1	Title: Climate change contributes to widespread declines among bumblebees across continents
2	Authors: Peter Soroye <sup>1</sup> *, Tim Newbold <sup>2</sup> , Jeremy Kerr <sup>1</sup>
3	Affiliations:
4	<sup>1</sup> Department of Biology, University of Ottawa, Ottawa, ON, Canada, K1N6N5.
5	<sup>2</sup> Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and
6	Environment, University College London, Gower Street, London WC1E 6BT, UK.
7	*Correspondence to: peter.soroye@gmail.com
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,

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 communityaveraged climatic position index (Figures 1 and S5).

Our measurements of bumblebee species occupancy over time provide evidence of rapid and widespread declines across Europe and North America. Probability of site occupancy declined on average by 46% (±3.3% SE) in North America and 17% (±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).

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; Table S2). Our model's capacity to predict change in occupancy (marginal  $R^2 = 0.11$ ) was 90

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<sup>2</sup> 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).

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 and increasing species richness toward warmingenvironments 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 changedriven 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.

139	Note	es and References:
140	1.	J. T. Kerr, A. Pindar, P. Galpern, L. Packer, S. G. Potts, S. M. Roberts, et al., Climate
141		change impacts on bumblebees converge across continents. Science. 349, 177–180 (2015).
142	2.	F. E. B. Spooner, R. G. Pearson, R. Freeman, Rapid warming is associated with
143		population decline among terrestrial birds and mammals globally. Glob. Chang. Biol. 24,
144		4521–4531 (2018).
145	3.	S. D. Veloz, J. W. Williams, J. L. Blois, F. He, B. Otto-Bliesner, Z. Liu, No-analog
146		climates and shifting realized niches during the late quaternary : implications for 21st-
147		century predictions by species distribution models. Glob. Chang. Biol. 18, 1698–1713
148		(2012).
149	4.	J. W. Williams, S. T. Jackson, Novel climates, no-analog communities, and ecological
150		surprises. Front. Ecol. Environ. 5, 475–482 (2007).
151	5.	M. C. Urban, Accelerating extinction risk from climate change. Science. 348, 571–573
152		(2015).
153	6.	K. D. T. Nguyen, S. A. Morley, C. H. Lai, M. S. Clark, K. S. Tan, A. E. Bates, et al.,
154		Upper temperature limits of tropical marine ectotherms: Global warming implications.
155		<i>PLoS One</i> . <b>6</b> , 6–13 (2011).
156	7.	J. M. Sunday, A. E. Bates, M. R. Kearney, R. K. Colwell, N. K. Dulvy, J. T. Longino, et
157		al., Thermal-safety margins and the necessity of thermoregulatory behavior across latitude
158		and elevation. Proc. Natl. Acad. Sci. 111, 5610–5615 (2014).

- S. G. Potts, J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, W. E. Kunin, Global
   pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25, 345–353 (2010).
- 161 9. Materials and methods are available as supplementary materials at the Science Website.
- 162 10. G. Sadoti, B. Zuckerberg, M. A. Jarzyna, W. F. Porter, Applying occupancy estimation
- and modelling to the analysis of atlas data. *Divers. Distrib.* **19**, 804–814 (2013).
- 164 11. S. H. Woodard, Bumble bee ecophysiology: integrating the changing environment and the
  165 organism. *Curr. Opin. Insect Sci.* 22, 101–108 (2017).
- 166 12. J. E. Ogilvie, S. R. Griffin, Z. J. Gezon, B. D. Inouye, N. Underwood, D. W. Inouye, et
- *al.*, Interannual bumble bee abundance is driven by indirect climate effects on floral
  resource phenology. *Ecol. Lett.*, 1–9 (2017).
- 169 13. C. A. Deutsch, J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak,
- 170 *et al.*, Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl.*
- 171 *Acad. Sci.* **105**, 6668–6672 (2008).
- 172 14. C. Sirois-Delisle, J. T. Kerr, Climate change-driven range losses among bumblebee
  173 species are poised to accelerate. *Sci. Rep.*, 1–10 (2018).
- 174 15. B. A. Woodcock, J. M. Bullock, R. F. Shore, M. S. Heard, M. G. Pereira, J. Redhead, et

175 *al.*, Country-specific effects of neonicotinoid pesticides on honey bees and wild bees.

- 176 Science. **356**, 1393–1395 (2017).
- 177 16. R. J. Gill, O. Ramos-Rodriguez, N. E. Raine, Combined pesticide exposure severely
  178 affects individual-and colony-level traits in bees. *Nature*. 491, 105–108 (2012).
- 179 17. D. Goulson, E. Nicholls, C. Botías, E. L. Rotheray, Bee declines driven by combined
- 180 stress from parasites, pesticides, and lack of flowers. *Science*. **347**, 1255957 (2015).
- 181 18. T. Newbold, Future effects of climate and land-use change on terrestrial vertebrate

183 C. S. Mantyka-Pringle, P. Visconti, M. Di Marco, T. G. Martin, C. Rondinini, J. R. 19. 184 Rhodes, Climate change modifies risk of global biodiversity loss due to land-cover 185 change. Biol. Conserv. 187, 103-111 (2015). 186 20. IPCC, "Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II 187 and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate 188 Change" (IPCC, Geneva, Switzerland, 2014), (available at www.ipcc.ch/report/ar5/syr/). 189 21. C. Polce, J. Maes, X. Rotllan-Puig, D. Michez, L. Castro, B. Cederberg, et al., 190 Distribution of bumblebees across europe. One Ecosyst. 3 (2018), 191 doi:10.3897/oneeco.3.e28143. 192 22. S. G. Potts, J. C. Biesmeijer, R. Bommarco, A. Felicioli, M. Fischer, P. Jokinen, et al., 193 Developing European conservation and mitigation tools for pollination services: 194 approaches of the STEP (Status and Trends of European Pollinators) project. J. Apic. Res. 195 **50**, 152–164 (2011). 196 23. P. H. Williams, R. W. Thorp, L. L. Richardson, S. R. Colla, Bumble bees of North 197 America: an identification guide (Princeton University Press, 2014). 198 24. P. Rasmont, M. Franzén, T. Lecocq, A. Harpke, S. P. M. Roberts, J. C. Biesmeijer, et al.,

community diversity under different scenarios. Proc. R. Soc. B, 20180792 (2018).

- 199 *Climatic Risk and Distribution Atlas of European Bumblebees* (Biorisk 10 (Special Issue),
  200 2015).
- 201 25. N. J. Gotelli, A. Chao, in *Encyclopedia of Biodiversity* (Elsevier, Waltham, MA, 2013;
- 202 http://www.sciencedirect.com/science/article/pii/B9780123847195004032), vol. 5, pp.
   203 195–211.
- 204 26. N. J. Gotelli, R. K. Colwell, in *Biological Diversity: Frontiers in measurement and*

205		assessment, A. E. Magurran, B. J. McGill, Eds. (Oxford University Press, New York, NY,
206		2011; http://www.uvm.edu/~ngotelli/manuscriptpdfs/Chapter 4.pdf), pp. 39-54.
207	27.	R Core Team, R: A Language and Environment for Statistical Computing. R Found. Stat.
208		<i>Comput.</i> <b>1</b> (2017), p. 2673.
209	28.	H. Wickham, tidyverse: Easily Install and Load "Tidyverse" Packages (2017), (available
210		at https://cran.r-project.org/package=tidyverse).
211	29.	R. Hijmans, J. van Etten, J. Cheng, M. Mattiuzzi, M. Sumner, J. A. Greenberg, et al.,
212		Package ' raster '. CRAN -R.2.5-8 (2016) (available at http://cran.r-
213		project.org/package=raster).
214	30.	J. A. Royle, M. Kéry, A Bayesian State-Space Formulation of Dynamic Occupancy
215		Models. Ecology. 88, 1813–1823 (2007).
216	31.	D. I. MacKenzie, J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, J. E. Hines,
217		Occupancy Estimation and Modeling : Inferring Patterns and Dynamics of Species
218		Occurrence (Elsevier Academic Press Inc., 2006).
219	32.	J. A. Royle, R. M. Dorazio, in Hierarchical Modeling and Inference in Ecology (2009;
220		http://linkinghub.elsevier.com/retrieve/pii/B9780123740977000119), pp. 297-324.
221	33.	M. Kéry, M. Schaub, in Bayesian Population Analysis using WinBUGS, M. Kéry, M.
222		Schaub, Eds. (Academic Press, Boston, 2012;
223		http://www.sciencedirect.com/science/article/pii/B9780123870209000134), pp. 413-461.
224	34.	D. I. MacKenzie, J. D. Nichols, M. E. Seamans, R. J. Gutierrez, Modeling species
225		occurance dynamics with multiple states and imperfect detection. <i>Ecology</i> . <b>90(3)</b> , 823–
226		835 (2009).

