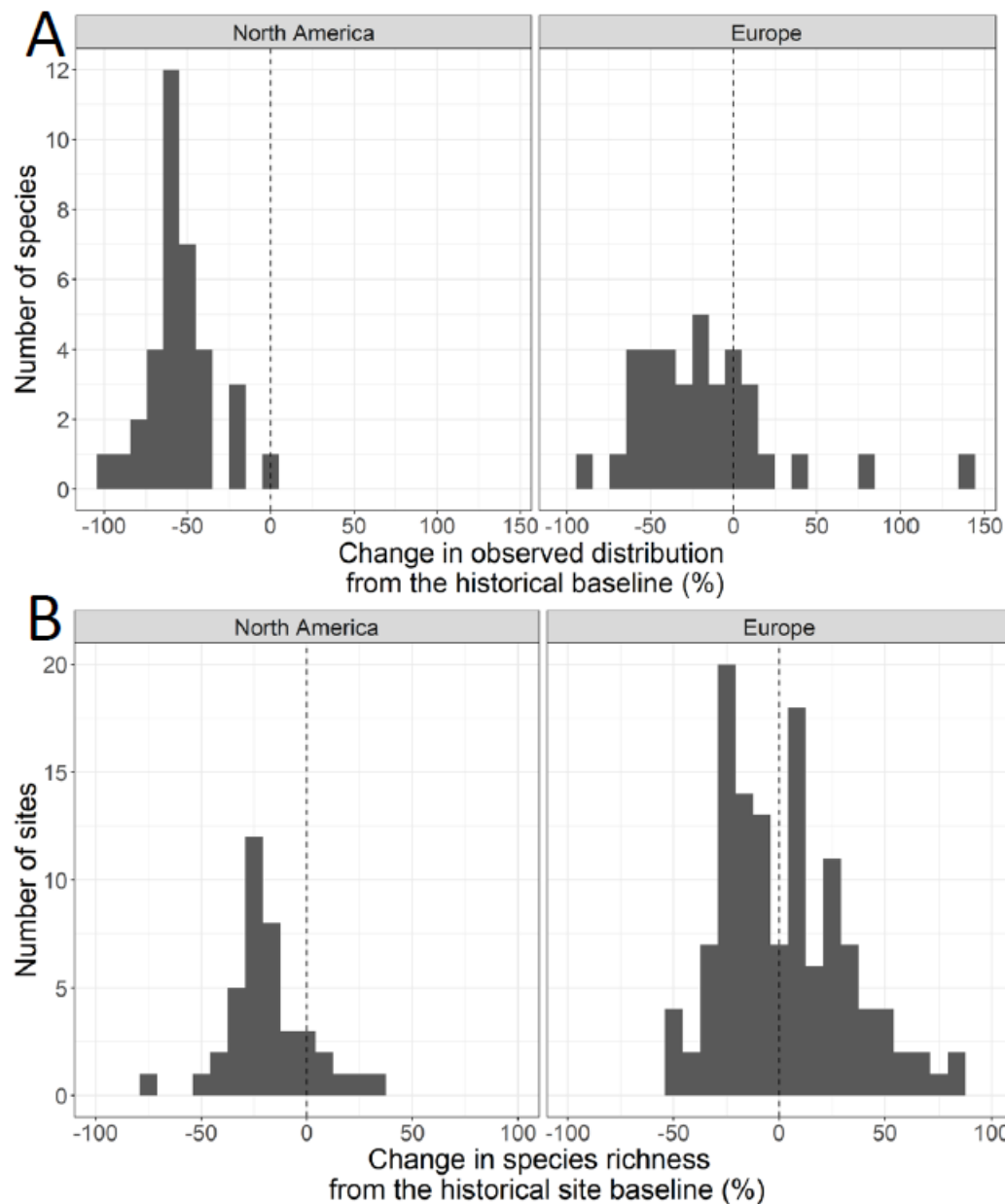


Figure S6. Change in species' observed distribution (A) and observed species richness (B) from the baseline (1901-1974) to recent period (2000-2014) in sites across the study area.

Observed species richness was only measured in sites with a minimum of 50 unique location-year-species observations in the baseline and most recent period. N= 164.

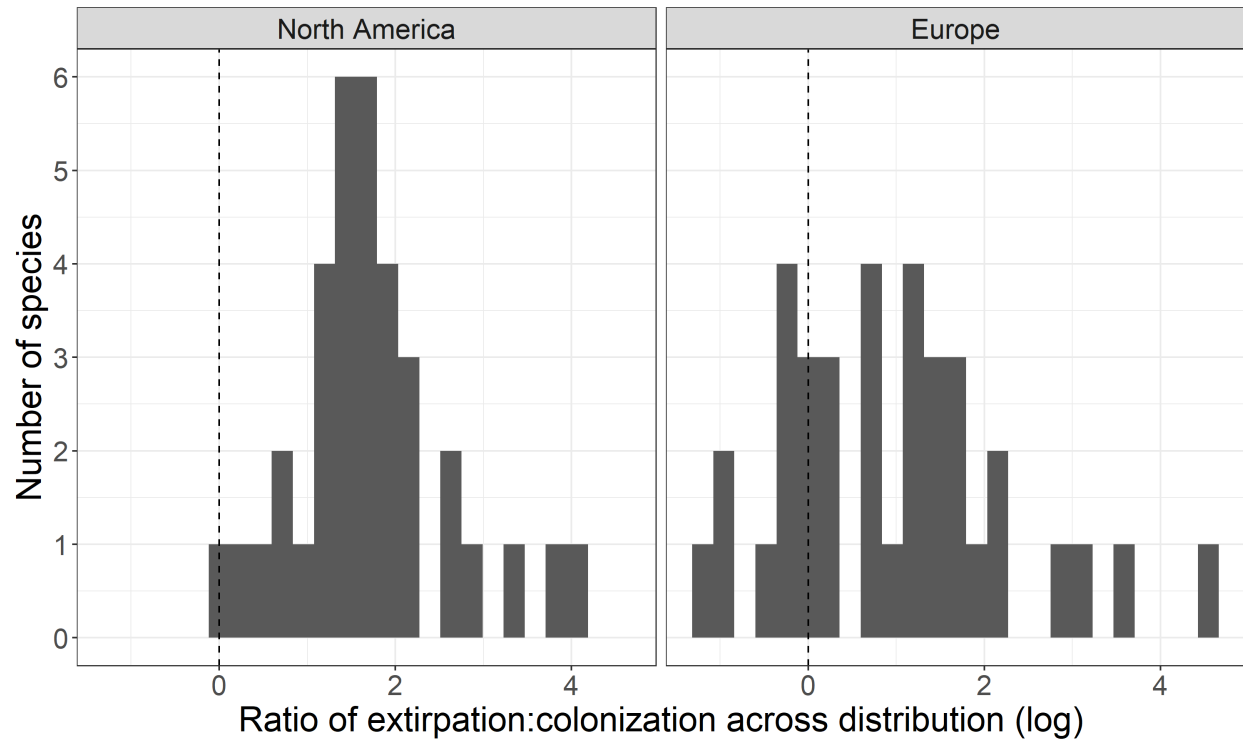
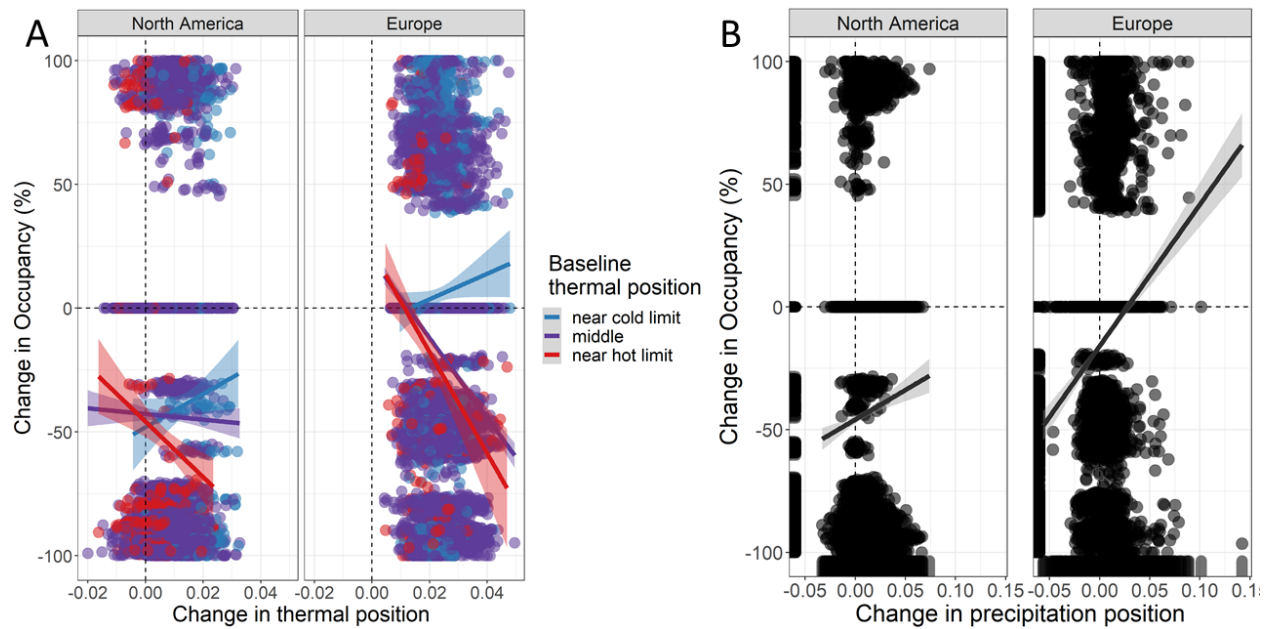


