

1 **Title:** Climate change contributes to widespread declines among bumblebees across continents

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8 **Abstract (120 words):** Climate change could increase species extinction risk as temperatures
9 and precipitation begin to exceed species' historically-observed tolerances. Using long-term data
10 for 66 bumblebee species across North America and Europe, we tested whether this mechanism
11 altered likelihoods of bumblebee species' extinction or colonization. Increasing frequency of
12 hotter temperatures predicts species' local extinction risk, chances of colonizing a new area, and
13 changing species richness. Effects are independent of changing land uses. The method developed
14 here permits spatially explicit predictions of climate change-related population extinction-
15 colonization dynamics within species that explains observed patterns of geographical range loss
16 and expansion across continents. Increasing frequencies of temperatures that exceed historically-
17 observed tolerances helps explain widespread bumblebee species decline. This mechanism may
18 contribute to biodiversity loss more generally.

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

21 **Main Text:**

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

30 While many mechanisms could alter how species fare as climate changes, discovering
31 processes that strongly affect species persistence remains among the foremost challenges in
32 conservation (5). Climate change could pose risks to species in part by increasing the frequency
33 of environmental conditions that exceed species' tolerances, causing population decline and
34 potentially extirpation (6, 7). Conversely, climate change may render marginal areas more
35 suitable for a species, making colonization of that locale more likely (1). Understanding and
36 predicting spatially explicit colonization and extinction likelihood could identify which species
37 are vulnerable to climate change and where, which species may benefit, and suggest
38 interventions to mitigate conservation risks. Colonization and extinction dynamics, in
39 combination across a regional species assemblage, determine how species richness changes.
40 Among taxa that contribute critically to ecosystem service provision, including pollinators such
41 as bumblebees (*Bombus*), species richness decline could impair ecosystem services (8).

42 We evaluated changes in bumblebee species occupancy and regional richness across North
43 America and Europe using a database of ~550,000 georeferenced occurrence records of 66
44 bumblebee species (Figure S1 and S2, Table S1; (1, 9)). We estimated species' distributions in

45 100 km by 100 km quadrats in a baseline (1901-1974) and recent period (2000-2014) (9).
46 Climate across Europe and North America has changed significantly between these time periods
47 (Figure S3). While the baseline period was substantially longer, there were 49% more records in
48 the recent period. Non-detection bias (i.e. difficulty distinguishing among true and false absences
49 due to imperfect detection) in opportunistic occurrence records can reduce measurement
50 accuracy of species distributions and overall richness (10). Consequently, we used detection-
51 corrected occupancy models to estimate probability of occurrence for each species in quadrats
52 within each time period (9). We calculated changes in species' probabilities of occupancy and
53 generated detection-corrected estimates of species richness change between periods (Figure S4).

54 We predict greater declines in bumblebee species occupancy and species richness where
55 changing climatic conditions more frequently exceed individual species' historically-observed
56 tolerances. Conversely, we predict greater occupancy and species richness in areas where climate
57 changes more frequently cause local weather to fall within species' historically-observed
58 tolerances. Temperature and precipitation can affect bumblebee mortality and fecundity directly
59 (e.g. (11)) and indirectly through changes to floral resources (12). For both periods, we
60 calculated proximity of climatic conditions within quadrats across these continents to estimated
61 thermal and precipitation limits of all 66 species. We averaged monthly temperatures and total
62 precipitation in localities where species were observed, and rescaled these measures relative to
63 each species' historically-observed climatic limits. Those limits were calculated from averages of
64 the five highest monthly maximum and lowest monthly minimum temperatures, or five highest
65 and lowest monthly total precipitation values, from among values for all location-year
66 combinations where that species was observed during the baseline. Although climate limits
67 inferred from observed distributions might not always identify actual physiological tolerances,

68 they can suggest such limits and can prove useful in the absence of more mechanistic data (1).
69 We calculated local changes in this new climatic position index between baseline and recent time
70 periods, and also averaged it across all species present per quadrat to calculate community-
71 averaged climatic position index (Figures 1 and S5).

72 Our measurements of bumblebee species occupancy over time provide evidence of rapid and
73 widespread declines across Europe and North America. Probability of site occupancy declined
74 on average by 46% ($\pm 3.3\%$ SE) in North America and 17% ($\pm 4.9\%$ SE) in Europe relative to the
75 baseline period (Figure 2). Declines were robust to detection-correction methods used (Figures
76 S6A and S7) and consistent with reductions in detection-corrected species richness (Figure S6B)
77 (9).

78 Declines among bumblebee species relate to the frequency and extent to which climatic
79 conditions approach or exceed species' historically observed climatic limits, particularly for
80 temperature. We modelled change in probability of site occupancy with phylogenetic generalized
81 linear mixed models using thermal position variables (baseline, change since baseline, and the
82 interaction between these), precipitation position variables (baseline, change since baseline, and
83 the interaction between these), the interaction between baseline thermal and precipitation
84 position terms, and the interaction between change in thermal position and change in
85 precipitation position. We controlled for continent (9). The models support our predictions:
86 probability of occupancy decreases when temperatures rise above species' upper thermal limits
87 (Figures 3A, S8A; Table S2), while warming in regions that were previously near species' cold
88 limits is associated with increasing occupancy. Evidence for precipitation influencing site
89 occupancy was mixed but declines were more likely in sites that became drier (Figures 3B, S8B;
90 Table S2). Our model's capacity to predict change in occupancy (marginal $R^2 = 0.11$) was

91 comparable to the predictive ability of other macroecological models of the biological impacts of
92 climate change (2), but models predicted extirpation and colonization more capably (marginal R^2
93 = 0.53-0.87 (9)). While there was weak evidence for a phylogenetic signal in the response of
94 occupancy (Pagel's $\lambda = 0.12$), modelling extirpation and colonization separately yields a stronger
95 signal (9). Results were robust to detection correction method for measuring species' presences
96 within quadrats, across spatial scales of analysis, and through a range of thresholds for inferring
97 absences from occurrence data (9).

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

107 Projections suggest that recent climate change has driven stronger and more widespread
108 bumblebee declines than have previously been reported, especially in Europe (Figure 4).
109 European estimates of observed richness rely particularly on observations from well-sampled
110 regions that were cooler in the baseline period and that have experienced less warming
111 subsequently (9), which may have contributed to underestimation of recent species richness
112 decline across that continent (Figures S6B, S9, S10). These findings contrast with those for other

113 taxa that predict widespread range expansions and increasing species richness toward warming
114 environments in the north (13, 14).

115 Changes in climatic position index predict biologically significant changes in bumblebee
116 presence, colonization, extirpation, and richness across two continents. Species-specific changes
117 in climatic position predict bumblebee diversity change as well as or better than using mean,
118 maximum, or minimum temperature or precipitation measures (models using climatic position
119 index: marginal R^2 2.6% lower to 23% higher, change in Deviance Information Criterion = 98.7-
120 241.9; (9)). Including land-use change in the models revealed a significant negative effect but did
121 not influence results for climatic position variables (Table S4) (9). At this scale, effects of
122 climate change on bumblebees appear distinct from effects of land-use. Other anthropogenic
123 changes, such as agricultural intensification, pesticide use, and pathogens can also affect
124 occupancy and extirpation risk of bumblebees (15–17). Interactions between these factors are
125 expected to accelerate biodiversity loss for bumblebees and other taxa over broad areas (18, 19).
126 Understanding how interactions between climate and land use changes alter extinction risk is
127 vital to conservation of pollinator species.

128 Climate is expected to warm rapidly in the future (20). Using a spatially explicit method of
129 measuring climatic position and its change over time, we show that risks of bumblebee
130 extirpation rise in areas where local temperatures more frequently exceed species' historical
131 tolerances, while colonization probabilities in other areas rise as climate changes cause
132 conditions to more frequently fall within species' thermal limits. Nevertheless, overall rates of
133 climate change-related extirpation among species greatly exceed those of colonization,
134 contributing to pronounced bumblebee species declines across both Europe and North America
135 with unknown consequences for the provision of ecosystem services. Mitigating climate change-

136 driven extinction risk among bumblebees requires efforts to manage habitats to reduce exposure
137 to growing frequency of temperatures that are extreme relative to species' historical tolerances.

138

139 **Notes and References:**

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284

285 **Acknowledgements**

286 The authors thank all data contributors for contributions to knowledge of bumblebee
287 distributions, especially Alana Pindar, Paul Galpern, Laurence Packer, Simon G. Potts, Stuart M.
288 Roberts, Pierre Rasmont, Oliver Schweiger, Sheila R. Colla, Leif L. Richardson, David L.
289 Wagner, Lawrence F. Gall, Derek S. Sikes, and Alberto Pantoja. See Supplemental for a full list
290 of contributors. **Funding:** J.T.K. is grateful for Discovery Grant and Discovery Accelerator
291 Supplement from the Natural Sciences and Engineering Research Council of Canada (NSERC),
292 and funds from his University Research Chair in Macroecology & Conservation at University of
293 Ottawa. J.T.K. is also supported through infrastructure funds from Canada Foundation for
294 Innovation. This collaboration was funded by a Royal Society grant to T.N. and J.T.K., and an
295 NSERC Postgraduate Scholarship award to P.S. to work with J.T.K. T.N. was supported by a
296 Royal Society University Research Fellowship and a grant from the UK Natural Environment

297 Research Council (NE/R010811/1). **Author contributions:** P.S., T.N., and J.T.K. created
298 techniques and designed the research. P.S. conducted analyses and with J.T.K. wrote the
299 manuscript. All authors contributed to editing manuscripts. **Competing interests:** None
300 declared. **Data and materials availability:** Bumblebee observations, gridded environmental
301 observations, and R scripts used to process data and generate all results are freely available
302 through figshare (DOI: 10.6084/m9.figshare.9956471).