227 35. C. T. Rota, R. J. Fletcher, R. M. Dorazio, M. G. Betts, Occupancy estimation and the

- 228 closure assumption. J. Appl. Ecol. 46, 1173–1181 (2009).
- 36. M. A. Jarzyna, W. Jetz, A near half-century of temporal change in different facets of avian
  diversity. *Glob. Chang. Biol.* 23, 2999–3011 (2017).
- 231 37. R. Bivand, T. Keitt, B. Rowlingson, rgdal: Bindings for the Geospatial Data Abstraction
- 232 Library (2017), (available at https://cran.r-project.org/package=rgdal).
- 38. M. Plummer, JAGS : A program for analysis of Bayesian graphical models using Gibbs
  sampling JAGS : Just Another Gibbs Sampler (2003).
- 39. Y.-S. Su, M. Yajima, R2jags: Using R to Run "JAGS" (2015), (available at https://cran.r project.org/package=R2jags).
- 237 40. S. P. Brooks, A. Gelman, General Methods for Monitoring Convergence of Iterative
- 238 Simulations General Methods for Monitoring Convergence of Iterative Simulations. J.

239 *Comput. Graph. Stat.* **7**, 434–455 (1998).

- 41. I. Harris, P. D. Jones, T. J. Osborn, D. H. Lister, Updated high-resolution grids of monthly
  climatic observations the CRU TS3.10 Dataset. *Int. J. Climatol.* 34, 623–642 (2014).
- 42. 42. S. Nakagawa, H. Schielzeth, A general and simple method for obtaining R2 from
- 243 generalized linear mixed-effects models. *Methods Ecol. Evol.* **4**, 133–142 (2013).
- 43. S. A. Cameron, H. M. Hines, P. H. Williams, A comprehensive phylogeny of the bumble
  bees (Bombus). *Biol. J. Linn. Soc.* 91, 161–188 (2007).
- 44. J. D. Hadfield, MCMC Methods for Multi-Response Generalized Linear Mixed Models:
  The MCMCglmm R Package. J. Stat. Softw. 33, 1–22 (2010).
- 248 45. E. Paradis, K. Schliep, ape 5.0: an environment for modern phylogenetics and
- evolutionary analyses in R (vers. 5.3). *Bioinformatics*. **35**, 526–528 (2018).
- 250 46. P. de Villemereuil, S. Nakagawa, in Modern Phylogenetic Comparative Methods and

- 251 *Their Application in Evolutionary Biology: Concepts and Practice*, L. Z. Garamszegi, Ed.
- 252 (Springer Berlin Heidelberg, Berlin, Heidelberg, 2014; https://doi.org/10.1007/978-3-662253 43550-2\_11), pp. 287–303.
- 47. M. P. Arbetman, G. Gleiser, C. L. Morales, P. Williams, M. A. Aizen, Global decline of
- bumblebees is phylogenetically structured and inversely related to species range size and
  pathogen incidence. *Proc. R. Soc. B.* 284, 20170204 (2017).
- 48. W. D. Kissling, G. Carl, Spatial autocorrelation and the selection of simultaneous
  autoregressive models. *Glob. Ecol. Biogeogr.* 17, 59–71 (2008).
- 259 49. C. F. Dormann, J. M. McPherson, M. B. Araújo, R. Bivand, J. Bolliger, G. Carl, et al.,
- Methods to account for spatial autocorrelation in the analysis of species distributional
  data: A review. *Ecography (Cop. ).* 30, 609–628 (2007).
- 262 50. D. Bates, M. Machler, B. M. Bolker, S. C. Walker, Fitting linear mixed-effects models
  263 using lme4. *J. Stat. Softw.* 67, 1–48 (2015).
- 264 51. R. Bivand, G. Piras, Comparing Implementations of Estimation Methods for Spatial
  265 Econometrics. J. Stat. Softw. 63 (2015), doi:10.18637/jss.v063.i18.
- 266 52. G. C. Hurtt, L. P. Chini, S. Frolking, R. A. Betts, J. Feddema, G. Fischer, et al.,
- 267 Harmonization of land-use scenarios for the period 1500-2100: 600 years of global
- 268 gridded annual land-use transitions, wood harvest, and resulting secondary lands. *Clim.*
- 269 *Change*. **109**, 117–161 (2011).
- 270 53. B. Sinervo, F. Mendez-de-la-Cruz, D. B. Miles, B. Heulin, E. Bastiaans, M. Villagran-
- 271 Santa Cruz, *et al.*, Erosion of Lizard Diversity by Climate Change and Altered Thermal
- 272 Niches. Science. **328**, 894–899 (2010).
- 273 54. J. M. Sunday, A. E. Bates, N. K. Dulvy, Thermal tolerance and the global redistribution

- 274 of animals. *Nat. Clim. Chang.* **2**, 686–690 (2012).
- 275 55. A. De Palma, M. Kuhlmann, S. P. M. Roberts, S. G. Potts, L. Börger, L. N. Hudson, et al.,
- 276 Ecological traits affect the sensitivity of bees to land-use pressures in European
- 277 agricultural landscapes. J. Appl. Ecol. **52**, 1567–1577 (2015).
- 278 56. C. P. Nadeau, M. C. Urban, J. R. Bridle, Coarse climate change projections for species
  279 living in a fine-scaled world. *Glob. Chang. Biol.* 23, 12–24 (2017).
- 280 57. C. P. Nadeau, M. C. Urban, J. R. Bridle, Climates Past, Present, and Yet-to-Come Shape
  281 Climate Change Vulnerabilities. *Trends Ecol. Evol.* 32, 786–800 (2017).
- 282 58. T. M. Blackburn, K. J. Gaston, Scale in macroecology. *Glob. Ecol. Biogeogr.* 11, 185–189
  283 (2002).

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)

- 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

Figure 2. Percent change in site occupancy since a baseline period (1901-1974) for 35 North
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 baseline thermal position variable has been split at the 1<sup>st</sup> and 3<sup>rd</sup> quantile to show sites that were 328 329 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.

- 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.



338	AAAS
339	
340	
341	Supplementary Materials for
342	
343	Climate change contributes to widespread declines among bumblebees across continents
344	Peter Soroye*, Tim Newbold, Jeremy Kerr.
345	
346	Correspondence to: peter.soroye@gmail.com
347	
348	
349	This PDF file includes:
350	
351	Materials and Methods
352	Supplementary Text
353	Supplementary Acknowledgements
354	Figures S1-S13
355	Tables S1-S8
356	References (21 - 58)
357	
358	
359	

#### 360 Materials and Methods

#### 361 <u>Bumblebee observations, observed distribution, and species richness</u>

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.

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 location383 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).

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.

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 (1). 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.

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

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.

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 S5). We did this for both periods, and then measured the change from the baseline to recent (Figure 1).

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).

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 calculated conditional and marginal  $R^2$  using the method proposed by (42). 540

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<sup>2</sup> 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  $\mathbb{R}^2$ , and 560 phylogenetic signal (Pagel's  $\lambda$ ) 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

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).

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 2<sup>nd</sup> 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.

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.

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).

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

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<sup>2</sup> 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 modelling, and we used Information Criterion and R<sup>2</sup> to compare between climatic position and 629 630 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

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

Using the detection-corrected species richness model (adjusted  $R^2 = 0.14$ ) and 0.5-degree 636 637 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 nondetection-corrected species richness model (adjusted  $R^2 = 0.44$ ; Figure S9). We used rescaled 639 640 climatic position and climatic position change layers at  $0.5 \times 0.5$  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 with land-use to pure climate change models using information criterion values and  $R^2$  and 652 653 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.