Figure S7. Ratio of local extirpation:colonization across species' observed distributions between the baseline (1900-1975) and recent period (2000-2015).

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875 **Figure S8. Change in probability of occupancy in response to change in thermal (A) and**
 876 **precipitation (B) position from the baseline (1901-1974) to recent period (2000-2014).** Note
 877 that this figure is identical to Figure 3 in the main text but shows raw data points. Thermal and
 878 precipitation position ranges from 0 to 1, with 1 indicating conditions at a site are at a species'
 879 hot or wet limit for the entire year, and zero meaning conditions are at a species' cold or dry limit
 880 for the entire year during the historic period. For ease of visualizing the significant interaction
 881 between baseline thermal position and change in thermal position, the continuous baseline
 882 thermal position variable has been split at the 1st and 3rd quantile to show sites that were
 883 historically close to species' hot limits (red; n=969), cold limits (blue; n=2,244), and middle of
 884 their observed climatic limits (purple; n=11,793). Rug plot shows the distribution of
 885 observations. Confidence intervals ($\pm 95\%$) are shown around linear trendlines.

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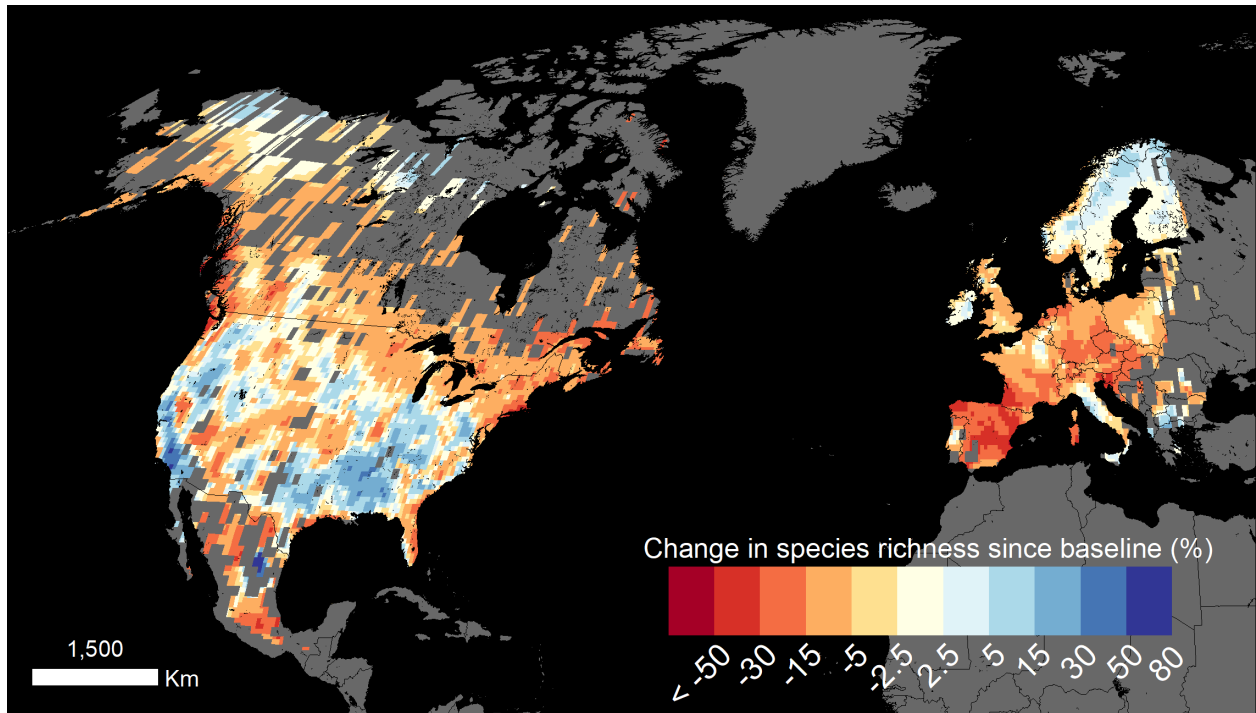


Figure S9. Spatial projections of climate change-related change in non-detection-corrected bumblebee species richness from a baseline period (1901-1974) to a recent period (2000-2014). Made using a model predicting percent change in non-detection-corrected bumblebee species richness as a function of mean community thermal and precipitation position ($R^2= 0.44$; see Materials and Methods for model details).