303

304 **Supplementary Materials**

305 Materials and Methods

306 Supplementary Text

307 Supplementary Acknowledgements

308 Figures S1-S13

309 Tables S1-S8

310 References (21 - 58)

311

312 **Figure Legends**

313 **Figure 1. Change in community-averaged thermal (A) and precipitation position (B) from**
314 **the baseline (1901-1974) to the recent period (2000-2015).** Increases indicate warmer or wetter
315 regions and that on average, species in that assemblage are closer to their hot/wet limits than
316 historically. Declines indicate cooling or drying regions and that on average, species in that
317 assemblage are closer to their cold/wet limits than historically.

318

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

321

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

324 Thermal and precipitation position ranges from 0 to 1, with 1 indicating conditions at a site are at
325 a species' hot or wet limit for the entire year, and zero meaning conditions are at a species' cold
326 or dry limit for the entire year during the historic period. For ease of visualizing the significant
327 interaction between baseline thermal position and change in thermal position, the continuous
328 baseline thermal position variable has been split at the 1st and 3rd quantile to show sites that were
329 historically close to species' hot limits (red; n=969), cold limits (blue; n=2,244), and middle of
330 their observed climatic limits (purple; n=11,793). Rug plot shows the distribution of
331 observations. Confidence intervals ($\pm 95\%$) are shown around linear trendlines.

332

333 **Figure 4. Climate change-related change in bumblebee species richness from a baseline**
334 **(1901-1974) to a recent period (2000-2014).** Predictions from a model predicting percent
335 change in detection-corrected bumblebee species richness as a function of mean community-
336 averaged thermal and precipitation position.

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Science



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Supplementary Materials for

Climate change contributes to widespread declines among bumblebees across continents
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This PDF file includes:

- Materials and Methods
- Supplementary Text
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- References (21 - 58)

360 **Materials and Methods**

361 Bumblebee observations, observed distribution, and species richness

362 We used a dataset comprising 557,622 observations of 66 bumblebee (*Bombus*) species from
363 1901-2015, from across North America and Europe. The dataset has been previously used in (1),
364 and contains data assembled from a variety of sources including (21–24), and other sources
365 acknowledged in the Supplementary Acknowledgements. To produce this database from the
366 assembled set of records, potentially unreliable records (including incomplete species, locality,
367 and sampling year information, or disagreement between record georeferencing and stated
368 country of origin) were flagged and removed. We assumed that records in the ocean less than
369 2500m from a high-resolution coastline were coastal observations with spatially-imprecise
370 georeferences and reassigned these to the nearest point on land. Approximately 6% of the
371 records obtained from GBIF lacked latitude-longitude coordinates for collection localities. For
372 these records, we obtained georeferencing data from a digital gazetteer, GeoNames
373 (<http://geonames.org>; Creative Commons Attribution 3.0 License). Among these records, we
374 retained those located near populated places for which reliable geographic coordinates were
375 available.

376 Of the 119 species present in the originally assembled data within our study area, we retained
377 66, which had at least 100 spatially unique records in the baseline period (1901-1974;
378 inclusively) and at least 30 in the recent period (2000-2014; inclusively). These 66 species
379 appeared well sampled across their ranges, including at range margins. The dataset included
380 264,494 observations of 36 North American species and 293,128 observations of 36 European
381 species, spread across 116,254 unique location-years (i.e. spatiotemporally unique observations;
382 Figure S1). The mean and median species-period sample size was 1887 and 848 unique location-

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

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

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

416 We combined the presence maps of the 66 species to build a map of regional species richness
417 for each period (Figure S10). Variation in sampling effort can bias the estimation of observed
418 biodiversity trends (25, 26), so we excluded quadrats without a minimum of 50 unique location-
419 year observations in the baseline and most recent period. This resulted in 40 North American and
420 124 European sites, within which we calculated the percent change in species richness from the
421 baseline to the most recent period. While the strict selection protocol limits the number of
422 quadrats in our species richness analysis, a less strict selection (e.g. including quadrats without a
423 minimum of 50 unique location-years observations) fails to account for sampling bias and
424 removes our ability to attribute changes in richness to any climatic variables. All data were
425 organized in R 3.4.1 (27) using packages *tidyverse* (28) and *raster* (29).

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

429 planning. To test the effect of spatial scale on our results, we repeated analyses at a i) 50km by
430 50km scale and ii) 200km by 200km scale.

431 Occupancy models

432 To correct for imperfect detection in our dataset of bumblebee observations, we used single-
433 species occupancy models to estimate occupancy for the 66 species in each period. These models
434 account for the possibility of false-absences within detection/non-detection data by explicitly
435 estimating detection probability (p) separately from probability of occurrence (30–34).
436 Estimating detection probability for a species during a period requires multiple “survey units” or
437 “visits” to sites within that period. We split each of our time periods into three “survey units”
438 (baseline: 1901-1924, 1925-1949, and 1950-1974; recent: 2000-2004, 2005-2009, and 2010-
439 2014). We used observations of a species during a survey unit to inform detection, and absence
440 of a species when others were seen as a non-detection. It is possible that there are biases in the
441 species sampled within our dataset. Bumblebees are a charismatic insect species that have been
442 collected by researchers and independent naturalists for hundreds of years, but, as with any
443 taxon, it is possible that agriculturally important species (e.g. *B. terrestris* and *B. impatiens*),
444 common species, and larger or more recognizable species have greater likelihoods of detection.
445 We used total number of records to help inform species-specific detection probabilities in our
446 occupancy models to account for sampling bias. Unfortunately, reliable inter- and intra-specific
447 data on other traits that may influence detection probability, such as body size, are not available
448 for all species to include in our models. A necessary assumption of occupancy modelling is that
449 there is no change in occupancy (or species turnover) within a survey period or between survey
450 units within the same period: the closure assumption (35). Estimates of site occupancy rely on
451 this assumption to calculate a probability of detection from the pattern of detection/non-

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

466 Occupancy models were fit using the Bayesian general-purpose modelling software JAGS
467 (38), with R v3.4.1 (27) and package *R2jags* (39). Each species- and season-specific model
468 computed season- and site-specific occupancy, using season-specific sampling effort (i.e. the
469 total number of unique location-year observations of any species in a cell) as a covariate for the
470 underlying detection process. We used noninformative Bayesian priors for all parameters and
471 each model ran three Markov chains for 100k iterations, discarding the first 50k as a burn-in and
472 thinning by 10, resulting in 5000 samples from the joint posterior distribution. We ran models
473 until values of the Brooks-Gelman-Rubin statistic suggested convergence had been reached
474 (<1.1) for all parameters (40). The JAGS code specifying our model, including the priors used, is

475 available with the rest of the data and materials (available on figshare DOI:
476 10.6084/m9.figshare.9956471).

477 Climatic position variables

478 For each of the 66 bumblebee species, we extracted the average of the five highest monthly
479 maximum and five lowest monthly minimum temperatures from among the values for all
480 location and year combinations within the species' geographic range in the baseline period
481 (1901-1975). These maximum and minimum temperatures were assumed to represent the
482 thermal limits for the species, and previous studies have found that this measure is robust to both
483 variation in the number of records used to calculate it and variation in species sampling effort
484 (*I*). Maximum and minimum precipitation limits were extracted from the five highest and five
485 lowest monthly total precipitation values from among all location and year combinations within
486 the species' geographic range in the baseline period. Climatic limits were rescaled for each
487 species to equal 0 for the lower climatic (i.e. cold/dry) limit and 1 for the upper climatic (i.e.
488 warm/wet) limit. While these derived environmental limits may not represent the actual critical
489 limits that a species can tolerate, they offer an indication of the species' environmental tolerances
490 and measuring the change in the environment relative to these derived limits enables tests of our
491 main hypotheses.

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

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

503 To calculate the community-averaged estimates of climatic position, we clipped each species'
504 thermal and precipitation position maps to their observed distribution in the baseline period, and
505 then overlapped all the position maps, averaging all index values in a given cell. This shows the
506 mean thermal or precipitation position for the entire estimated assemblage of species in that
507 region (Figure S5). We did this for both periods, and then measured the change from the baseline
508 to recent (Figure 1).