660

## 661 Supplemental Text

## 662 <u>Non-detection corrected declines</u>

*Occupancy, extirpation, and colonization.* Consistent with measured declines in occupancy
(Figure 2), observed distributions declined on average by 54% (±3.4% SE) in North America and
18% (±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% (±2.2% SE) and 669 49% (±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 ( $\pm 1.7$  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.

Non-detection corrected species richness. Since the baseline period, local (non-detection
corrected) species richness has declined by about 18.6% (±3.2% SE) in North America, while
richness in Europe has stayed relatively constant (2.2% increase since the baseline ±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.

## 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 undoubtably 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

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

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

and colonization models (marginal  $R^2 0.87$  vs 0.53) could suggest that the process of 720 721 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).

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  $\lambda$ = 0.88) being stronger than the signal for colonization (Pagel's  $\lambda$ = 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.

#### 735 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

743 position variables instead of mean climate variables produces models that better predict 744 extinction, colonization, and change in occupancy (marginal  $\mathbb{R}^2$  7% lower to 12.5% higher) and 745 are more informative ( $\Delta$ DIC ~ 202.4,  $\Delta$ DIC ~ 102.8 and  $\Delta$ DIC ~ 164.9 respectively). This 746 increase in explanatory power was consistent when comparing to models using average annual 747 maximum (marginal  $\mathbb{R}^2$  1.6% to 23% higher;  $\Delta DIC = 98.7-157.5$ ) or minimum temperatures 748 (marginal  $R^2$  2.6% lower to 21.3% higher;  $\Delta DIC = 128.2-241.9$ ). 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 <u>Climatic sampling across continents</u>

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 =  $7.0 \times 10^{-3}$  and 758  $4.8 \times 10^{-5}$ , 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 =  $5.1 \times 10^{-3}$  and 0.03, df = 41.5 and 40.2, 764 respectively).

#### 765 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).

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

*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.

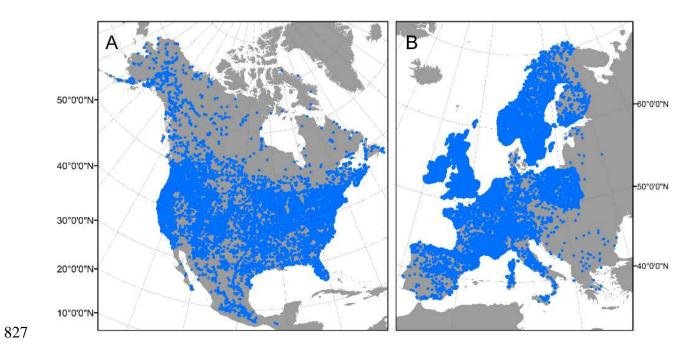
792	Absence threshold. When converting our occurrence records into presence absence data, we
793	inferred absence of a species when the focal species was not seen but at least one other species
794	was (absence threshold of one). A liberal absence threshold could result in overestimating
795	absences (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	

#### 802 Supplementary Acknowledgements

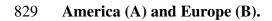
803 The authors would like to thank all contributors to the bumblebee dataset, and the tireless hours 804 of those who helped put it together, especially Alana Pindar, Paul Galpern, Laurence Packer, 805 Simon G. Potts, Stuart M. Roberts, Pierre Rasmont, Oliver Schweiger, Sheila R. Colla, Leif L. 806 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.

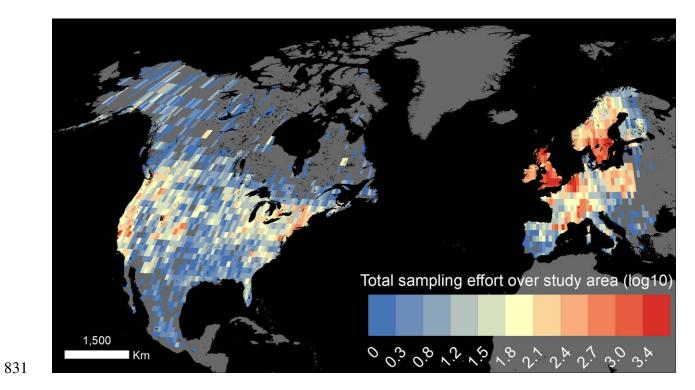
### 825 Supplemental Figures

826

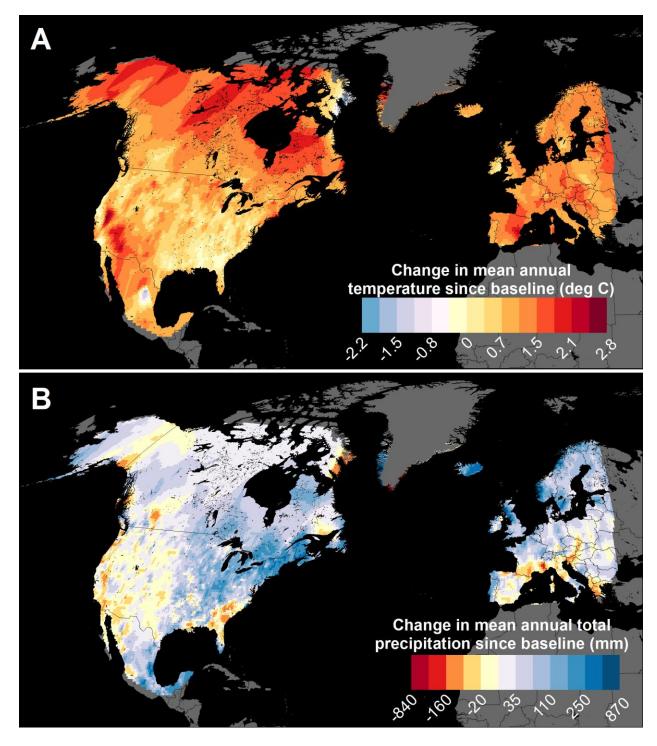


828 Figure S1. Distribution of unique species-location-year sampling locations from North



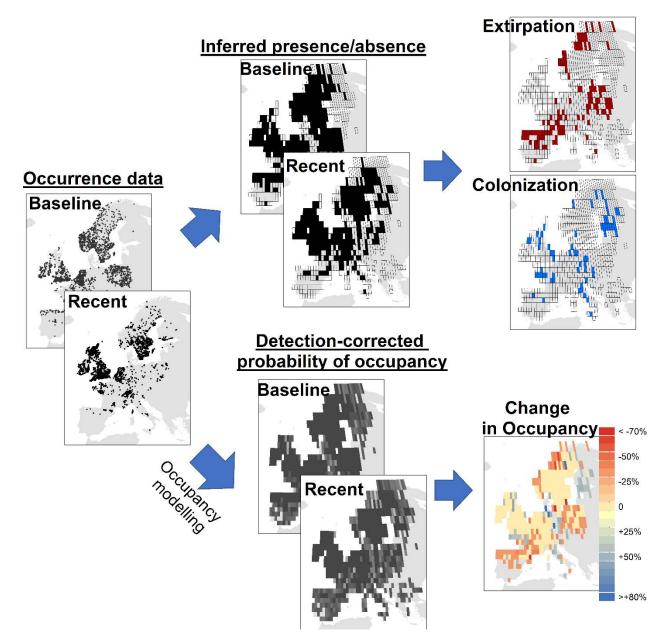


- 832 Figure S2. Density of unique location-year observations per 100km by 100km grid cell
- 833 across North America and Europe.
- 834
- 835