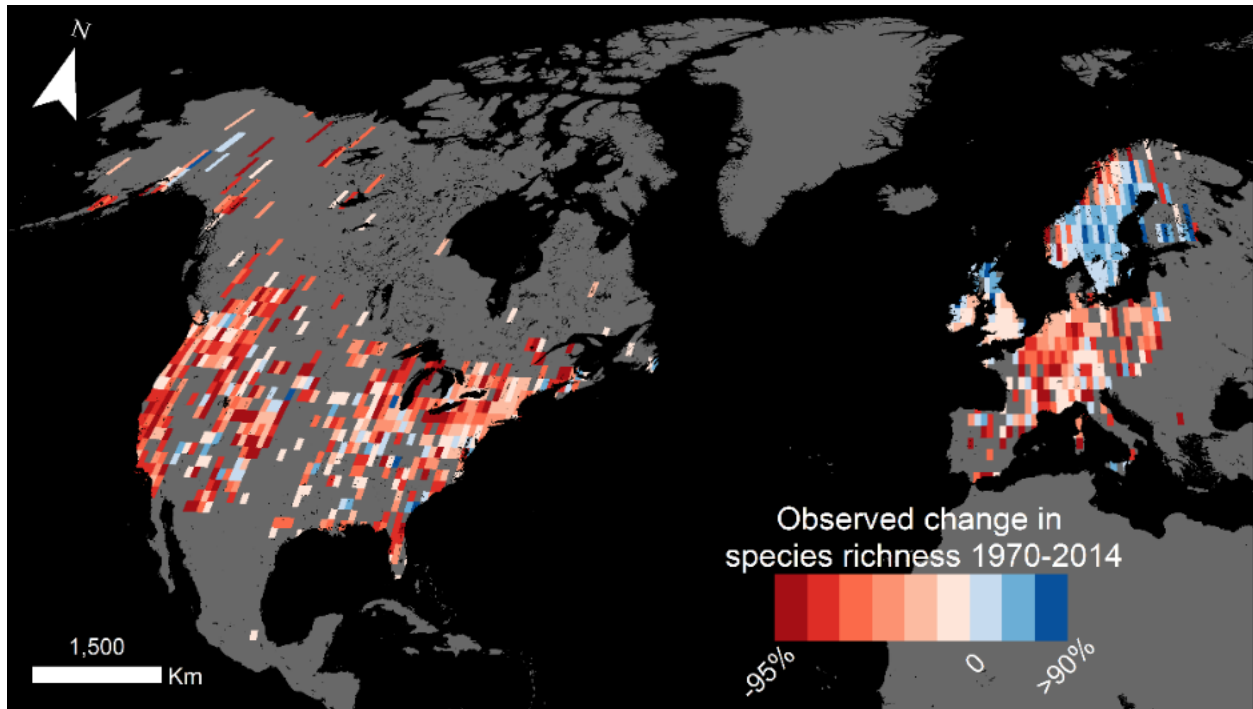


Figure S10. Percent change in observed bumblebee species richness across North America from the baseline (1901-1974) to recent period (2000-2014). Grid cells shown are 100 km by 100 km, in an equal area projection. No sampling-based selection (see methods) applied here.

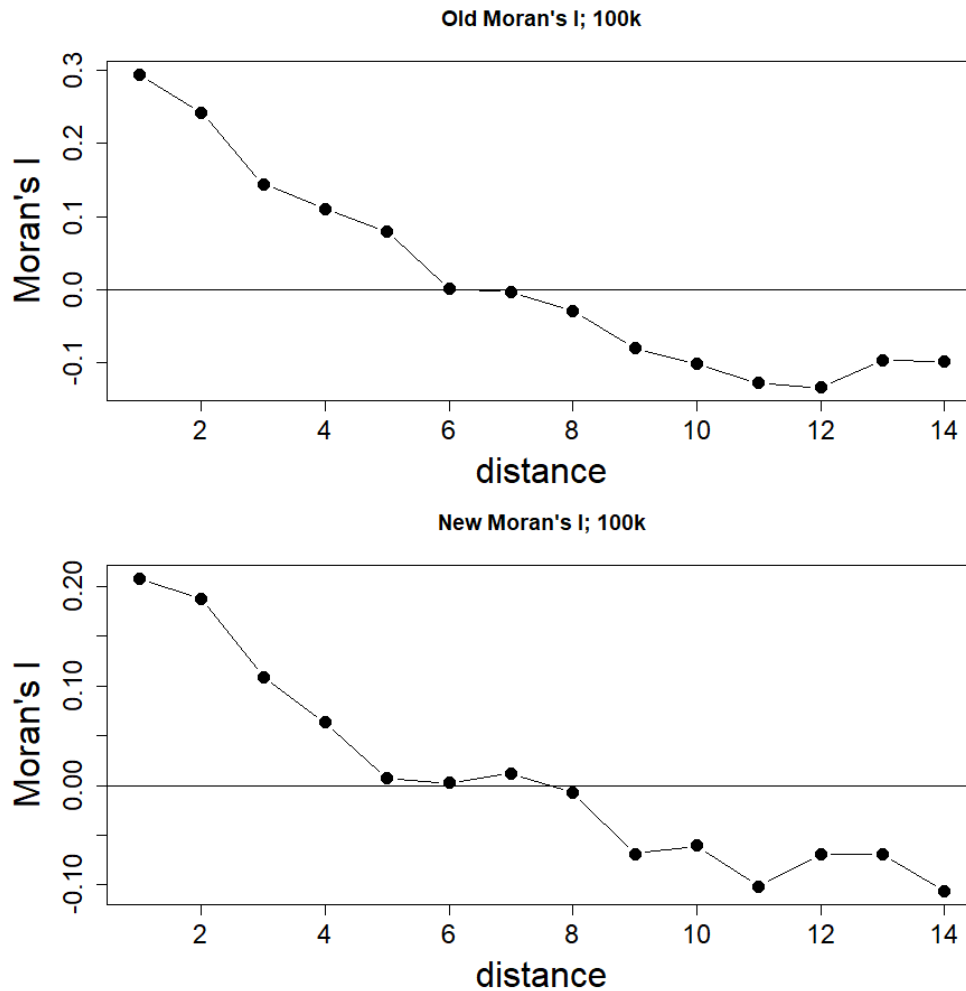


Figure S11. Correlogram of Moran's I for non-detection corrected species richness model.

Moran's I calculated from a) ordinary least squares regression model and b) simultaneous autoregressive (SAR) error model. SAR model was a significantly better fit (according to log likelihood). Model coefficients were qualitatively similar between both models.