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

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

520 Statistical analyses

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

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

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

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

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

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

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

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

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

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

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

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

611 each period, the occupancy models estimate a probability of 1 (or very close) for cells where the
612 species was detected in any one of the survey units, and they estimate some probability between
613 0 and 1 for cells where a species was never detected. This latter occupancy probability depends
614 on the species-period-specific detection probability and the total sampling effort in that cell. For
615 most species the occupancy probability of cells where they were not detected is between 0 and
616 0.4. As detection probability and sampling effort vary by period, the same cell can have a
617 different occupancy estimate in the baseline and recent period, even when the species was never
618 observed there or when it has persisted through both periods. This between-period variation
619 reflects the uncertainty within estimates of occupancy probability during a period, and likely
620 drives the lower adjusted R^2 values we see when comparing the detection-corrected and observed
621 species richness models. A similar reasoning likely explains the differences between marginal R^2
622 of change in occupancy models (0.11) compared to extinction and colonization models (0.87 and
623 0.53, respectively).

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

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

635 Spatial projection across recent period

636 Using the detection-corrected species richness model (adjusted $R^2 = 0.14$) and 0.5-degree
637 resolution climate data (41), we spatially projected the predicted change in species richness since
638 the baseline across the entire study area (Figure 4). We also projected change using the non-
639 detection-corrected species richness model (adjusted $R^2 = 0.44$; Figure S9). We used rescaled
640 climatic position and climatic position change layers at 0.5×0.5 degree grid resolution and used
641 the respective model coefficients to predict what percent climate-change-induced change in
642 assemblage richness occurred from the baseline period (1901-1974) to the recent period (2000-
643 2014).

644 Effects of land-use change

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

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

660

661 **Supplemental Text**

662 Non-detection corrected declines

663 *Occupancy, extirpation, and colonization.* Consistent with measured declines in occupancy
664 (Figure 2), observed distributions declined on average by 54% ($\pm 3.4\%$ SE) in North America and
665 18% ($\pm 7.2\%$ SE) in Europe relative to the baseline period (Figure S6A).

666 Rates of observed extirpation and colonization were calculated for each species as the
667 proportion of extirpation or colonization events relative to the total number of cells occupied
668 historically. Across all species in North America and Europe there was a 72% ($\pm 2.2\%$ SE) and
669 49% ($\pm 2.8\%$ SE) chance, respectively, that a given bumblebee species was lost from a quadrat it
670 occupied historically. Globally, extirpation events were 8 times (± 1.7 SE) more likely than
671 colonization events, with ratios being higher in North America (Figure S7). Imperfect species
672 detection and patchy sampling mean that extirpation can be overestimated in opportunistic
673 datasets, so observed extirpation rates likely represent the upper bound of true extinction
674 probability.

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

680 Response of change in occupancy to precipitation position

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

691 Response of extirpation and colonization to climatic position

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

697 interaction (Table S2). Increasing thermal position was linked to greater probability of
698 extirpation for species in regions that were already near their upper thermal limit, and lower
699 probability of extirpation for species in regions historically closer to their cold limits (Figure
700 S13A). As with occupancy, precipitation position showed more ambiguous associations. While
701 sites that became drier had higher probability of extirpation, the effect of baseline precipitation
702 was not significant and there was no significant interaction between these two effects (Figure
703 S13C). Our model explained most of the variation in the response of extirpation to climatic
704 position (marginal $R^2 = 0.87$). The strong relationship between temperature warming and
705 extirpation risk among bumblebee species is consistent with previous work demonstrating that
706 extinction risk depends on shifts in the spatial distributions of thermal niches in other taxa (53,
707 54) and is of particular importance since bumblebee species are being pushed towards their upper
708 thermal limits across most of North America and Europe (Figure 1A).

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

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

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

735 Comparing climatic position models to mean climate variables

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

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

752 Climatic sampling across continents

753 We tested whether the most well-sampled quadrats in our analysis (which were used for the
754 non-detection-corrected species richness analysis) presented a representative sample of historic
755 climate and climatic patterns across North America and Europe, and found that well-sampled
756 regions in European tended to be cooler in the baseline and experience less warming between
757 periods (Welch's two-sample t-test results: t-statistics = 2.72 and 4.16, p-values = 7.0×10^{-3} and
758 4.8×10^{-5} , df = 227 and 206, respectively). Previous estimates of European bumblebee richness
759 change extrapolating from well-sampled areas may have systematically underestimated recent
760 richness declines. Well-sampled quadrats in North America appeared representative of the
761 general temperature trends experienced over the continent as a whole, but tended to be
762 historically wetter and have gotten wetter than the continental average (Welch's two-sample t-
763 test results: t-statistics = 2.95 and 2.30, p-values = 5.1×10^{-3} and 0.03, df = 41.5 and 40.2,
764 respectively).

765 Land-use change

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

772 We did not find any statistically significant relationship between percent of species'
773 geographical range covered by cropland and unique location-year observations (t-value= -0.79,
774 p-value= 0.43, d.f.= 64), mean change in probability of occupancy (t-value= 0.07, p-value= 0.94,
775 d.f.= 64), or mean change in observed distribution (t-value= 1.24, p-value= 0.22, d.f.= 64). It
776 appears that rates of species decline do not appear to strongly differ between species more
777 associated with agricultural areas, although we note that our subset of well-sampled species is
778 likely already biased toward species more associated with agricultural and urban areas. This is
779 consistent with previous work that concluded latitudinal range shifts in bumblebees appeared
780 strongly sensitive to climate change but not especially sensitive to agriculture (1).

781 Additional tests of modelling robustness

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

789 change. Repeating analyses in 50km by 50km cells and 200km by 200km cells produced results
790 that were qualitatively similar (Tables S5 and S6), suggesting our analyses were robust to the
791 scale used.

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

799

800

801

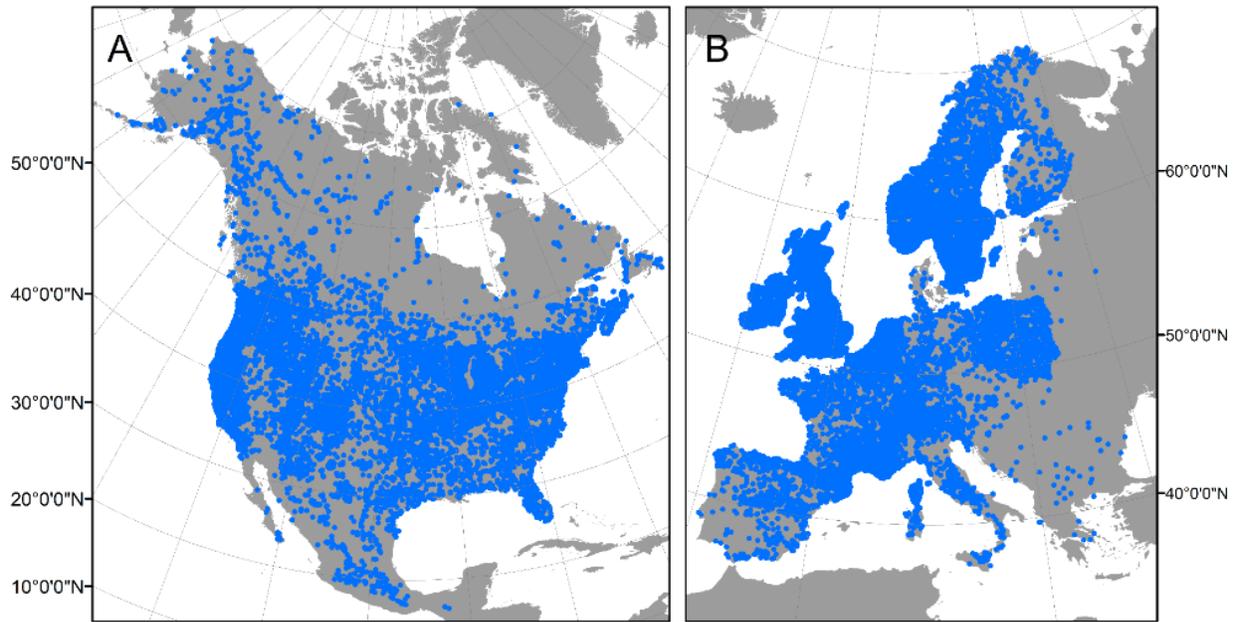
802 **Supplementary Acknowledgements**

803 The authors would like to thank all contributors to the bumblebee dataset, and the tireless hours
804 of those who helped put it together, especially Alana Pindar, Paul Galpern, Laurence Packer,
805 Simon G. Potts, Stuart M. Roberts, Pierre Rasmont, Oliver Schweiger, Sheila R. Colla, Leif L.
806 Richardson, David L. Wagner, Lawrence F. Gall, Derek S. Sikes, and Alberto Pantoja. We are
807 grateful to data contributors from North America: Bee Biology and Systematics Lab, USDA-
808 ARS, Utah State University; John Ascher, National University of Singapore and American
809 Museum of Natural History, New York, USA; Doug Yanega, University of California, Riverside
810 (NSF-DBI #0956388 and #0956340), California, USA; Illinois Natural History Survey, Illinois,
811 USA; Packer Lab Research Collection, York University, Canada; Canadian National Collection,
812 Agriculture and Agri-Food Canada; Canada; Peabody Museum, Yale University; Sam Droege,
813 USGS Patuxent Wildlife Research Center, USA; Boulder Museum of Natural History,
814 University of Colorado, Colorado, USA. From Europe: Status and Trends of European
815 Pollinators (STEP) Collaborative Project (grant 244090, www.STEP-project.net); Bees, Wasps
816 and Ants Recording Society; BDFGM Banque de Données Fauniques (P. Rasmont & E.
817 Haubruge); BWARS (UK, S.P.M. Roberts); SSIC (Sweden, B. Cederberg); Austria (J.
818 Neumayer); EISN (Netherland, M. Reemer); CSCF (Suisse, Y. Gonseth); Poland (T.
819 Pawlikowski); NBDC (Eire, U. FitzPatrick); FMNH (Finland, J. Paukkunen); Czech Republic (J.
820 Straka, L. Dvorak); France (G. Mahé); NSIC (Norway, F. Odegaard); UK (S.P.M. Roberts); Italy
821 (A. Manino); Spain (L. Castro) Global Biodiversity Information Facility (GBIF), <http://gbif.org>
822 for records from North America and Europe. P.S. would also like to thank A. Abdelgadir and J-
823 Y. Maba for support.