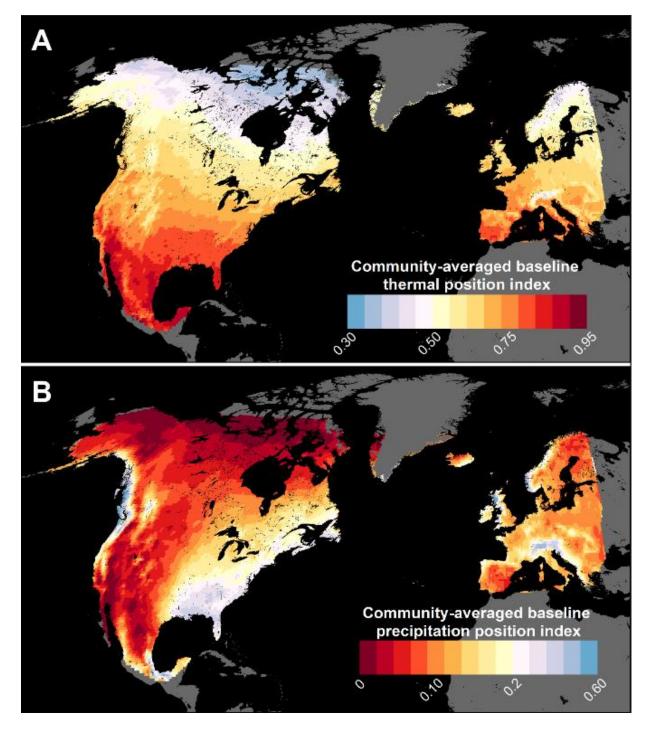


836

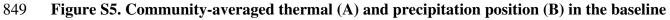
- **Figure S3.** Change in mean annual mean temperature (A) and mean total precipitation (B)
- 838 from the baseline (1901-1974) to the recent period (2000-2015) across North America and
- 839 Europe.
- 840



- 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*.

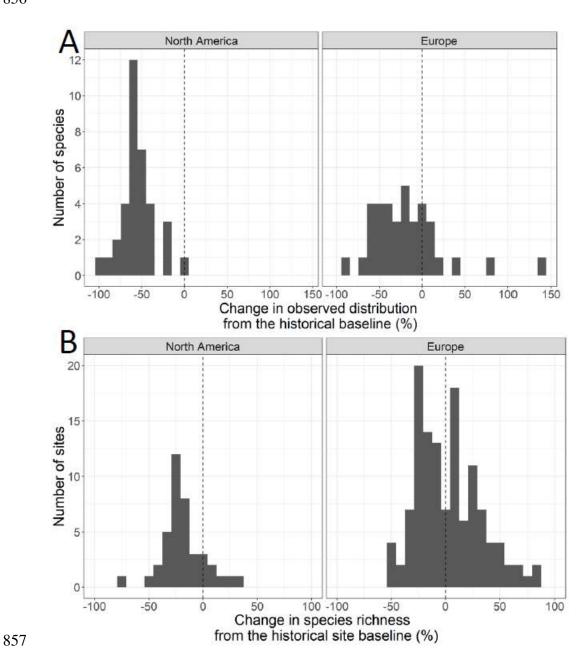


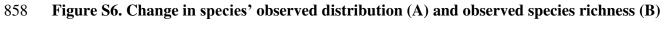


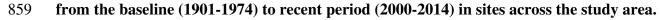


- 850 period (1901-1974) across North America and Europe. Both thermal and precipitation
- position indices have a potential range of 0 to 1. Zero indicates that species in the assemblage are
- 852 on average at their cold/dry tolerance limit for the entirety of the year in the period. One

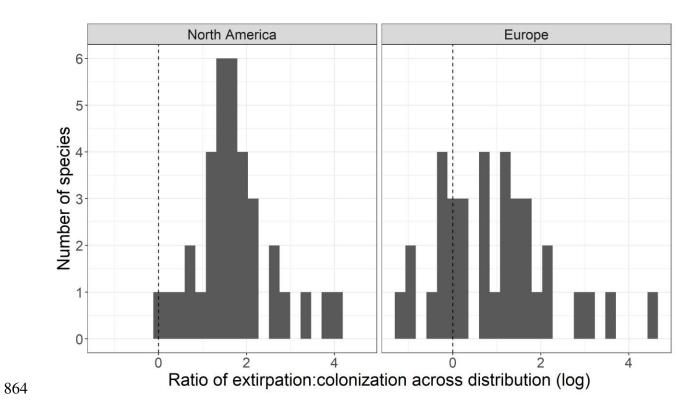
- 853 indicates that species in the assemblage are on average at their hot/wet tolerance limit for the
- entirety of the year in the period.
- 855





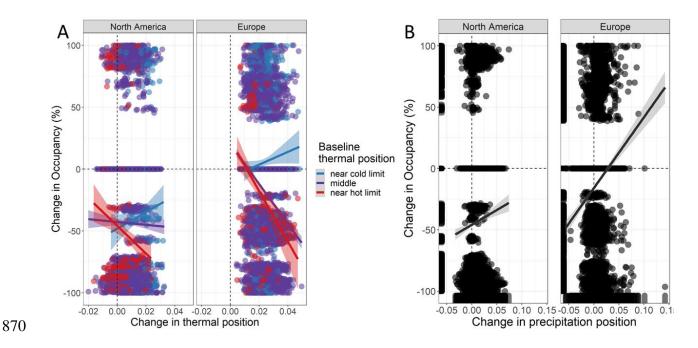


- 860 Observed species richness was only measured in sites with a minimum of 50 unique location-
- 861 year-species observations in the baseline and most recent period. N= 164.
- 862
- 863

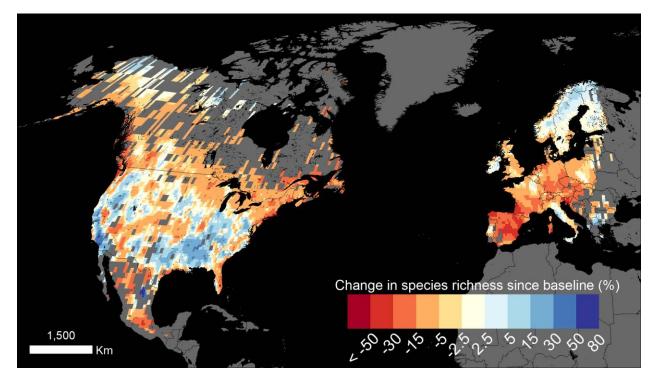


865 Figure S7. Ratio of local extirpation:colonization across species' observed distributions

<sup>866</sup> between the baseline (1900-1975) and recent period (2000-2015).



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 site are 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 thermal position variable has been split at the 1<sup>st</sup> and 3<sup>rd</sup> quantile to show sites that were 878 879 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 (±95%) are shown around linear trendlines.





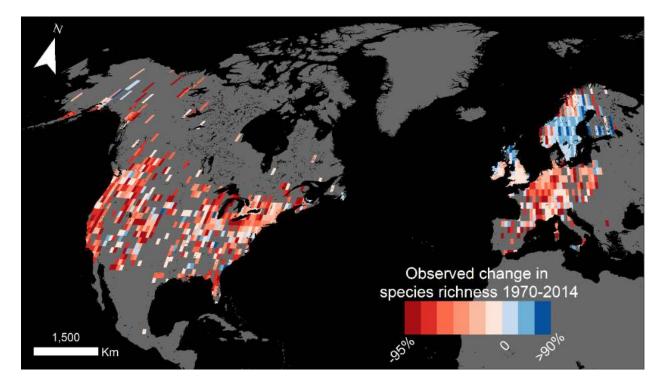
885 Figure S9. Spatial projections of climate change-related change in non-detection-corrected

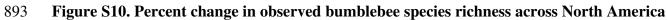
886 bumblebee species richness from a baseline period (1901-1974) to a recent period (2000-

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

- species richness as a function of mean community thermal and precipitation position ( $R^2 = 0.44$ ;
- 889 see Materials and Methods for model details).

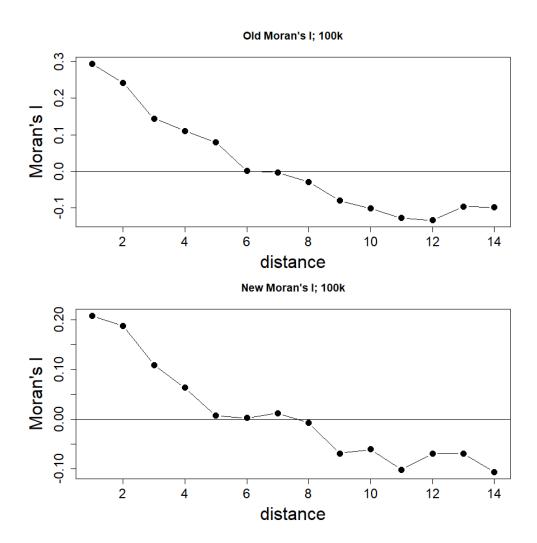
890





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.