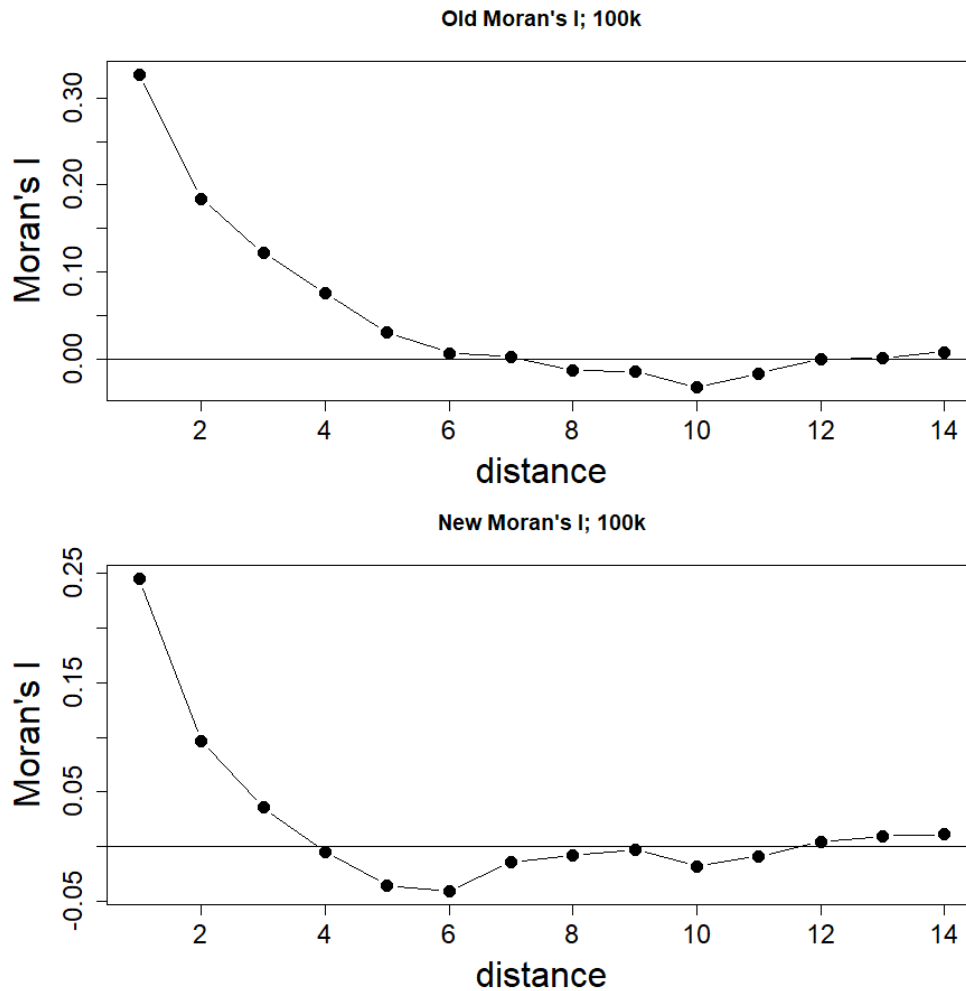


Figure S12. Correlogram of Moran's I for detection-corrected species richness response model. Moran's I calculated from a) ordinary least squares regression model and b) simultaneous autoregressive (SAR) error model. SAR model was a significantly better fit (according to log likelihood). Model coefficients were qualitatively similar between both models.

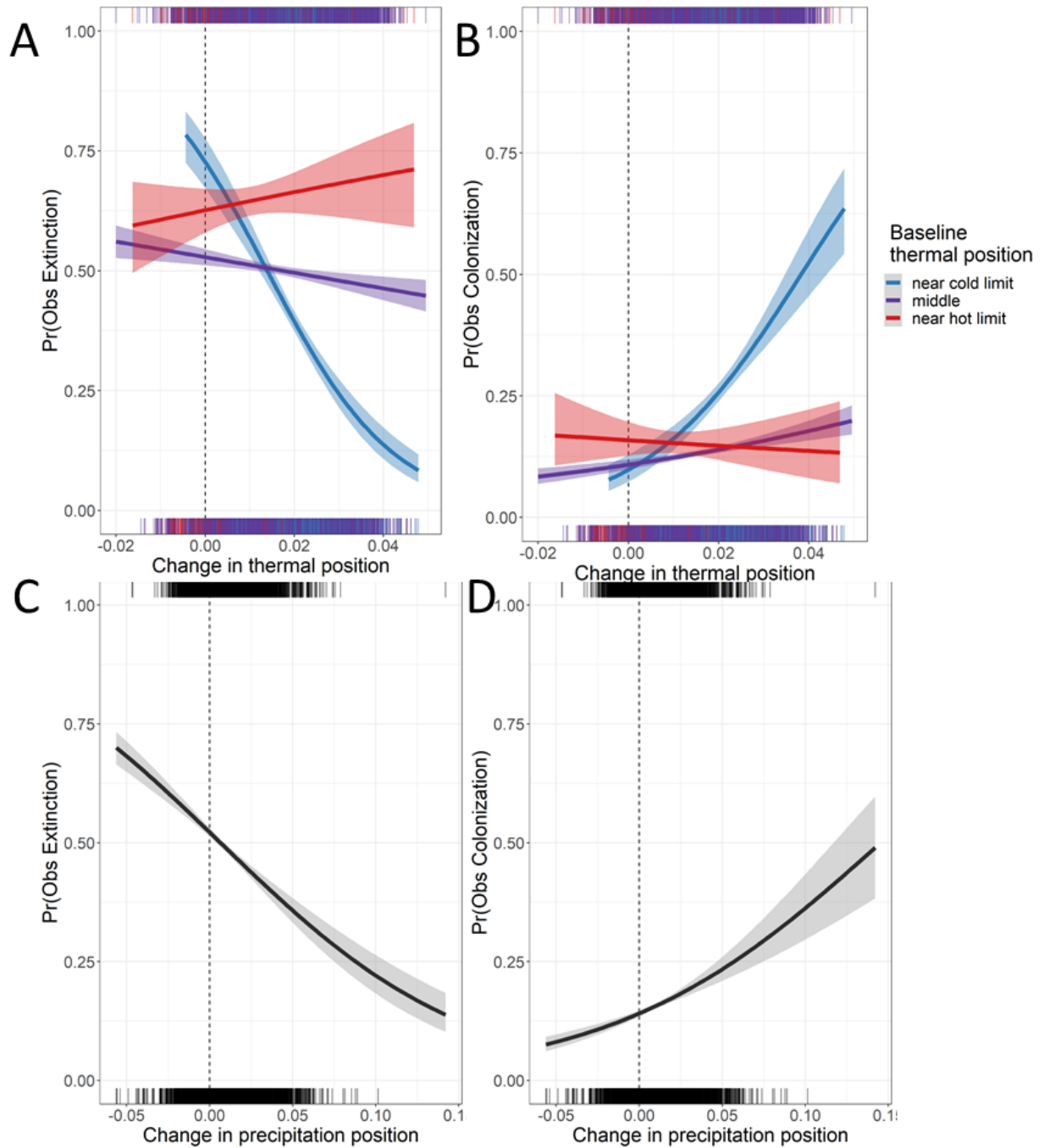


Figure S13. Probability of local extinction (A, C) and colonization (B, D) in response to change in thermal (A, B) and precipitation (C, D) position from the baseline (1901-1974) to recent period (2000-2014). Thermal and precipitation position ranges from 0 to 1, with 1 indicating conditions at a site are at a species' hot or wet limit for the entire year, and zero meaning conditions are at a species' 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 1st and 3rd quantile to show sites that were historically close to species' hot limits (red; n=969), cold limits (blue; n=2,244), and middle of their observed climatic limits (purple; n=11,793). Rug plot shows the distribution of observations. Confidence intervals ($\pm 95\%$) are shown around linear trendlines.

Table S1. Summary of unique location-year observations per period for the 66 bumblebee (*Bombus*) species in the analysis dataset.