824

825 **Supplemental Figures**

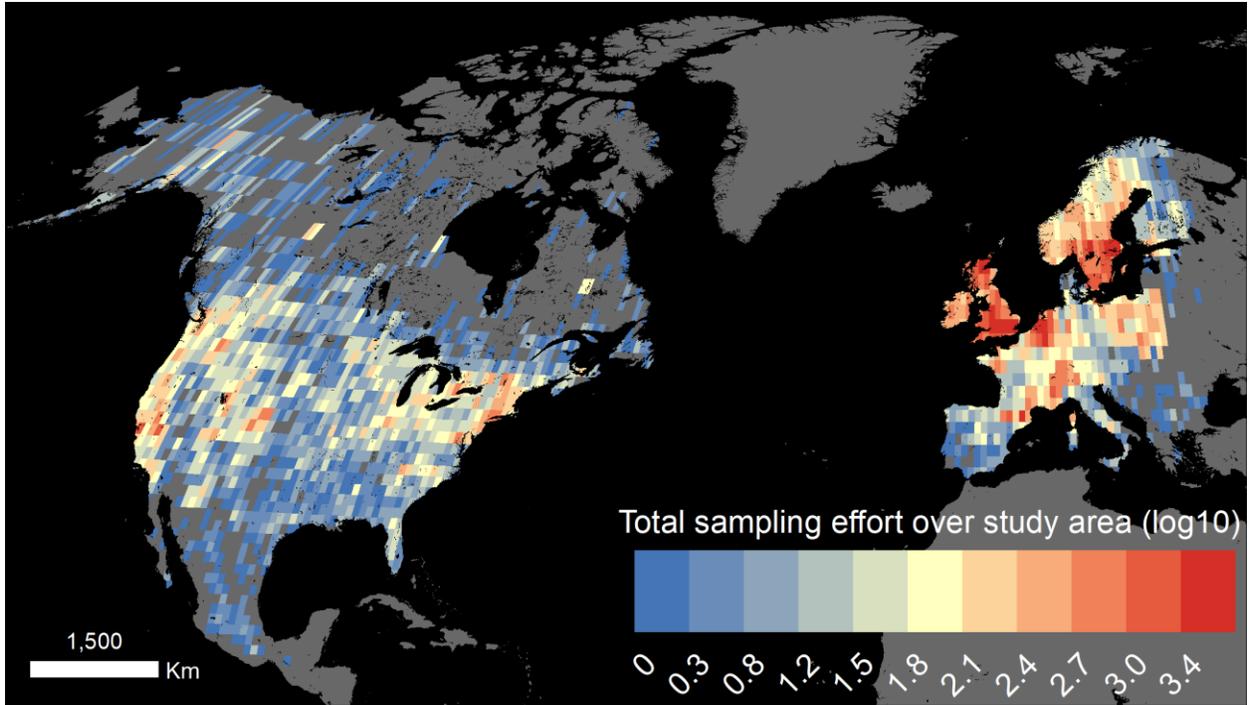
826



828 **Figure S1. Distribution of unique species-location-year sampling locations from North**

829 **America (A) and Europe (B).**

830



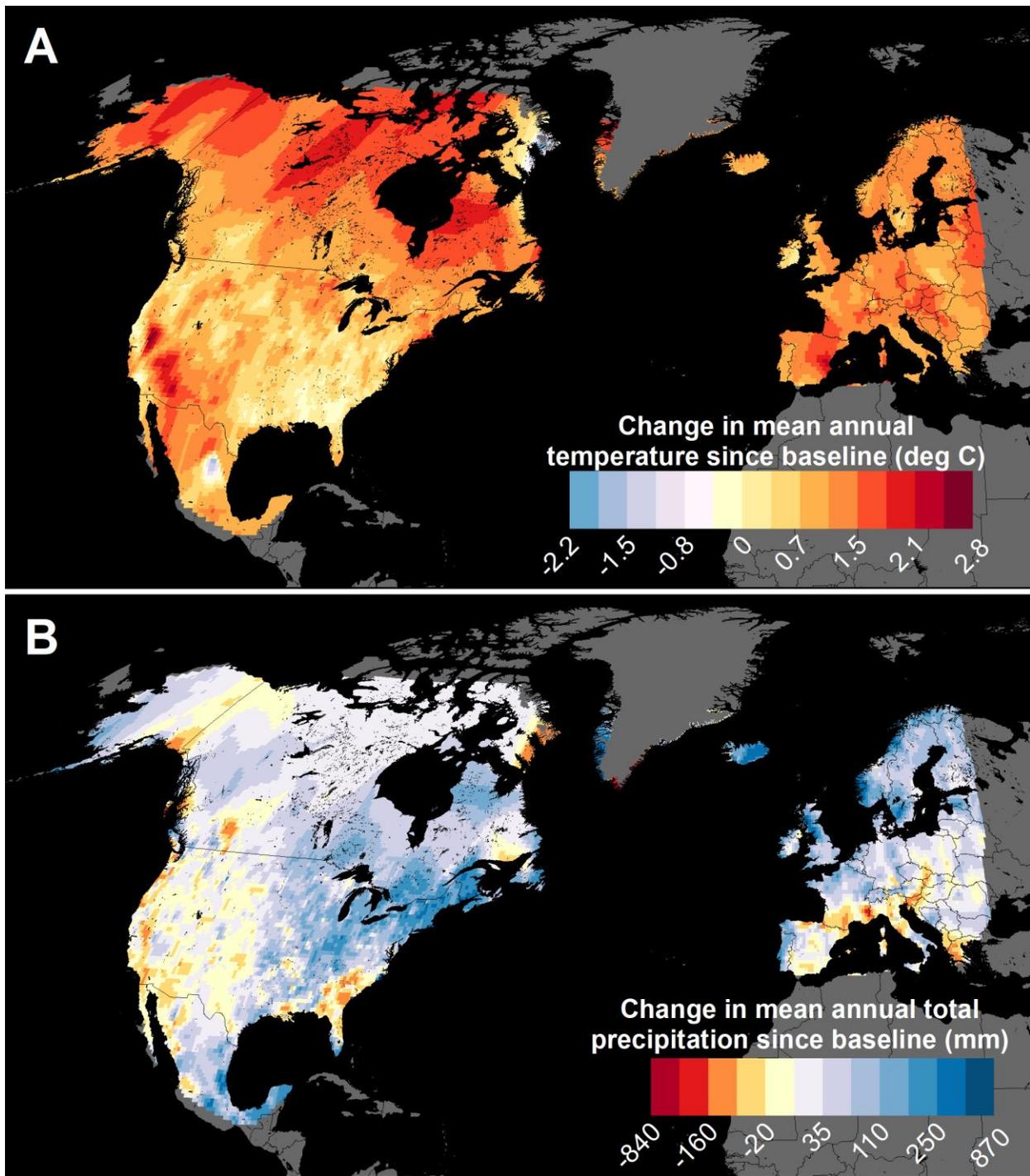
831

832 **Figure S2. Density of unique location-year observations per 100km by 100km grid cell**