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

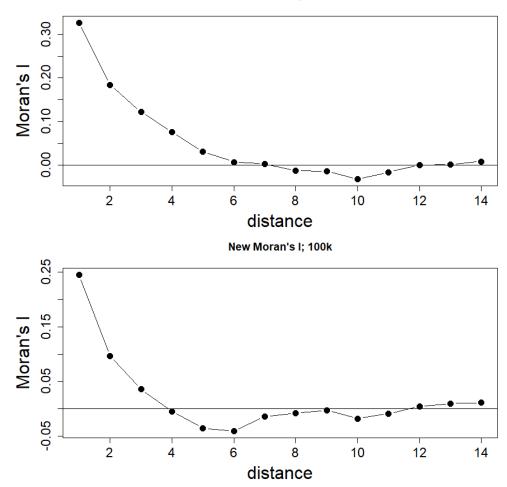
901 autoregressive (SAR) error model. SAR model was a significantly better fit (according to log

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

903

898

Old Moran's I; 100k



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

905

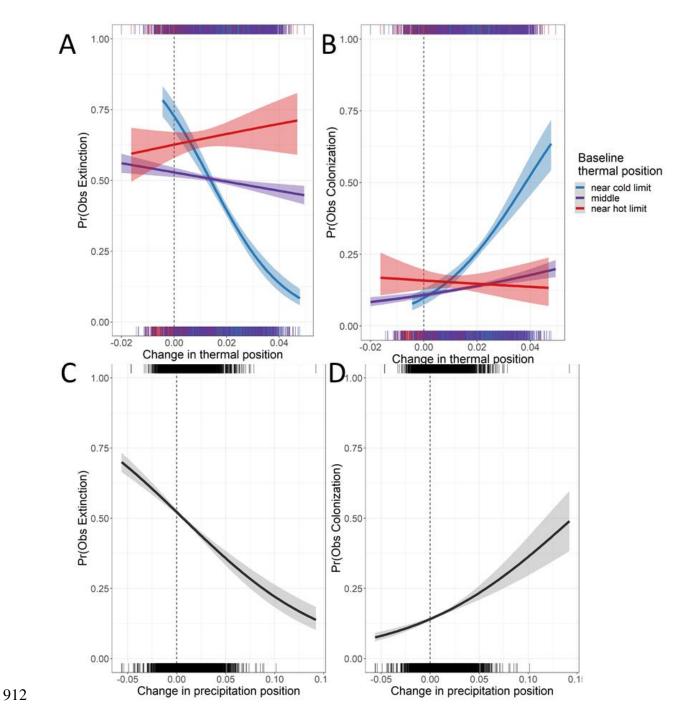


Figure S13. Probability of local extinction (A, C) and colonization (B, D) in response to
change in thermal (A, B) and precipitation (C, D) position from the baseline (1901-1974) to
recent period (2000-2014). Thermal and precipitation position ranges from 0 to 1, with 1
indicating conditions at a site 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

- 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 1<sup>st</sup> and 3<sup>rd</sup> 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 (±95%) are shown around
- 923 linear trendlines.
- 924

# 926 Supplementary Tables

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

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

**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<sup>2</sup> (for PGLMM) and adjusted-R<sup>2</sup> (for ANCOVA models).

	Occupan	cy (PGLMM)	Extinctio	on (PGLMM)	Coloniza	tion (PGLMM)	Species ric (ancova		Detecti corrected richness (a	species
	Posterior		Posterior		Posterior		Estimate	t	Estimate	t
	mean	95% CI	mean	95% CI	mean	95% CI	(SE)	value	(SE)	value
		-100.93 -					-10.94		-15.41	-
Intercept	-46.29	6.96	0.87	-1.53 - 3.21	-2.55	-4.750.32	(4.26)	-2.57	(0.52)	29.38
<u>Thermal position</u> variables										
Baseline (1st order				22.31 -			-161.33		-0.49	
polynomial)	-8.46	-10.396.33	27.38	32.65	-12.91	-19.856.16	(34.39)	-4.69	(0.43)	-1.14
Baseline (2nd order				12.43 -			-62.53			
polynomial)			17.44	22.16	13.27	6.77 - 19.46	(26.68)	-2.34		
Change since									-2.16	
baseline	-4.54	-6.083.01	0.29	0.23 - 0.36	-0.09	-0.170.01	-4.86 (2.92)	-1.67	(0.55)	-3.91
Baseline:Change									-2.77	
interaction	-10.76	-12.828.76	0.53	0.43 - 0.63	-0.43	-0.550.29	-9.74 (4.31)	-2.34	(0.44)	0
Precipitation positio	n variables									
Baseline (1st order						-39.56			-0.73	
polynomial)	-1.63	-3.040.25	-0.89	-7.39 - 6.14	-30.56	21.29	-5.57 (2.09)	-2.67	(0.44)	-1.64

Baseline (2nd order polynomial) Change since			-2.56	-8.56 - 2.96	13.56	6.53 - 20.55				
baseline Baseline:Change	3.9	2.55 - 5.13	-0.14	-0.210.09	0.21	0.13 - 0.29	-1.27 (2.47)	-0.51	0.26 (0.5) 0.47	0.53
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	(0.34)	1.38
<u>Climatic position inte</u> Baseline thermal:Baseline	eractions								0.00	
precipitation interaction Change in thermal:Change in	-0.05	-1.82 - 1.69	0.02	-0.05 - 0.1	0.12	0.03 - 0.21			-0.39 (0.39)	-1.01
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>									7.87	
Continent (Europe) Sampling Effort	39.35 	32.95 - 45.45	-1.98 -0.59	-2.221.71 -0.650.55	1.27 -0.17	0.96 - 1.56 -0.210.13	12.2 (5.13)	2.38	(1.13)	6.95 
<u>Random effects</u> Species	<u>Varian</u> 181.4	<u>ice (95% CI)</u> 117 - 256.2	<u>Varian</u> 0.3	<u>ce (95% CI)</u> <b>0.19 - 0.44</b>	<u>Variar</u> 0.26	nce (95% CI) <b>0.15 - 0.39</b>				
Model summary Number observations (n)	46	17-5264	30.	8-1035.5	118	5.5-1730.1	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-R<sup>2</sup>.

	Species richne	ess SAR	Detection-corre richness	-
	Estimate	z value	Estimate	z value
Intercept	-12.64 (11.27)	-1.12	-14.19 (1.98)	-7.16
Thermal position variables				
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
Precipitation position variables				
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 Change in thermal:Change in			0.36 (0.55)	0.65
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) Variation explained (R2)	164 0.44		184 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-R<sup>2</sup> (for ANCOVA models), and Nagelkerke pseudo-R<sup>2</sup>.