Bumblebee species	Baseline (1900-1975)	Recent (2000-2015)
<i>affinis</i>	1386	76
<i>appositus</i>	622	178
<i>auricomus</i>	407	224
<i>barbutellus</i>	1053	494
<i>bifarius</i>	2921	644
<i>bimaculatus</i>	981	794
<i>bohemicus</i>	1957	4171
<i>borealis</i>	542	142
<i>campestris</i>	1495	1847
<i>centralis</i>	1038	344
<i>citrinus</i>	344	334
<i>cryptarum</i>	336	717
<i>distinguendus</i>	1409	1735
<i>fervidus</i>	2798	856
<i>flavifrons</i>	1078	421
<i>fraternus</i>	323	80
<i>frigidus</i>	350	195
<i>griseocollis</i>	1070	1089
<i>hortorum</i>	3856	9238
<i>humilis</i>	2006	2055
<i>huntii</i>	1252	449
<i>hypnorum</i>	2333	6214
<i>impatiens</i>	2914	1632
<i>insularis</i>	840	332
<i>jonellus</i>	1753	4162
<i>lapidarius</i>	4124	14547
<i>lucorum</i>	4646	15076
<i>magnus</i>	348	587
<i>melanopygus</i>	1242	454
<i>mendax</i>	166	111
<i>mesomelas</i>	351	447
<i>mixtus</i>	860	452
<i>monticola</i>	410	2125
<i>morrisoni</i>	858	257
<i>mucidus</i>	194	147
<i>muscorum</i>	1974	2012
<i>nevadensis</i>	517	207

<i>norvegicus</i>	165	578
<i>occidentalis</i>	3217	398
<i>pascuorum</i>	7883	22236
<i>pensylvanicus</i>	3953	443
<i>perplexus</i>	581	442
<i>pomorum</i>	483	38
<i>pratorum</i>	3928	11142
<i>pyrenaeus</i>	271	308
<i>quadricolor</i>	106	356
<i>runderarius</i>	2565	2355
<i>runderatus</i>	1731	398
<i>rufocinctus</i>	1097	435
<i>rupestris</i>	1011	2117
<i>sicheli</i>	223	332
<i>soroeensis</i>	1725	4028
<i>sporadicus</i>	188	411
<i>subterraneus</i>	1355	1522
<i>sylvarum</i>	2492	3235
<i>sylvestris</i>	1252	2598
<i>sylvicola</i>	471	310
<i>ternarius</i>	677	459
<i>terrestris</i>	4027	15206
<i>terricola</i>	1886	337
<i>vagans</i>	1191	564
<i>vandykei</i>	182	150
<i>vestalis</i>	936	2874
<i>veteranus</i>	1221	145
<i>vosnesenskii</i>	3249	410
<i>wurflenii</i>	1042	426

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Table S2. Estimated model coefficients for the five main models. Posterior means and 95% Bayesian credible intervals are shown for PGLMM models. t-values (for analysis of covariance models, ANCOVA) are included as a measure of significance. Generally, coefficients with t-values < -2 and > 2 are considered significant, these and coefficients where the 95% CI does not overlap zero are in bold text in the table. Variance explained is expressed in terms of marginal R^2 (for PGLMM) and adjusted- R^2 (for ANCOVA models).

	Occupancy (PGLMM)		Extinction (PGLMM)		Colonization (PGLMM)		Species richness (ancova)		Detection-corrected species richness (ancova)	
	Posterior mean	95% CI	Posterior mean	95% CI	Posterior mean	95% CI	Estimate (SE)	t value	Estimate (SE)	t value
Intercept	-46.29	-100.93 - 6.96	0.87	-1.53 - 3.21	-2.55	-4.75 - -0.32	-10.94 (4.26)	-2.57	-15.41 (0.52)	- 29.38
<u>Thermal position variables</u>										
Baseline (1st order polynomial)	-8.46	-10.39 - -6.33	27.38	22.31 - 32.65	-12.91	-19.85 - -6.16	-161.33 (34.39)	-4.69	-0.49 (0.43)	-1.14
Baseline (2nd order polynomial)	--	--	17.44	12.43 - 22.16	13.27	6.77 - 19.46	-62.53 (26.68)	-2.34	--	--
Change since baseline	-4.54	-6.08 - -3.01	0.29	0.23 - 0.36	-0.09	-0.17 - -0.01	-4.86 (2.92)	-1.67	-2.16 (0.55)	-3.91
Baseline:Change interaction	-10.76	-12.82 - -8.76	0.53	0.43 - 0.63	-0.43	-0.55 - -0.29	-9.74 (4.31)	-2.34	-2.77 (0.44)	0
<u>Precipitation position variables</u>										
Baseline (1st order polynomial)	-1.63	-3.04 - -0.25	-0.89	-7.39 - 6.14	-30.56	-39.56 - -21.29	-5.57 (2.09)	-2.67	-0.73 (0.44)	-1.64

Baseline (2nd order polynomial)	--	--	-2.56	-8.56 - 2.96	13.56	6.53 - 20.55	--	--	--	--
Change since baseline	3.9	2.55 - 5.13	-0.14	-0.21 - -0.09	0.21	0.13 - 0.29	-1.27 (2.47)	-0.51	0.26 (0.5)	0.53
Baseline:Change interaction	-0.11	-0.81 - 0.69	0.02	-0.02 - 0.05	-0.03	-0.08 - 0.02	-9.74 (4.31)	-2.26	0.47 (0.34)	1.38

Climatic position interactions

Baseline thermal:Baseline precipitation interaction	-0.05	-1.82 - 1.69	0.02	-0.05 - 0.1	0.12	0.03 - 0.21	--	--	-0.39 (0.39)	-1.01
Change in thermal:Change in precipitation interaction	-0.15	-1.17 - 0.85	0.02	-0.02 - 0.06	0.06	0 - 0.12	--	--	2.04 (0.39)	5.26

Covariates

Continent (Europe)	39.35	32.95 - 45.45	-1.98	-2.22 - -1.71	1.27	0.96 - 1.56	12.2 (5.13)	2.38	7.87 (1.13)	6.95
Sampling Effort	--	--	-0.59	-0.65 - -0.55	-0.17	-0.21 - -0.13	--	--	--	--

Random effects

Species	181.4	117 - 256.2	0.3	0.19 - 0.44	0.26	0.15 - 0.39	--	--
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Model summary

Number observations (n)	4617-5264	30.8-1035.5	118.5-1730.1	164	1849
Variation explained (R2)	0.11	0.87	0.53	0.38	0.07

Table S3. Model coefficients (and standard error) for the simultaneous autoregressive (SAR) error species richness models correcting for spatial autocorrelation. Z values are included as a measure of significance. Generally, coefficients with z values < -2 and > 2 are considered significant, these are in bold text in the table. Variance explained is expressed in terms of Nagelkerke pseudo-R².