833 **across North America and Europe.**

834

835



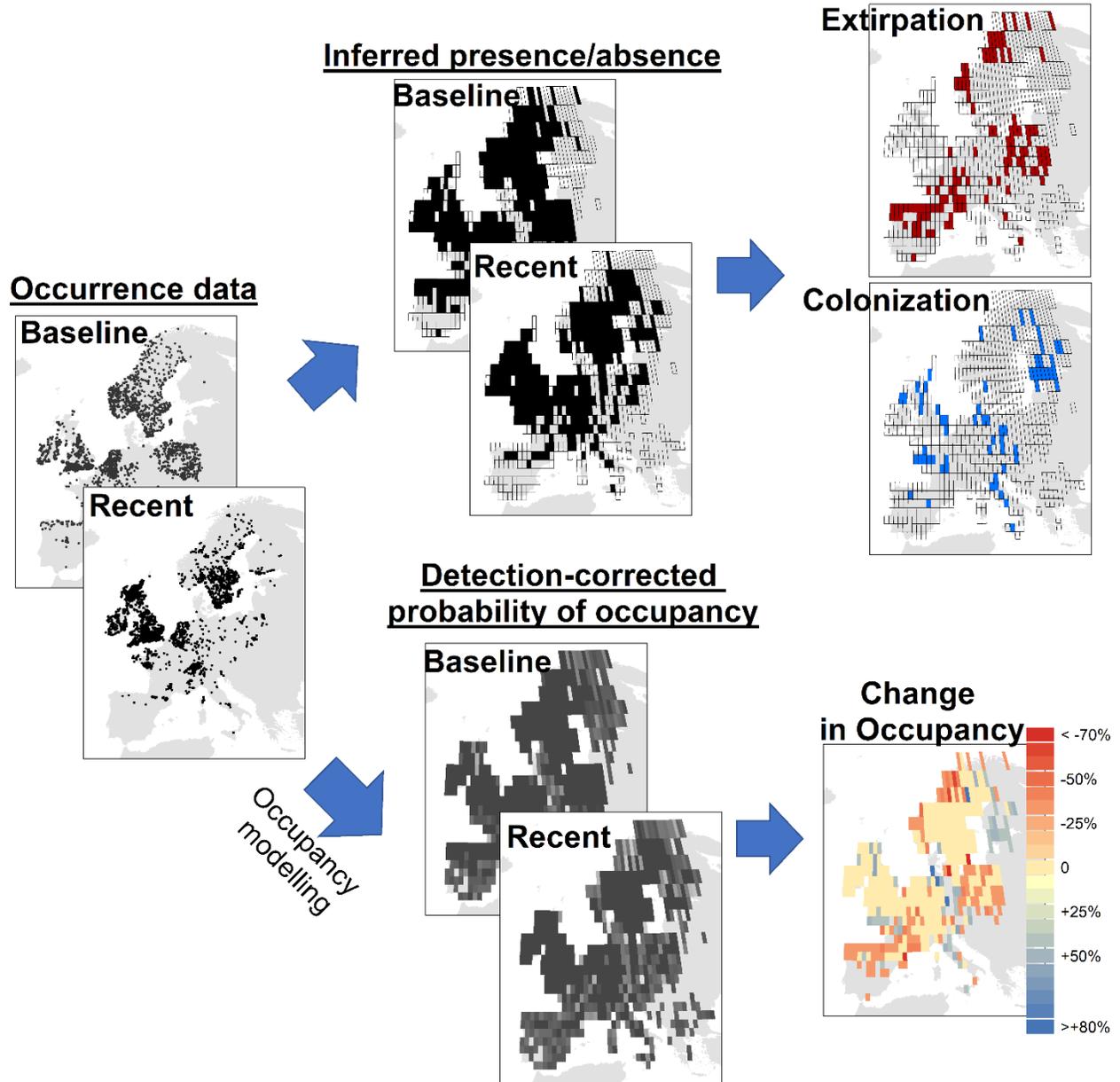
836

837 **Figure S3. Change in mean annual mean temperature (A) and mean total precipitation (B)**

838 **from the baseline (1901-1974) to the recent period (2000-2015) across North America and**

839 **Europe.**

840

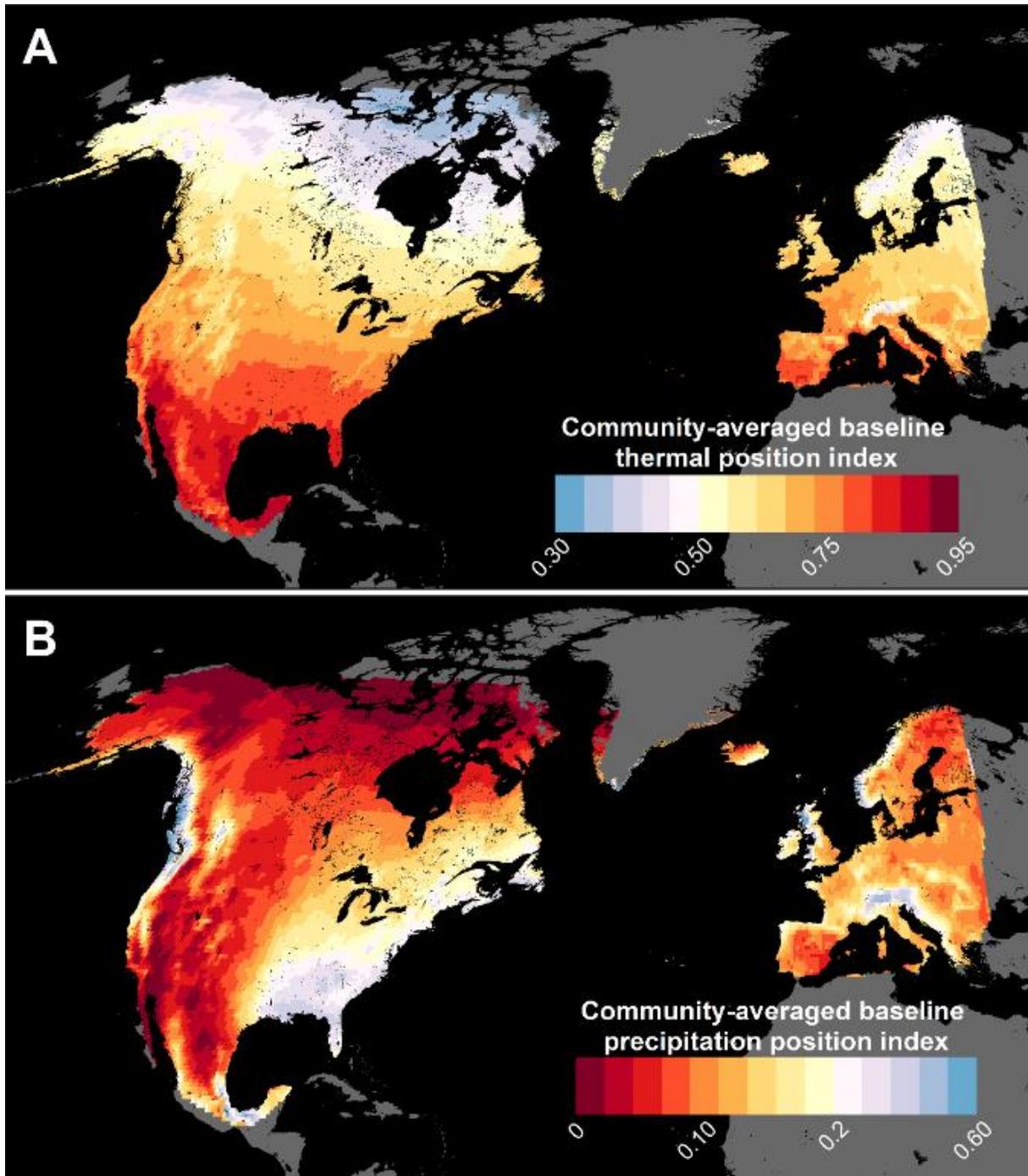


842

843 **Figure S4. Graphical description of methods visualizing relation between occurrence**
 844 **records and eventual measures of detection-corrected change in occupancy, extirpation,**
 845 **and colonization for *Bombus hortorum*.**