	Occupan	Occupancy (PGLMM)		Extinction (PGLMM)		Colonization (PGLMM)		chness VA)	Detection- corrected species richness (SAR error model)	
	Posterior		Posterior		Posterior		Estimate	t	Estimate	Z
	mean	95% CI	mean	95% CI	mean	95% CI	(SE)	value	(SE)	value
		-102.49 -					-15.62	-	<u> </u>	
Intercept	-46.47	10.76	0.91	-1.28 - 3.33	-2.96	-5.380.29	(0.56)	27.73	-14.2 (2)	-7.11
Thermal position variables										
Baseline (1st order				21.01 -			-0.67		-0.26	
polynomial)	-8.18	-10.296.18	26.77	31.65	-14.9	-246.14	(0.47)	-1.43	(0.85)	-0.31
Baseline (2nd order							× ,		× ,	
polynomial)			15.56	10.31 - 20.7	16.08	7.69 - 25.05				
P 0 1 J/						••••	-2.24		-1.95	
Change since baseline	-4.22	-5.752.68	0.29	0.22 - 0.34	-0.09	-0.19 - 0.01	(0.56)	-4.01	(0.64)	-3.06
Baseline:Change	••	<b>UNU</b>	<b>V1</b>		0.02	0.17 0.01	-2.7		-1.18	••••
interaction	-11.06	-13.098.93	0.52	0.43 - 0.61	-0.5	-0.680.34	(0.45)	-6	(0.56)	-2.1

Precipitation position variables

Baseline (1st order polynomial) Baseline (2nd order	-2	-3.440.58	1.9	-4.63 - 7.57	-35.49	-47.78 23.32	-0.59 (0.46)	-1.28	0.12 (0.62)	0.19
polynomial)			-4.05	-10.46 - 2.35	15.95	6.79 - 25.15				
Change since baseline Baseline:Change	3.78	2.46 - 5.03	-0.14	-0.20.09	0.24	0.14 - 0.34	0.25 (0.5) 0.48	0.5	0.32 (0.64) -0.04	0.5
interaction	-0.02	-0.76 - 0.74	0.02	-0.02 - 0.05	-0.03	-0.08 - 0.02	(0.34)	1.4	(0.38)	-0.1
Climatic position interactions	5									
Baseline thermal:Baseline	_						-0.32		0.36	
precipitation interaction	-0.3	-2.02 - 1.4	0.04	-0.04 - 0.11	0.13	0.03 - 0.25	(0.4)	-0.81	(0.55)	0.65
Change in thermal: Change	0.1	1.00 0.05	0.02	0.00	0.07	0 0 1 4	2.01	<b>F</b> 1 4	0.7	1.(2
in precipitation interaction	-0.1	-1.08 - 0.95	0.02	-0.02 - 0.06	0.07	0 - 0.14	(0.39)	5.14	(0.43)	1.63
<u>Human dominated land-</u> use										
							3.72		0.11	
Land-use change	-16.4	-27.336.46	0.92	0.44 - 1.39	-0.61	-1.3 - 0.15	(3.73)	1	(4.35)	0.03
Covariates							8.21		7.11	
Continent (Europe)	38.78	33.03 - 45.31	-1.96	-2.251.67	1.43	1 - 1.91	0.21 (1.18)	6.94	(3.74)	1.9
Sampling Effort			-0.57	-0.640.53	-0.19	-0.250.14				
r 8										
Random effects	<u>Variar</u>	nce (Std.dev.)	<u>Varian</u>	ce (Std.dev.)	<u>Varian</u>	ce (Std.dev.)				
Species	181.6	118.1 - 256.8	0.31	0.19 - 0.43	1.32	0.14 - 3.66				
N 11										
<u>Model summary</u> Number observations (n)	7	235-7500	18	4-1464.9	57	9-1551.6	184	0	184	0
Variation explained (R2)	12	0.11	10.	0.87	57.	0.27	0.0		0.1	
· manon explained (112)		····		,		··-/	0.0		5.1	•

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  $R^2$  (for PGLMM), ad`usted- $R^2$  (for ANCOVA models), and Nagelkerke pseudo-R2.

	Occupand	cy (PGLMM)	Extinctio	on (PGLMM)	Coloniza	ation (PGLMM)	Spec richn (ANCC	iess	Detect correct species r (SAR mod	cted richness error
	Posterior		Posterior		Posterior		Estimate	t	Estimate	/
	mean	95% CI	mean	95% CI	mean	95% CI	(SE)	value		value
		-115.76 -					-21.59		-21.02	i
Intercept	-53.03	10.83	1.54	-1.04 - 4.04	-2.27	-4.410.2	(0.28)	-78.3	(1.13)	-18.6
Thermal position variables										I
Baseline (1st order							-0.05			I
polynomial)	-6.17	-7.654.76	32.56	27.47 - 37.66	-16.86	-23.2511.77	(0.21)	-0.23	0.5 (0.4)	1.27
Baseline (2nd order										I
polynomial)			28.47	23.31 - 33.69	2.02	-3.6 - 7.4				
							-0.83		-0.63	I
Change since baseline	-3.45	-4.562.36	0.24	0.2 - 0.29	-0.21	-0.260.16	(0.29)	-2.87	(0.33)	-1.9
Baseline:Change							-1.41		-0.68	I
interaction	-7.12	-8.455.58	0.47	0.4 - 0.53	-0.32	-0.390.24	(0.22)	-6.29	(0.28)	-2.38

Precipitation position variables

Baseline (1st order polynomial)	-0.88	-2.02 - 0.19	0.73	-5.91 - 7.46	-23.4	-30.6115.15	-0.26 (0.21)	-1.23	0.13 (0.31)	0.44
Baseline (2nd order polynomial)			-10.36	-15.675.18	13.49	6.85 - 20.92	0.25		0.25	
Change since baseline Baseline:Change	4.99	4.01 - 6.04	-0.26	-0.30.22	0.22	0.17 - 0.27	(0.23 (0.24) 0.3	1.03	(0.23) (0.33) -0.01	0.76
interaction	-0.31	-0.97 - 0.38	0.08	0.05 - 0.11	-0.02	-0.05 - 0.02	(0.17)	1.81	(0.19)	-0.04
<u>Climatic position interaction</u> Baseline thermal:Baseline precipitation interaction	<u>s</u> 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	-0.090.02	0.01	-0.03 - 0.05	1.04 (0.2)	5.25	0.4 (0.23)	1.79
<u>Covariates</u>							3.96		3.06	
Continent (Europe) Sampling Effort	37.1 	31.46 - 42.32	-1.87 -0.53	-2.091.65 -0.560.5	1.46 -0.09	1.23 - 1.69 -0.110.07	(0.57)	6.95 	(1.97)	1.55 
Random effects Species	<u>Variar</u> 238.8	<u>nce (Std.dev.)</u> 160.1 - 334	<u>Variar</u> 0.37	<u>lce (Std.dev.)</u> 0.23 - 0.52	<u>Varia</u> 0.25	nce (Std.dev.) 0.16 - 0.36				
<u>Model summary</u> Number observations (n) Variation explained (R2)	50	000-5490 0.1	40	).3-5608 0.84	58	3.8-2410.7 0.61	485 0.0	-	485 0.0	-

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.

	Occupan	Occupancy (PGLMM)		Extinction (PGLMM)		tion (PGLMM)	Species richness (ANCOVA)		Detection- corrected specie richness (SAR error model)	
	Posterior		Posterior		Posterior		Estimate	t	Estimate	Z
	mean	95% CI	mean	95% CI	mean	95% CI	(SE)	value	(SE)	value
							5.23		6.75	-
Intercept	-36.36	-85.99 - 13.45	0.07	-2.85 - 2.79	-4.64	-12.080.63	(1.16)	4.52	(2.88)	2.35
Thermal position variables										
Baseline (1st order							1.46		-0.9	
polynomial)	-6.14	-9.063.06	13.46	6.36 - 21.36	-11.78	-33.65 - 1.39	(0.99)	1.47	(1.66)	-0.54
Baseline (2nd order							````			
polynomial)			12.3	5.42 - 19.56	35.46	15.18 - 81.11				
							-0.69		-1.88	
Change since baseline	-3.08	-5.231.06	0.22	0.09 - 0.37	0.1	-0.13 - 0.42	(1.18)	-0.58	(1.26)	-1.5
Baseline:Change							-5.5		-2.97	
interaction	-9.96	-12.876.94	0.54	0.33 - 0.81	-0.47	-1.160.08	(0.99)	-5.55	(1.11)	-2.69