	Species richness SAR		Detection-corrected species richness SAR	
	Estimate	z value	Estimate	z value
Intercept	-12.64 (11.27)	-1.12	-14.19 (1.98)	-7.16
<u>Thermal position variables</u>				
Baseline (1st order polynomial)	-107.69 (38.08)	-2.83	-0.26 (0.84)	-0.31
Baseline (2nd order polynomial)	-13.86 (25)	-0.55	--	--
Change since baseline	0.63 (3.08)	0.21	-1.95 (0.64)	-3.06
Baseline:Change interaction	1.5 (4.46)	0.34	-1.18 (0.56)	-2.11
<u>Precipitation position variables</u>				
Baseline (1st order polynomial)	0.94 (2.59)	0.36	0.12 (0.62)	0.19
Baseline (2nd order polynomial)	--	--	--	--
Change since baseline	-3.33 (2.66)	-1.25	0.32 (0.64)	0.5
Baseline:Change interaction	1.15 (1.87)	0.62	-0.04 (0.38)	-0.1
<u>Climatic position interactions</u>				
Baseline thermal:Baseline precipitation interaction	--	--	0.36 (0.55)	0.65
Change in thermal:Change in precipitation interaction	--	--	0.7 (0.43)	1.63
<u>Covariates</u>				
Continent (Europe)	14.47 (12.99)	1.11	7.1 (3.72)	1.91
<u>Model summary</u>				
Number observations (n)	164		1849	
Variation explained (R ²)	0.44		0.14	

Table S4. Estimated model coefficients for the change in occupancy, extirpation, colonization, and detection-corrected species richness models including land-use. Posterior means and 95% Bayesian credible intervals presented for PGLMM models, model coefficients (and standard error) presented for analysis of covariance (ANCOVA) and spatial autoregressive (SAR) error models. t-values (for analysis of covariance models) and z-values (for SAR error models) are included as a measure of significance. Generally, coefficients with t-values < -2 and > 2 are considered significant, these and coefficients where the 95% CI does not overlap zero are in bold text in the table. Variance explained is expressed in terms of marginal R² (for PGLMM), adjusted-R² (for ANCOVA models), and Nagelkerke pseudo-R².

	Occupancy (PGLMM)		Extinction (PGLMM)		Colonization (PGLMM)		Species richness (ANCOVA)		Detection-corrected species richness (SAR error model)	
	Posterior mean	95% CI	Posterior mean	95% CI	Posterior mean	95% CI	Estimate (SE)	t value	Estimate (SE)	z value
Intercept	-46.47	-102.49 - 10.76	0.91	-1.28 - 3.33	-2.96	-5.38 - -0.29	-15.62 (0.56)	-27.73	-14.2 (2)	-7.11
<u>Thermal position variables</u>										
Baseline (1st order polynomial)	-8.18	-10.29 - -6.18	26.77	21.01 - 31.65	-14.9	-24 - -6.14	-0.67 (0.47)	-1.43	-0.26 (0.85)	-0.31
Baseline (2nd order polynomial)	--	--	15.56	10.31 - 20.7	16.08	7.69 - 25.05	--	--	--	--
Change since baseline	-4.22	-5.75 - -2.68	0.29	0.22 - 0.34	-0.09	-0.19 - 0.01	-2.24 (0.56)	-4.01	-1.95 (0.64)	-3.06
Baseline:Change interaction	-11.06	-13.09 - -8.93	0.52	0.43 - 0.61	-0.5	-0.68 - -0.34	-2.7 (0.45)	-6	-1.18 (0.56)	-2.1
<u>Precipitation position variables</u>										

Baseline (1st order polynomial)	-2	-3.44 - -0.58	1.9	-4.63 - 7.57	-35.49	-47.78 - -23.32	-0.59 (0.46)	-1.28	0.12 (0.62)	0.19
Baseline (2nd order polynomial)	--	--	-4.05	-10.46 - 2.35	15.95	6.79 - 25.15	--	--	--	--
Change since baseline	3.78	2.46 - 5.03	-0.14	-0.2 - -0.09	0.24	0.14 - 0.34	0.25 (0.5)	0.5	0.32 (0.64)	0.5
Baseline:Change interaction	-0.02	-0.76 - 0.74	0.02	-0.02 - 0.05	-0.03	-0.08 - 0.02	0.48 (0.34)	1.4	-0.04 (0.38)	-0.1
<u>Climatic position interactions</u>										
Baseline thermal:Baseline precipitation interaction	-0.3	-2.02 - 1.4	0.04	-0.04 - 0.11	0.13	0.03 - 0.25	-0.32 (0.4)	-0.81	0.36 (0.55)	0.65
Change in thermal:Change in precipitation interaction	-0.1	-1.08 - 0.95	0.02	-0.02 - 0.06	0.07	0 - 0.14	2.01 (0.39)	5.14	0.7 (0.43)	1.63
<u>Human dominated land-use</u>										
Land-use change	-16.4	-27.33 - -6.46	0.92	0.44 - 1.39	-0.61	-1.3 - 0.15	3.72 (3.73)	1	0.11 (4.35)	0.03
<u>Covariates</u>										
Continent (Europe)	38.78	33.03 - 45.31	-1.96	-2.25 - -1.67	1.43	1 - 1.91	8.21 (1.18)	6.94	7.11 (3.74)	1.9
Sampling Effort	--	--	-0.57	-0.64 - -0.53	-0.19	-0.25 - -0.14	--	--	--	--
<u>Random effects</u>										
Species	Variance (Std.dev.) 181.6 118.1 - 256.8		Variance (Std.dev.) 0.31 0.19 - 0.43		Variance (Std.dev.) 1.32 0.14 - 3.66		--		--	
<u>Model summary</u>										
Number observations (n)	7235-7500		18.4-1464.9		57.9-1551.6		1849		1849	
Variation explained (R2)	0.11		0.87		0.27		0.07		0.14	

Table S5. Estimated model coefficients for the change in occupancy, extirpation, colonization, and detection-corrected species richness models at a 50km by 50km scale. Posterior means and 95% Bayesian credible intervals presented for PGLMM models, model coefficients (and standard error) presented for analysis of covariance (ANCOVA) and spatial autoregressive (SAR) error models. t-values (for analysis of covariance models) and z-values (for SAR error models) are included as a measure of significance. Generally, coefficients with t-values < -2 and > 2 are considered significant, these and coefficients where the 95% CI does not overlap zero are in bold text in the table. Variance explained is expressed in terms of marginal R² (for PGLMM), adjusted-R² (for ANCOVA models), and Nagelkerke pseudo-R².

	Occupancy (PGLMM)		Extinction (PGLMM)		Colonization (PGLMM)		Species richness (ANCOVA)		Detection-corrected species richness (SAR error model)	
	Posterior mean	95% CI	Posterior mean	95% CI	Posterior mean	95% CI	Estimate (SE)	t value	Estimate (SE)	z value
Intercept	-53.03	-115.76 - 10.83	1.54	-1.04 - 4.04	-2.27	-4.41 - -0.2	-21.59 (0.28)	-78.3	-21.02 (1.13)	-18.6
<u>Thermal position variables</u>										
Baseline (1st order polynomial)	-6.17	-7.65 - -4.76	32.56	27.47 - 37.66	-16.86	-23.25 - -11.77	-0.05 (0.21)	-0.23	0.5 (0.4)	1.27
Baseline (2nd order polynomial)	--	--	28.47	23.31 - 33.69	2.02	-3.6 - 7.4	--	--	--	--
Change since baseline	-3.45	-4.56 - -2.36	0.24	0.2 - 0.29	-0.21	-0.26 - -0.16	-0.83 (0.29)	-2.87	-0.63 (0.33)	-1.9
Baseline:Change interaction	-7.12	-8.45 - -5.58	0.47	0.4 - 0.53	-0.32	-0.39 - -0.24	-1.41 (0.22)	-6.29	-0.68 (0.28)	-2.38
<u>Precipitation position variables</u>										