846

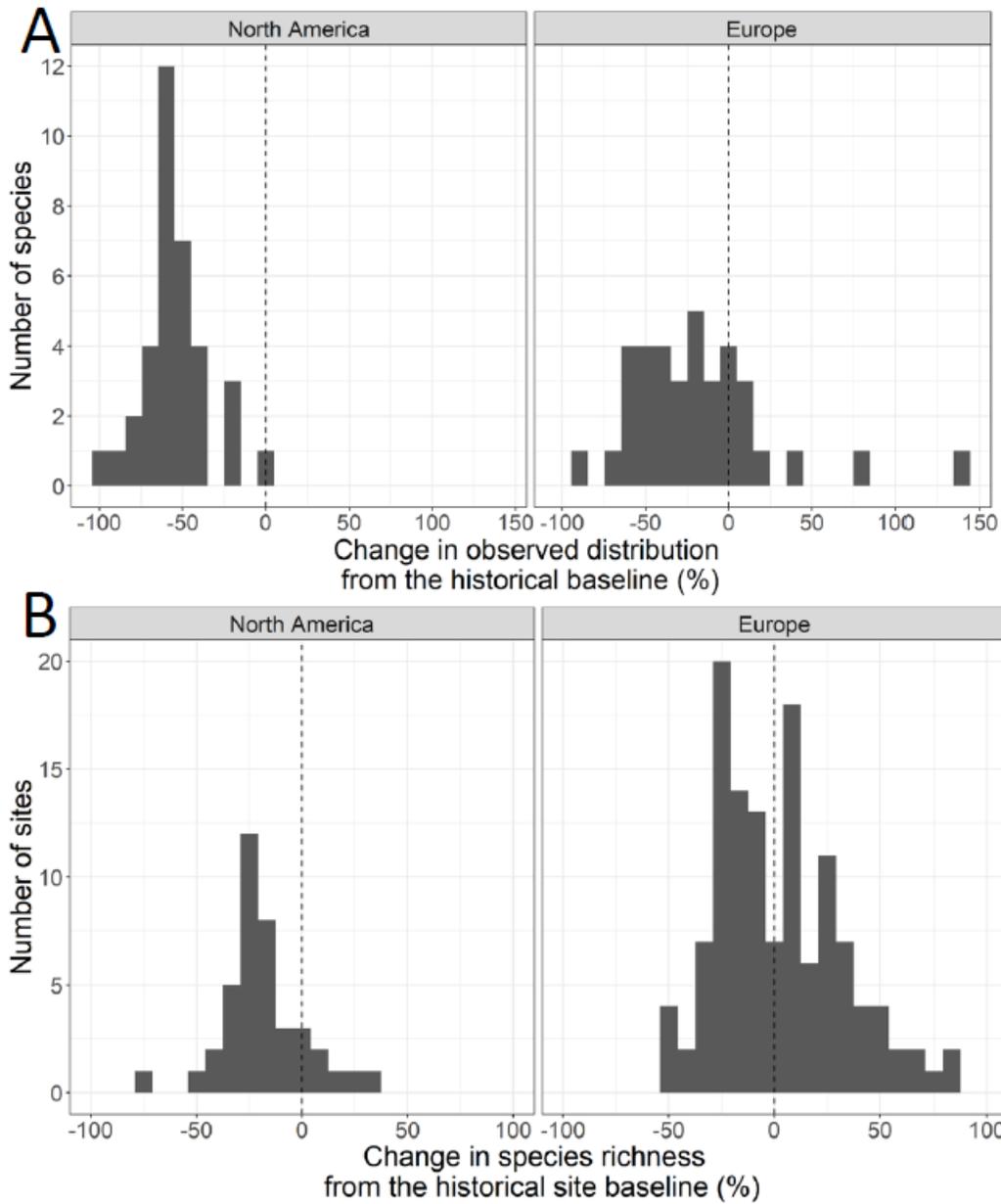
847



848

849 **Figure S5. Community-averaged thermal (A) and precipitation position (B) in the baseline**
 850 **period (1901-1974) across North America and Europe. Both thermal and precipitation**
 851 **position indices have a potential range of 0 to 1. Zero indicates that species in the assemblage are**
 852 **on average at their cold/dry tolerance limit for the entirety of the year in the period. One**

853 indicates that species in the assemblage are on average at their hot/wet tolerance limit for the
854 entirety of the year in the period.
855
856

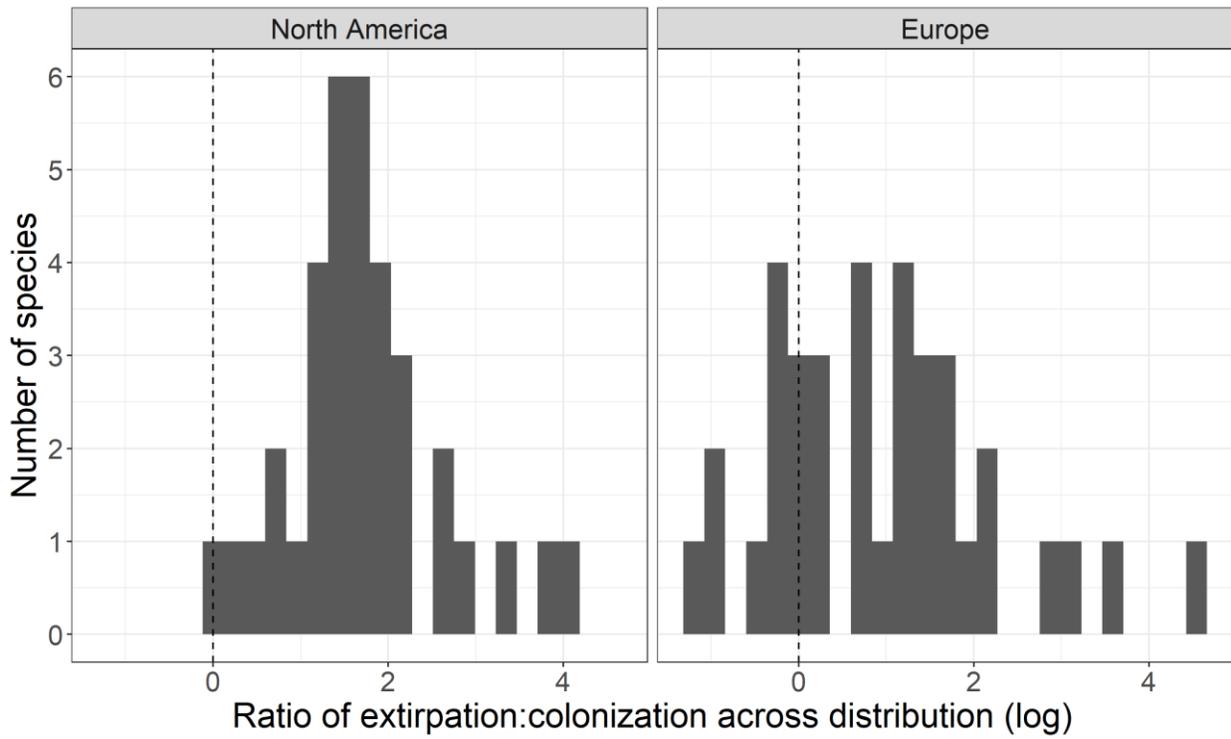


857
858 **Figure S6. Change in species' observed distribution (A) and observed species richness (B)**
859 **from the baseline (1901-1974) to recent period (2000-2014) in sites across the study area.**