Precipitation position variables

Baseline (1st order polynomial)	-2.89	-4.890.91	0.07	-7.03 - 7.34	-37.24	-83.914.07	-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	0.26		0.48	
Change since baseline Baseline:Change	4.33	2.59 - 6.08	-0.13	-0.250.02	0.49	0.17 - 1.15	(1.16) 0.77	0.23	(1.33) 0.48	0.36
interaction	0.26	-0.72 - 1.16	-0.05	-0.12 - 0.02	-0.12	-0.34 - 0.03	(0.94)	0.83	(0.99)	0.49
<u>Climatic position interaction</u> Baseline thermal:Baseline	<u>s</u>						1.1		1.28	
precipitation interaction Change in thermal:Change	1.07	-1.54 - 3.83	0.05	-0.07 - 0.2	0.28	-0.01 - 0.74	(0.89) 2.42	1.23	(1.09) 1.2	1.18
in precipitation interaction	0.57	-0.88 - 1.92	0.02	-0.06 - 0.09	0.25	0.05 - 0.59	(0.9)	2.68	(0.93)	1.29
<u>Covariates</u>							1.5		0.50	
Continent (Europe) Sampling Effort	38.47	31 - 45.34	-2.13 -0.72	-3.181.46 -0.930.54	1.55 -0.34	0.55 - 3.55 -0.790.14	-1.5 (2.52) 	-0.6 	-0.52 (5.76) 	-0.09 
Random effects Species	<u>Variar</u> 133.8	<u>nce (Std.dev.)</u> 75.62 - 193.4	<u>Varian</u> 0.41	<u>ce (Std.dev.)</u> 0.16 - 0.82	<u>Variar</u> 0.66	<u>ace (Std.dev.)</u> 0.09 - 2.47				
<u>Model summary</u> Number observations (n) Variation explained (R2)	41	181-5284 0.1	10.	5-1428.2 0.71	6	.5-382.6 0.14	584 0.0		584 0.1	

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  $R^2$  (for PGLMM), adjusted- $R^2$  (for ANCOVA models), and Nagelkerke pseudo- $R^2$ .

	Occupancy (PGLMM)		Extinction (PGLMM)		Colonizat	tion (PGLMM)	Species richness (ANCOVA)		Detection-corrected species richness (SAR error model)	
	Posterior		Posterior	Posterior			Estimate	t	Estimate	Z
	mean	95% CI	mean	95% CI	mean	95% CI	(SE)	value	(SE)	value
		-102.49 -					-15.36	-	-14.85	-
Intercept	-45.15	11.21	0.89	-1.41 - 3.21	-2.52	-4.730.33	(0.74)	20.69	(1.47)	10.09
										,
Thermal position										ļ
variables										<b>!</b>
Baseline (1st order										
polynomial)	-5.4	-7.183.58	20.67	15.2 - 25.93	-7.69	-14.720.65	-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				1
Change since										ļ
baseline	-3.69	-5.232.17	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	-11.247.75	0.44	0.35 - 0.52	-0.36	-0.470.26	-3.97 (0.59)	-6.71	-2.94 (0.66)	-4.46
Draginitation position	n voriablaa									

Precipitation position variables

Baseline (1st order polynomial) Baseline (2nd order	-1.93	-3.340.5	0.63	-6 - 6.94	-33.81	-42.725.37	-1 (0.58)	-1.74	-0.61 (0.67)	-0.91
polynomial)			-5.52	-11.5 - 0.4	15.51	8.38 - 22.84				
Change since baseline Baseline:Change	4.63	3.21 - 6.01	-0.19	-0.250.13	0.25	0.16 - 0.33	0.4 (0.65)	0.61	1.11 (0.76)	1.46
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 inte</u> Baseline thermal:Baseline precipitation										
interaction Change in thermal:Change in precipitation	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
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
Covariates										
Continent (Europe) Sampling Effort	38.03 	31.62 - 44.05	-1.99 -0.56	-2.291.7 -0.620.51	1.26 -0.17	0.93 - 1.59 -0.210.13	9.48 (1.51)	6.29 	10.17 (2.63) 	3.87 
Random effects Species	<u>Variar</u> 185.1	<u>nce (Std.dev.)</u> 115.6 - 256	<u>Varian</u> 0.3	<u>ce (Std.dev.)</u> 0.18 - 0.43	<u>Varian</u> 0.27	<u>ice (Std.dev.)</u> 0.16 - 0.4				
<u>Model summary</u> Number observations (n) Variation explained	4596-5481		69.4-2453.7		201.6-4627.8		1374		1374	
(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  $R^2$  (for PGLMM), adjusted- $R^2$  (for ANCOVA models), and Nagelkerke pseudo- $R^2$ .

	Occupan	cy (PGLMM)	Extinction	on (PGLMM)	Colonizat	ion (PGLMM)	Species richness (ANCOVA)		Detection- corrected species richness (SAR error model)	
	Posterior		Posterior		Posterior		Estimate	t	Estimate	Z
	mean	95% CI	mean	95% CI	mean	95% CI	(SE)	value	(SE)	value
							-14.76	-	-13.73	
Intercept	-43.16	-96.07 - 13.89	0.8	-1.56 - 2.98	-2.56	-4.880.25	(0.91)	16.27	(2.16)	-6.34
Thermal position variables										
Baseline (1st order							0.37		1.4	
polynomial)	-3.81	-5.572.12	17	11.13 - 22.42	-4.41	-11.67 - 2.67	(0.65)	0.58	(1.01)	1.39
Baseline (2nd order										
polynomial)			12.82	6.57 - 17.84	14.83	8.72 - 21.08				
							-2.96		-2.37	
Change since baseline	-3.47	-5.051.9	0.25	0.19 - 0.31	-0.07	-0.15 - 0.02	(0.92)	-3.21	(1.06)	-2.24
Baseline:Change							-4.66		-2.43	
interaction	-9.07	-10.737.5	0.42	0.34 - 0.5	-0.32	-0.420.22	(0.66)	-7.05	(0.83)	-2.92
monucion	-7.07	-10,757,5	V•74	0.54 - 0.5	-0.54	-0.720.22	(0.00)	-1.03	(0.03)	- 20 - 2

Precipitation position variables

Baseline (1st order polynomial)	-1.99	-3.470.59	-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	-12.941.84	16.85	9.68 - 23.69				
Change since baseline	4.7	3.39 - 6.19	-0.19	-0.260.11	0.26	0.18 - 0.35	0.62 (0.76) 0.37	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	(0.49)	0.75	-0.38 (0.53)	-0.72
<u>Climatic position interactions</u> Baseline thermal:Baseline	<u>.</u>						-0.17		0.17	
precipitation interaction	0.31	-1.11 - 1.65	-0.02	-0.07 - 0.04	0.08	0.02 - 0.16	(0.51) <b>2.16</b>	-0.34	(0.69) 0.74	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	2.10 (0.61)	3.56	0.74 (0.69)	1.07
<u>Covariates</u>							9.44		0 11	
Continent (Europe) Sampling Effort	<b>38.09</b> 	31.68 - 44.28	-1.97 -0.54	-2.271.67 -0.60.48	1.34 -0.17	0.99 - 1.67 -0.210.13	9.44 (1.74) 	5.42	8.44 (3.63) 	2.32
<u>Random effects</u> Species	<u>Variar</u> 185.9	<u>nce (Std.dev.)</u> 120.9 - 265.9	<u>Variar</u> 0.3	nce (Std.dev.) 0.18 - 0.43	<u>Varian</u> 0.31	<u>ce (Std.dev.)</u> 0.17 - 0.46				
<u>Model summary</u> Number observations (n) Variation explained (R2)	50	000-5324 0.1	25	.3-2121.9 0.86	175	.4-3736.8 0.53	113 0.1	-	113 0.1	-

#### 938 Supplemental references

- 939 21. 21. C. Polce, J. Maes, X. Rotllan-Puig, D. Michez, L. Castro, B. Cederberg, et al.,
- 940 Distribution of bumblebees across europe. One Ecosyst. 3 (2018),
- 941 doi:10.3897/oneeco.3.e28143.
- 942 22. S. G. Potts, J. C. Biesmeijer, R. Bommarco, A. Felicioli, M. Fischer, P. Jokinen, et al.,
- 943 Developing European conservation and mitigation tools for pollination services:
- 944 approaches of the STEP (Status and Trends of European Pollinators) project. J. Apic. Res.
  945 50, 152–164 (2011).
- 946 23. P. H. Williams, R. W. Thorp, L. L. Richardson, S. R. Colla, Bumble bees of North

947 America: an identification guide (Princeton University Press, 2014).

- 948 24. P. Rasmont, M. Franzén, T. Lecocq, A. Harpke, S. P. M. Roberts, J. C. Biesmeijer, et al.,
  949 Climatic Risk and Distribution Atlas of European Bumblebees (Biorisk 10 (Special Issue),
- 950 2015).
- 951 25. N. J. Gotelli, A. Chao, in Encyclopedia of Biodiversity (Elsevier, Waltham, MA, 2013;
- 952 http://www.sciencedirect.com/science/article/pii/B9780123847195004032), vol. 5, pp.
- 953 195–211.
- 954 26. N. J. Gotelli, R. K. Colwell, in Biological Diversity: Frontiers in measurement and

955 assessment, A. E. Magurran, B. J. McGill, Eds. (Oxford University Press, New York, NY,

- 956 2011; http://www.uvm.edu/~ngotelli/manuscriptpdfs/Chapter 4.pdf), pp. 39–54.
- 957 27. R Core Team, R: A Language and Environment for Statistical Computing. R Found. Stat.
  958 Comput. 1 (2017), p. 2673.
- 959 28. H. Wickham, tidyverse: Easily Install and Load "Tidyverse" Packages (2017), (available
  960 at https://cran.r-project.org/package=tidyverse).