Baseline (1st order polynomial)	-0.88	-2.02 - 0.19	0.73	-5.91 - 7.46	-23.4	-30.61 - -15.15	-0.26 (0.21)	-1.23	0.13 (0.31)	0.44
Baseline (2nd order polynomial)	--	--	-10.36	-15.67 - -5.18	13.49	6.85 - 20.92	--	--	--	--
Change since baseline	4.99	4.01 - 6.04	-0.26	-0.3 - -0.22	0.22	0.17 - 0.27	0.25 (0.24)	1.03	0.25 (0.33)	0.76
Baseline:Change interaction	-0.31	-0.97 - 0.38	0.08	0.05 - 0.11	-0.02	-0.05 - 0.02	0.3 (0.17)	1.81	-0.01 (0.19)	-0.04
<u>Climatic position interactions</u>										
Baseline thermal:Baseline precipitation interaction	0.71	-0.62 - 1.9	-0.06	-0.11 - 0	0.12	0.07 - 0.18	-0.21 (0.18)	-1.2	0.01 (0.25)	0.05
Change in thermal:Change in precipitation interaction	-0.3	-1.09 - 0.46	-0.05	-0.09 - -0.02	0.01	-0.03 - 0.05	1.04 (0.2)	5.25	0.4 (0.23)	1.79
<u>Covariates</u>										
Continent (Europe)	37.1	31.46 - 42.32	-1.87	-2.09 - -1.65	1.46	1.23 - 1.69	3.96 (0.57)	6.95	3.06 (1.97)	1.55
Sampling Effort	--	--	-0.53	-0.56 - -0.5	-0.09	-0.11 - -0.07	--	--	--	--
<u>Random effects</u>										
Species	<u>Variance (Std.dev.)</u> 238.8 160.1 - 334		<u>Variance (Std.dev.)</u> 0.37 0.23 - 0.52		<u>Variance (Std.dev.)</u> 0.25 0.16 - 0.36		--		--	
<u>Model summary</u>										
Number observations (n)	5000-5490		40.3-5608		58.8-2410.7		4856		4856	
Variation explained (R2)	0.1		0.84		0.61		0.03		0.06	

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Table S6. Estimated model coefficients for the change in occupancy, extirpation, colonization, and detection-corrected species richness models at a 200km by 200km scale. Posterior means and 95% Bayesian credible intervals presented for PGLMM models, model coefficients (and standard error) presented for analysis of covariance (ANCOVA) and spatial autoregressive (SAR) error models. t-values (for analysis of covariance models) and z-values (for SAR error models) are included as a measure of significance. Generally, coefficients with t-values < -2 and > 2 are considered significant, these and coefficients where the 95% CI does not overlap zero are in bold text in the table. Variance explained is expressed in terms of marginal R2 (for PGLMM), adjusted-R2 (for ANCOVA models), and Nagelkerke pseudo-R2.

	Occupancy (PGLMM)		Extinction (PGLMM)		Colonization (PGLMM)		Species richness (ANCOVA)		Detection-corrected species richness (SAR error model)	
	Posterior mean	95% CI	Posterior mean	95% CI	Posterior mean	95% CI	Estimate (SE)	t value	Estimate (SE)	z value
Intercept	-36.36	-85.99 - 13.45	0.07	-2.85 - 2.79	-4.64	-12.08 - -0.63	5.23 (1.16)	4.52	6.75 (2.88)	2.35
<u>Thermal position variables</u>										
Baseline (1st order polynomial)	-6.14	-9.06 - -3.06	13.46	6.36 - 21.36	-11.78	-33.65 - 1.39	1.46 (0.99)	1.47	-0.9 (1.66)	-0.54
Baseline (2nd order polynomial)	--	--	12.3	5.42 - 19.56	35.46	15.18 - 81.11	--	--	--	--
Change since baseline	-3.08	-5.23 - -1.06	0.22	0.09 - 0.37	0.1	-0.13 - 0.42	-0.69 (1.18)	-0.58	-1.88 (1.26)	-1.5
Baseline:Change interaction	-9.96	-12.87 - -6.94	0.54	0.33 - 0.81	-0.47	-1.16 - -0.08	-5.5 (0.99)	-5.55	-2.97 (1.11)	-2.69
<u>Precipitation position variables</u>										

Baseline (1st order polynomial)	-2.89	-4.89 - -0.91	0.07	-7.03 - 7.34	-37.24	-83.9 - -14.07	-1.04 (1.05)	-0.99	0.31 (1.26)	0.24
Baseline (2nd order polynomial)	--	--	3.68	-4.3 - 11.65	11.72	-6.28 - 38.02	--	--	--	--
Change since baseline	4.33	2.59 - 6.08	-0.13	-0.25 - -0.02	0.49	0.17 - 1.15	0.26 (1.16)	0.23	0.48 (1.33)	0.36
Baseline:Change interaction	0.26	-0.72 - 1.16	-0.05	-0.12 - 0.02	-0.12	-0.34 - 0.03	0.77 (0.94)	0.83	0.48 (0.99)	0.49
<u>Climatic position interactions</u>										
Baseline thermal:Baseline precipitation interaction	1.07	-1.54 - 3.83	0.05	-0.07 - 0.2	0.28	-0.01 - 0.74	1.1 (0.89)	1.23	1.28 (1.09)	1.18
Change in thermal:Change in precipitation interaction	0.57	-0.88 - 1.92	0.02	-0.06 - 0.09	0.25	0.05 - 0.59	2.42 (0.9)	2.68	1.2 (0.93)	1.29
<u>Covariates</u>										
Continent (Europe)	38.47	31 - 45.34	-2.13	-3.18 - -1.46	1.55	0.55 - 3.55	-1.5 (2.52)	-0.6	-0.52 (5.76)	-0.09
Sampling Effort	--	--	-0.72	-0.93 - -0.54	-0.34	-0.79 - -0.14	--	--	--	--
<u>Random effects</u>										
Species	Variance (Std.dev.) 133.8 75.62 - 193.4		Variance (Std.dev.) 0.41 0.16 - 0.82		Variance (Std.dev.) 0.66 0.09 - 2.47		--		--	
<u>Model summary</u>										
Number observations (n)	4181-5284		10.5-1428.2		6.5-382.6		584		584	
Variation explained (R2)	0.1		0.71		0.14		0.08		0.19	

Table S7. Estimated model coefficients for the change in occupancy, extirpation, colonization, and detection-corrected species richness models using an absence threshold of three. Posterior means and 95% Bayesian credible intervals presented for PGLMM models, model coefficients (and standard error) presented for analysis of covariance (ANCOVA) and spatial autoregressive (SAR) error models. t-values (for analysis of covariance models) and z-values (for SAR error models) are included as a measure of significance. Generally, coefficients with t-values < -2 and > 2 are considered significant, these and coefficients where the 95% CI does not overlap zero are in bold text in the table. Variance explained is expressed in terms of marginal R² (for PGLMM), adjusted-R² (for ANCOVA models), and Nagelkerke pseudo-R².