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

862

863



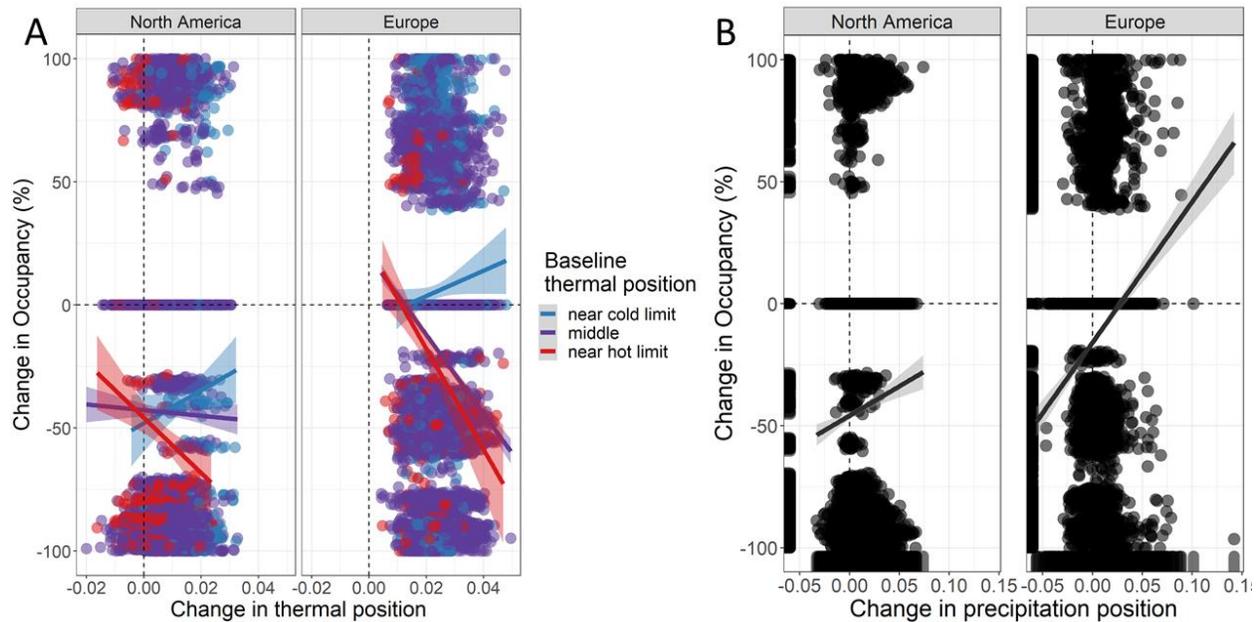
864

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

867

868

869

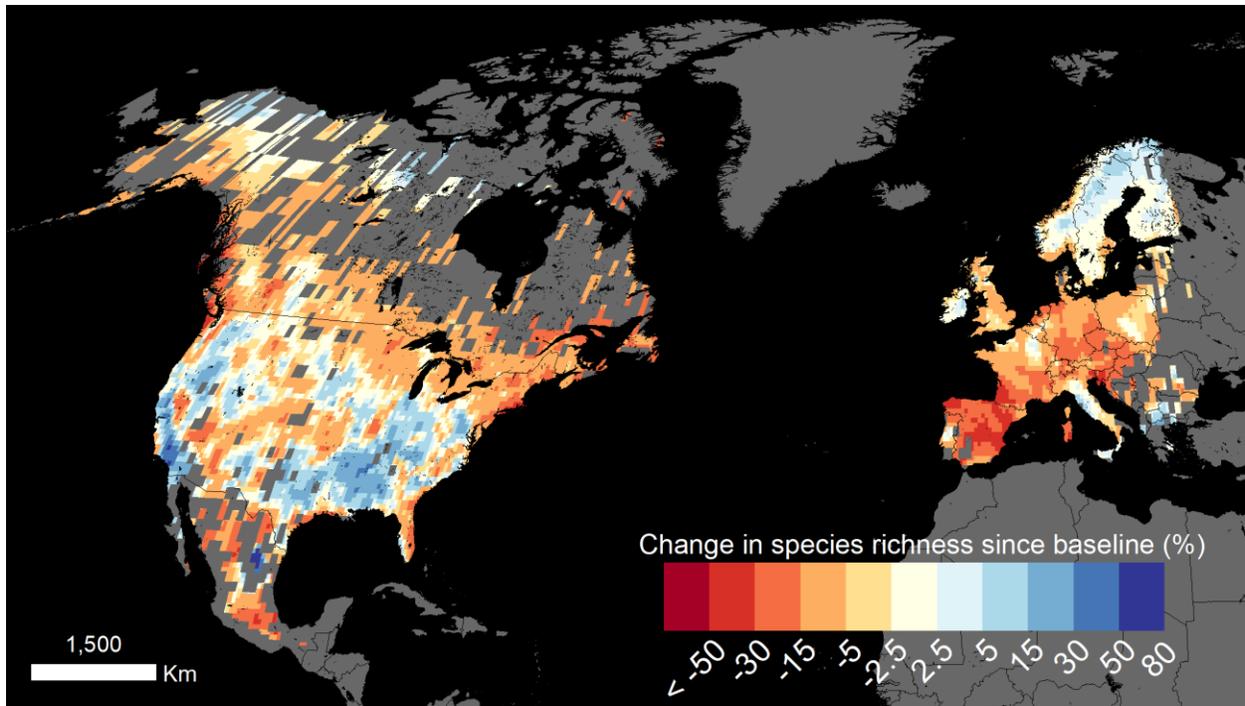


870

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

882

883



884

885 **Figure S9. Spatial projections of climate change-related change in non-detection-corrected**

886 **bumblebee species richness from a baseline period (1901-1974) to a recent period (2000-**

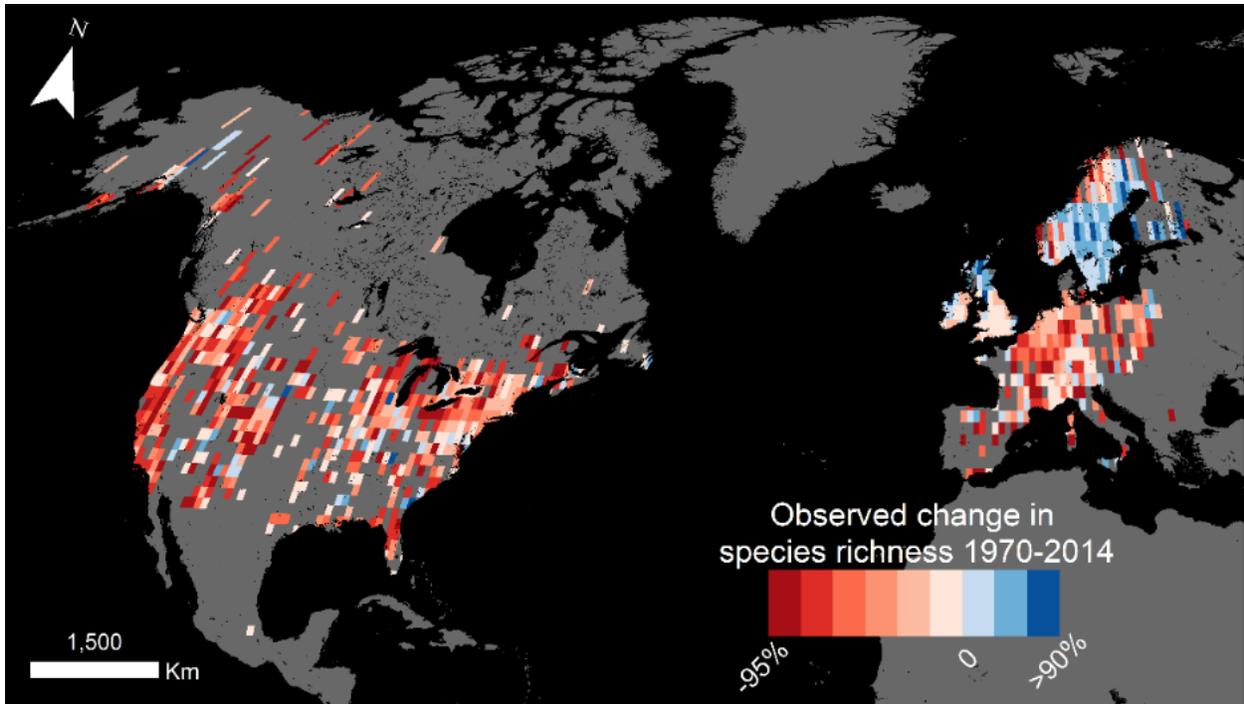
887 **2014).** Made using a model predicting percent change in non-detection-corrected bumblebee

888 species richness as a function of mean community thermal and precipitation position ($R^2= 0.44$;

889 see Materials and Methods for model details).

890

891



892

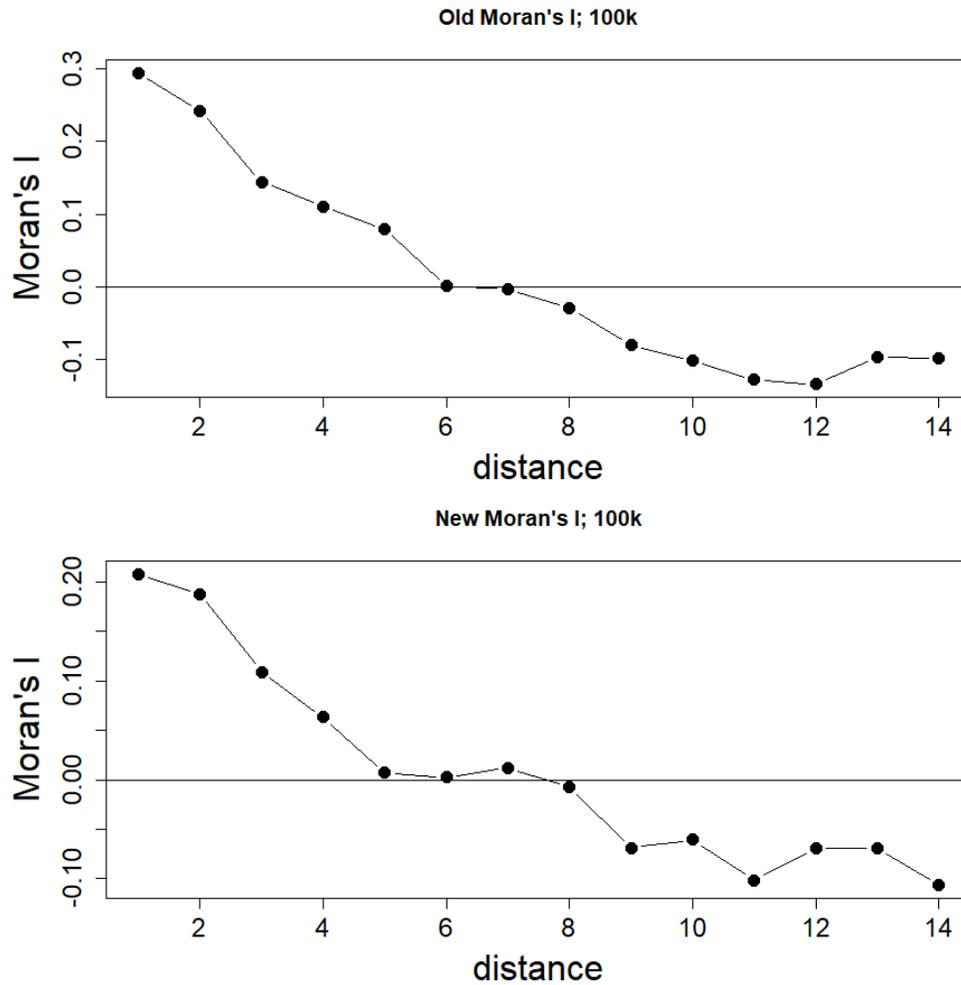
893 **Figure S10. Percent change in observed bumblebee species richness across North America**

894 **from the baseline (1901-1974) to recent period (2000-2014).** Grid cells shown are 100 km by

895 100 km, in an equal area projection. No sampling-based selection (see methods) applied here.