- 961 29. R. Hijmans, J. van Etten, J. Cheng, M. Mattiuzzi, M. Sumner, J. A. Greenberg, et al.,
  962 Package ' raster '. CRAN -R.2.5-8 (2016) (available at http://cran.r-
- 963 project.org/package=raster).
- 30. J. A. Royle, M. Kéry, A Bayesian State-Space Formulation of Dynamic Occupancy
  Models. Ecology. 88, 1813–1823 (2007).
- 966 31. D. I. MacKenzie, J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, J. E. Hines,
- 967 Occupancy Estimation and Modeling : Inferring Patterns and Dynamics of Species
  968 Occurrence (Elsevier Academic Press Inc., 2006).
- 969 32. J. A. Royle, R. M. Dorazio, in Hierarchical Modeling and Inference in Ecology (2009;
- 970 http://linkinghub.elsevier.com/retrieve/pii/B9780123740977000119), pp. 297–324.
- 33. M. Kéry, M. Schaub, in Bayesian Population Analysis using WinBUGS, M. Kéry, M.
  Schaub, Eds. (Academic Press, Boston, 2012;
- 973 http://www.sciencedirect.com/science/article/pii/B9780123870209000134), pp. 413–461.
- 974 34. D. I. MacKenzie, J. D. Nichols, M. E. Seamans, R. J. Gutierrez, Modeling species
- 975 occurance dynamics with multiple states and imperfect detection. Ecology. 90(3), 823–
  976 835 (2009).
- 977 35. C. T. Rota, R. J. Fletcher, R. M. Dorazio, M. G. Betts, Occupancy estimation and the
  978 closure assumption. J. Appl. Ecol. 46, 1173–1181 (2009).
- M. A. Jarzyna, W. Jetz, A near half-century of temporal change in different facets of avian
  diversity. Glob. Chang. Biol. 23, 2999–3011 (2017).
- 981 37. R. Bivand, T. Keitt, B. Rowlingson, rgdal: Bindings for the Geospatial Data Abstraction
  982 Library (2017), (available at https://cran.r-project.org/package=rgdal).
- 983 38. M. Plummer, JAGS : A program for analysis of Bayesian graphical models using Gibbs

984 sampling JAGS : Just Another Gibbs Sampler (2003).

- 985 39. Y.-S. Su, M. Yajima, R2jags: Using R to Run "JAGS" (2015), (available at https://cran.r986 project.org/package=R2jags).
- 987 40. S. P. Brooks, A. Gelman, General Methods for Monitoring Convergence of Iterative
- 988 Simulations General Methods for Monitoring Convergence of Iterative Simulations. J.
- 989 Comput. Graph. Stat. 7, 434–455 (1998).
- 41. I. Harris, P. D. Jones, T. J. Osborn, D. H. Lister, Updated high-resolution grids of monthly
  climatic observations the CRU TS3.10 Dataset. Int. J. Climatol. 34, 623–642 (2014).
- 992 42. S. Nakagawa, H. Schielzeth, A general and simple method for obtaining R2 from
- generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142 (2013).
- 994 43. S. A. Cameron, H. M. Hines, P. H. Williams, A comprehensive phylogeny of the bumble
  995 bees (Bombus). Biol. J. Linn. Soc. 91, 161–188 (2007).
- 996 44. J. D. Hadfield, MCMC Methods for Multi-Response Generalized Linear Mixed Models:
- 997 The MCMCglmm R Package. J. Stat. Softw. 33, 1–22 (2010).
- 998 45. E. Paradis, K. Schliep, ape 5.0: an environment for modern phylogenetics and
- 999 evolutionary analyses in R (vers. 5.3). Bioinformatics. 35, 526–528 (2018).
- 1000 46. P. de Villemereuil, S. Nakagawa, in Modern Phylogenetic Comparative Methods and
- 1001 Their Application in Evolutionary Biology: Concepts and Practice, L. Z. Garamszegi, Ed.
- 1002 (Springer Berlin Heidelberg, Berlin, Heidelberg, 2014; https://doi.org/10.1007/978-3-6621003 43550-2\_11), pp. 287–303.
- 1004 47. M. P. Arbetman, G. Gleiser, C. L. Morales, P. Williams, M. A. Aizen, Global decline of
- 1005 bumblebees is phylogenetically structured and inversely related to species range size and
- 1006 pathogen incidence. Proc. R. Soc. B. 284, 20170204 (2017).

- 48. W. D. Kissling, G. Carl, Spatial autocorrelation and the selection of simultaneous
  autoregressive models. Glob. Ecol. Biogeogr. 17, 59–71 (2008).
- 1009 49. C. F. Dormann, J. M. McPherson, M. B. Araújo, R. Bivand, J. Bolliger, G. Carl, et al.,
- 1010 Methods to account for spatial autocorrelation in the analysis of species distributional
- 1011 data: A review. Ecography (Cop.). 30, 609–628 (2007).
- 1012 50. D. Bates, M. Machler, B. M. Bolker, S. C. Walker, Fitting linear mixed-effects models
  1013 using lme4. J. Stat. Softw. 67, 1–48 (2015).
- 1014 51. R. Bivand, G. Piras, Comparing Implementations of Estimation Methods for Spatial
- 1015 Econometrics. J. Stat. Softw. 63 (2015), doi:10.18637/jss.v063.i18.
- 1016 52. G. C. Hurtt, L. P. Chini, S. Frolking, R. A. Betts, J. Feddema, G. Fischer, et al.,
- 1017 Harmonization of land-use scenarios for the period 1500-2100: 600 years of global
- 1018 gridded annual land-use transitions, wood harvest, and resulting secondary lands. Clim.
- 1019 Change. 109, 117–161 (2011).
- 1020 53. B. Sinervo, F. Mendez-de-la-Cruz, D. B. Miles, B. Heulin, E. Bastiaans, M. Villagran-
- 1021 Santa Cruz, et al., Erosion of Lizard Diversity by Climate Change and Altered Thermal
- 1022 Niches. Science. 328, 894–899 (2010).
- 1023 54. J. M. Sunday, A. E. Bates, N. K. Dulvy, Thermal tolerance and the global redistribution of
  1024 animals. Nat. Clim. Chang. 2, 686–690 (2012).
- 1025 55. A. De Palma, M. Kuhlmann, S. P. M. Roberts, S. G. Potts, L. Börger, L. N. Hudson, et al.,
- 1026 Ecological traits affect the sensitivity of bees to land-use pressures in European
- 1027 agricultural landscapes. J. Appl. Ecol. 52, 1567–1577 (2015).
- 1028 56. C. P. Nadeau, M. C. Urban, J. R. Bridle, Coarse climate change projections for species
- 1029 living in a fine-scaled world. Glob. Chang. Biol. 23, 12–24 (2017).

- 1030 57. C. P. Nadeau, M. C. Urban, J. R. Bridle, Climates Past, Present, and Yet-to-Come Shape
- 1031 Climate Change Vulnerabilities. Trends Ecol. Evol. 32, 786–800 (2017).
- 1032 58. T. M. Blackburn, K. J. Gaston, Scale in macroecology. Glob. Ecol. Biogeogr. 11, 185–189
- 1033 (2002).