	Occupancy (PGLMM)		Extinction (PGLMM)		Colonization (PGLMM)		Species richness (ANCOVA)		Detection-corrected species richness (SAR error model)	
	Posterior mean	95% CI	Posterior mean	95% CI	Posterior mean	95% CI	Estimate (SE)	t value	Estimate (SE)	z value
Intercept	-45.15	-102.49 - 11.21	0.89	-1.41 - 3.21	-2.52	-4.73 - -0.33	-15.36 (0.74)	-20.69	-14.85 (1.47)	-10.09
<u>Thermal position variables</u>										
Baseline (1st order polynomial)	-5.4	-7.18 - -3.58	20.67	15.2 - 25.93	-7.69	-14.72 - -0.65	-0.08 (0.56)	-0.15	0.52 (0.72)	0.72
Baseline (2nd order polynomial)	--	--	13.85	9.03 - 19.04	14.45	8.32 - 20.34	--	--	--	--
Change since baseline	-3.69	-5.23 - -2.17	0.27	0.21 - 0.34	-0.05	-0.14 - 0.03	-2.85 (0.78)	-3.66	-3.12 (0.8)	-3.88
Baseline:Change interaction	-9.51	-11.24 - -7.75	0.44	0.35 - 0.52	-0.36	-0.47 - -0.26	-3.97 (0.59)	-6.71	-2.94 (0.66)	-4.46
<u>Precipitation position variables</u>										

Baseline (1st order polynomial)	-1.93	-3.34 - -0.5	0.63	-6 - 6.94	-33.81	-42.7 - -25.37	-1 (0.58)	-1.74	-0.61 (0.67)	-0.91
Baseline (2nd order polynomial)	--	--	-5.52	-11.5 - 0.4	15.51	8.38 - 22.84	--	--	--	--
Change since baseline	4.63	3.21 - 6.01	-0.19	-0.25 - -0.13	0.25	0.16 - 0.33	0.4 (0.65)	0.61	1.11 (0.76)	1.46
Baseline:Change interaction	-0.25	-1.05 - 0.55	0.04	0 - 0.08	-0.04	-0.08 - 0.01	0.39 (0.44)	0.9	0.06 (0.46)	0.13
<u>Climatic position interactions</u>										
Baseline thermal:Baseline precipitation interaction	0.13	-1.41 - 1.58	0.01	-0.06 - 0.08	0.11	0.03 - 0.18	-0.36 (0.46)	-0.78	-0.19 (0.54)	-0.35
Change in thermal:Change in precipitation interaction	-0.24	-1.29 - 0.84	0.02	-0.02 - 0.07	0.05	-0.01 - 0.11	2.29 (0.52)	4.42	1.63 (0.54)	3.04
<u>Covariates</u>										
Continent (Europe)	38.03	31.62 - 44.05	-1.99	-2.29 - -1.7	1.26	0.93 - 1.59	9.48 (1.51)	6.29	10.17 (2.63)	3.87
Sampling Effort	--	--	-0.56	-0.62 - -0.51	-0.17	-0.21 - -0.13	--	--	--	--
<u>Random effects</u>										
Species	<u>Variance (Std.dev.)</u>		<u>Variance (Std.dev.)</u>		<u>Variance (Std.dev.)</u>					
	185.1	115.6 - 256	0.3	0.18 - 0.43	0.27	0.16 - 0.4	--	--	--	--
<u>Model summary</u>										
Number observations (n)	4596-5481		69.4-2453.7		201.6-4627.8		1374		1374	
Variation explained (R2)	0.1		0.85		0.56		0.09		0.1	

Table S8. Estimated model coefficients for the change in occupancy, extirpation, colonization, and detection-corrected species richness models using an absence threshold of five. Posterior means and 95% Bayesian credible intervals presented for PGLMM models, model coefficients (and standard error) presented for analysis of covariance (ANCOVA) and spatial autoregressive (SAR) error models. t-values (for analysis of covariance models) and z-values (for SAR error models) are included as a measure of significance. Generally, coefficients with t-values < -2 and > 2 are considered significant, these and coefficients where the 95% CI does not overlap zero are in bold text in the table. Variance explained is expressed in terms of marginal R² (for PGLMM), adjusted-R² (for ANCOVA models), and Nagelkerke pseudo-R².

	Occupancy (PGLMM)		Extinction (PGLMM)		Colonization (PGLMM)		Species richness (ANCOVA)		Detection-corrected species richness (SAR error model)	
	Posterior mean	95% CI	Posterior mean	95% CI	Posterior mean	95% CI	Estimate (SE)	t value	Estimate (SE)	z value
Intercept	-43.16	-96.07 - 13.89	0.8	-1.56 - 2.98	-2.56	-4.88 - -0.25	-14.76 (0.91)	-16.27	-13.73 (2.16)	-6.34
<u>Thermal position variables</u>										
Baseline (1st order polynomial)	-3.81	-5.57 - -2.12	17	11.13 - 22.42	-4.41	-11.67 - 2.67	0.37 (0.65)	0.58	1.4 (1.01)	1.39
Baseline (2nd order polynomial)	--	--	12.82	6.57 - 17.84	14.83	8.72 - 21.08	-2.96 (0.92)	--	-2.37 (1.06)	--
Change since baseline	-3.47	-5.05 - -1.9	0.25	0.19 - 0.31	-0.07	-0.15 - 0.02	-4.66 (0.66)	-3.21	-2.43 (0.83)	-2.24
Baseline:Change interaction	-9.07	-10.73 - -7.5	0.42	0.34 - 0.5	-0.32	-0.42 - -0.22		-7.05		-2.92
<u>Precipitation position variables</u>										

Baseline (1st order polynomial)	-1.99	-3.47 - -0.59	-0.14	-6.21 - 6.16	-36.96	-45.96 - -28.29	-0.94 (0.65)	-1.45	-0.04 (0.87)	-0.05
Baseline (2nd order polynomial)	--	--	-7.41	-12.94 - -1.84	16.85	9.68 - 23.69	-- 0.62 (0.76)	--	-- 0.73 (0.98)	-- 0.74
Change since baseline	4.7	3.39 - 6.19	-0.19	-0.26 - -0.11	0.26	0.18 - 0.35	0.37 (0.49)	0.82	-0.38 (0.53)	-0.72
Baseline:Change interaction	-0.16	-1.03 - 0.65	0.03	-0.01 - 0.07	-0.03	-0.08 - 0.02		0.75		
<u>Climatic position interactions</u>										
Baseline thermal:Baseline precipitation interaction	0.31	-1.11 - 1.65	-0.02	-0.07 - 0.04	0.08	0.02 - 0.16	-0.17 (0.51)	-0.34	0.17 (0.69)	0.25
Change in thermal:Change in precipitation interaction	-0.66	-1.75 - 0.38	0.05	-0.01 - 0.1	0.04	-0.02 - 0.11	2.16 (0.61)	3.56	0.74 (0.69)	1.07
<u>Covariates</u>										
Continent (Europe)	38.09	31.68 - 44.28	-1.97	-2.27 - -1.67	1.34	0.99 - 1.67	9.44 (1.74)	5.42	8.44 (3.63)	2.32
Sampling Effort	--	--	-0.54	-0.6 - -0.48	-0.17	-0.21 - -0.13	--	--	--	--
<u>Random effects</u>										
Species	Variance (Std.dev.) 185.9 120.9 - 265.9		Variance (Std.dev.) 0.3 0.18 - 0.43		Variance (Std.dev.) 0.31 0.17 - 0.46		--		--	
<u>Model summary</u>										
Number observations (n)	5000-5324		25.3-2121.9		175.4-3736.8		1133		1133	
Variation explained (R2)	0.1		0.86		0.53		0.1		0.18	

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