896

897



898

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

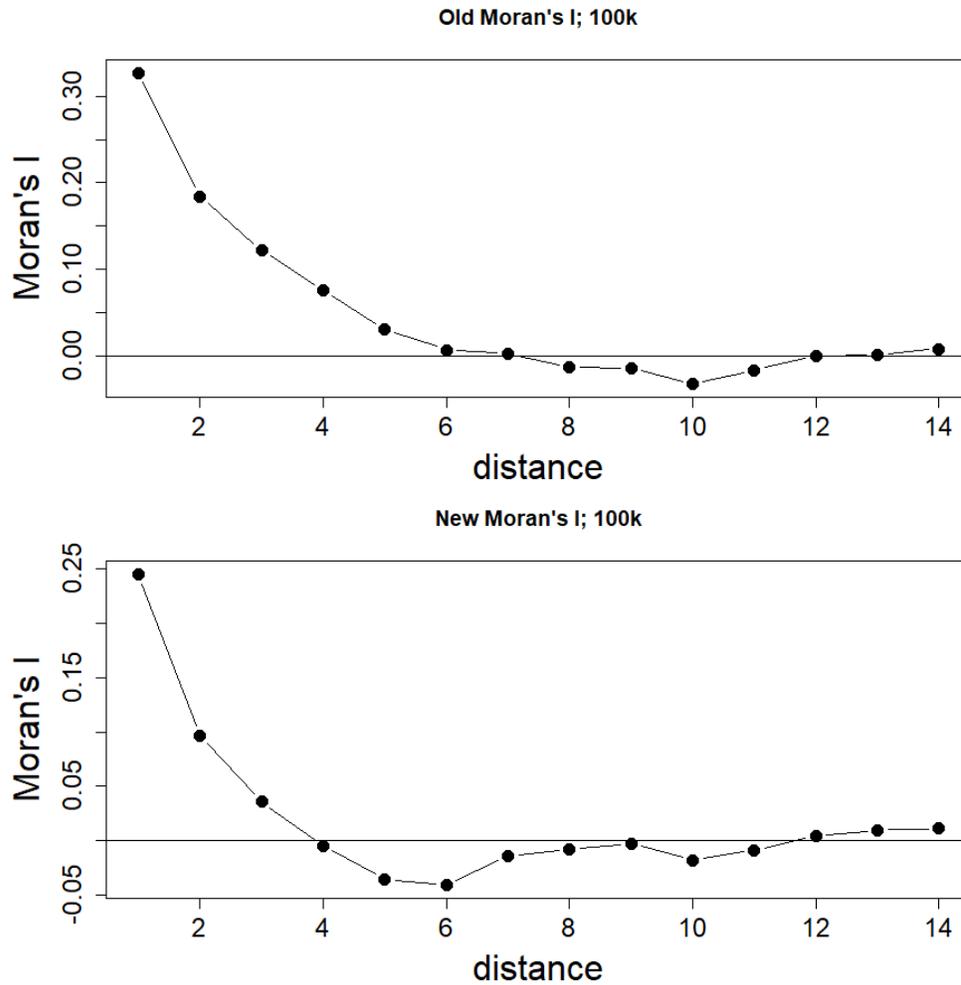
900 Moran's I calculated from a) ordinary least squares regression model and b) simultaneous

901 autoregressive (SAR) error model. SAR model was a significantly better fit (according to log

902 likelihood). Model coefficients were qualitatively similar between both models.

903

904

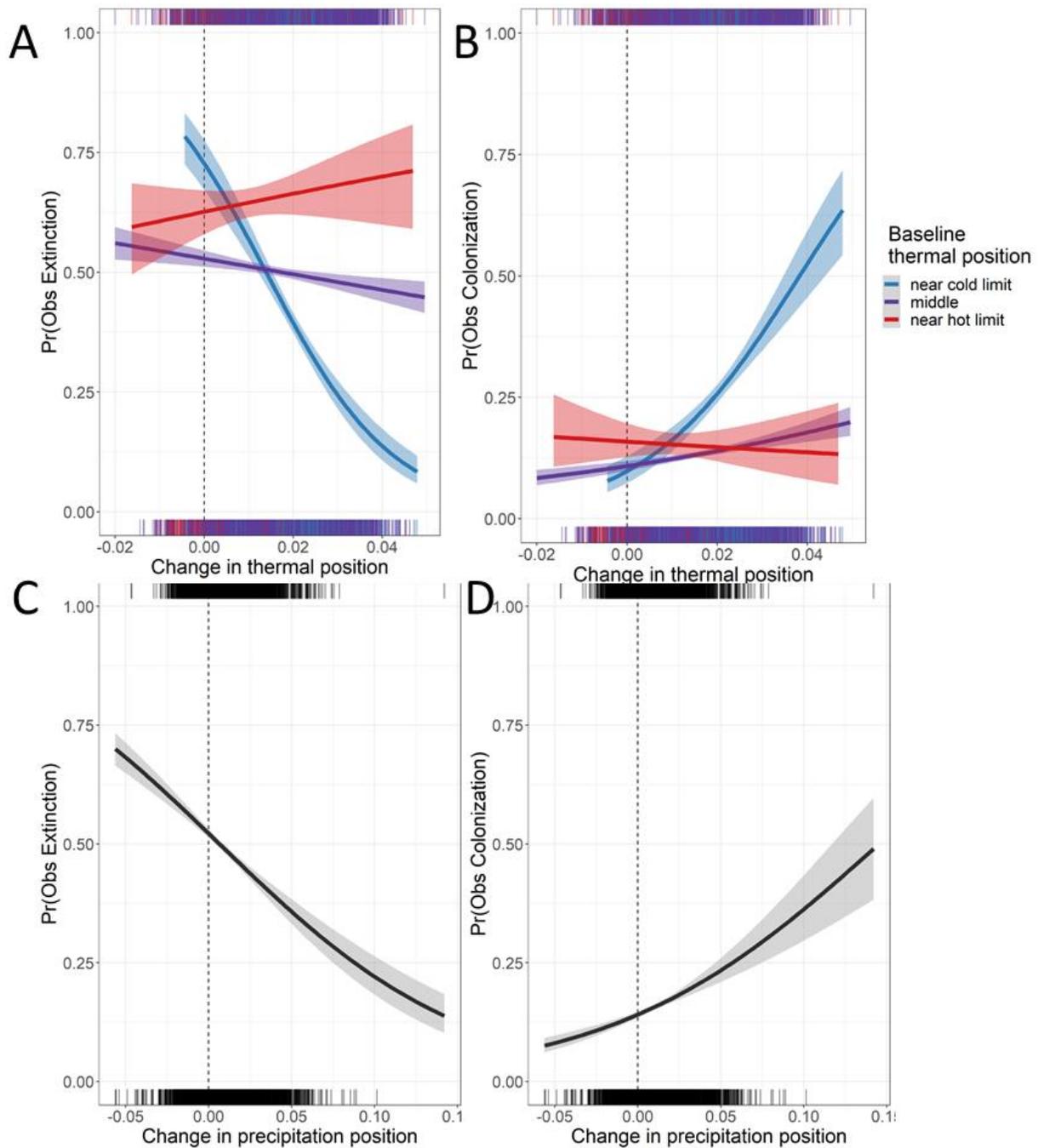


905

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

910

911



912

913 **Figure S13. Probability of local extinction (A, C) and colonization (B, D) in response to**
 914 **change in thermal (A, B) and precipitation (C, D) position from the baseline (1901-1974) to**
 915 **recent period (2000-2014). Thermal and precipitation position ranges from 0 to 1, with 1**
 916 **indicating conditions at a site are at a species' hot or wet limit for the entire year, and zero**
 917 **meaning conditions are at a species' cold or dry limit for the entire year during the historic**

918 period. For ease of visualizing the significant interaction between baseline thermal position and
919 change in thermal position, the continuous baseline thermal position variable has been split at the
920 1st and 3rd quantile to show sites that were historically close to species' hot limits (red; n=969),
921 cold limits (blue; n=2,244), and middle of their observed climatic limits (purple; n=11,793). Rug
922 plot shows the distribution of observations. Confidence intervals ($\pm 95\%$) are shown around
923 linear trendlines.

924

925

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>soroensis</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

927

928

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 R² (for PGLMM) and adjusted-R² (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
<u>Climatic position interactions</u>										
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
<u>Covariates</u>										
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	--	--	--	--
<u>Random effects</u>										
Species	181.4	117 - 256.2	0.3	0.19 - 0.44	0.26	0.15 - 0.39	--	--	--	--
<u>Model summary</u>										
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	(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	(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	<u>Variance (Std.dev.)</u>		<u>Variance (Std.dev.)</u>		<u>Variance (Std.dev.)</u>		--	--	--	--
	181.6	118.1 - 256.8	0.31	0.19 - 0.43	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	4856	4856
Variation explained (R2)	0.1		0.84		0.61		0.03	0.03	0.06	0.06

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	<u>Variance (Std.dev.)</u>		<u>Variance (Std.dev.)</u>		<u>Variance (Std.dev.)</u>		--	--	--	--
	133.8	75.62 - 193.4	0.41	0.16 - 0.82	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	

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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	--	--	--	--
Change since baseline	-3.47	-5.05 - -1.9	0.25	0.19 - 0.31	-0.07	-0.15 - 0.02	-2.96 (0.92)	-3.21	-2.37 (1.06)	-2.24
Baseline:Change interaction	-9.07	-10.73 - -7.5	0.42	0.34 - 0.5	-0.32	-0.42 - -0.22	-4.66 (0.66)	-7.05	-2.43 (0.83)	-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	--	--	--	--
Change since baseline	4.7	3.39 - 6.19	-0.19	-0.26 - -0.11	0.26	0.18 - 0.35	0.62 (0.76)	0.82	0.73 (0.98)	0.74
Baseline:Change interaction	-0.16	-1.03 - 0.65	0.03	-0.01 - 0.07	-0.03	-0.08 - 0.02	0.37 (0.49)	0.75	-0.38 (0.53)	-0.72
<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	<u>Variance (Std.dev.)</u> 185.9 120.9 - 265.9		<u>Variance (Std.dev.)</u> 0.3 0.18 - 0.43		<u>Variance (Std.dev.)</u> 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	1133	1133
Variation explained (R2)	0.1		0.86		0.53		0.1	0.1	0.18	0.18

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