Climate change and land-use change impacts on bumblebees

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“What you do makes a difference, and you have to decide what kind of difference you want to make.”

- Jane Goodall

"Everybody likes bumblebees."

- Bumble Bees of North America (2014), by Paul Williams, Robbin Thorp, Leif Richardson, and Sheila Colla

"I knew I’d done something harder than I’d ever done in my life, and I knew I’d never work that hard again."

- Brett Beattie, uncredited stunt double for Gimli in Peter Jackson's Lord of the Rings Trilogy

Abstract

Biodiversity is declining across the globe, and human-driven climate change and land-use change are among the primary drivers of this loss. Understanding the mechanisms causing declines is critical for developing effective conservation and management strategies which will not only slow biodiversity loss, but reverse it. This is relevant for virtually all species on the planet, but given the ecosystem services that they provide, pollinators are an especially important group in which to study this. Among the wild pollinators native to North America and Europe, bumblebees (*Bombus*) are a particularly important and beautiful group. In this thesis, I identify how climate change and land-use change interact to influence population and community change in North American and European bumblebees, and I explore the potential role of protected areas in mitigating declines. I find that climate change has increased local extinction risk for bumblebees by exposing them to temperatures beyond their historic tolerances, and I introduce a broadly applicable method which improves prediction of this climate change-related risk (Chapter 2). Examining the interactions between climate change and land-use change shows that the risk from increasing temperatures and temperature extremes is worse in historically degraded areas, and that climate change and land-use change may be driving biotic homogenization in bumblebee communities. Yet, landscape-scale patterns suggest that human land-use can be managed to have minimal, or even positive, effects on pollinators (Chapter 3). In the face of these global pressures, protected areas represent one way to conserve species. I find that increasing the amount of protected area in a region, regardless of size or management category of the protected areas, is related to reduced local extinction risk for bumblebees across North America and Europe. This benefit is especially strong in areas with high human land-use, highlighting the importance of protected areas in highly human-dominated landscapes (Chapter 4). The work within my thesis improves our understanding of how climate change and land-use change drive shifts in species and communities, and can inform on the effectiveness of specific conservation actions from gardens and urban greenspaces, to Other Effective Area-Based Conservation Measures (Chapter 5).

Résumé

La biodiversité diminue à travers le monde, et les principaux facteurs de cette perte sont le changement climatique et le changement d'utilisation des terres induits par l'homme. Nous devons comprendre les mécanismes à l'origine du déclin si nous voulons développer des stratégies de conservation et de gestion efficaces qui non seulement ralentiront la perte de biodiversité, mais l'inverseront. Ceci est pertinent pour pratiquement toutes les espèces de la planète, mais les pollinisateurs sont un groupe particulièrement important dans lequel étudier cela compte tenu des services écosystémiques qu'ils fournissent. Parmi les pollinisateurs sauvages originaires d'Amérique du Nord et d'Europe, les bourdons (Bombus) constituent un groupe particulièrement important et magnifique. Dans cette thèse, j'identifie comment le changement climatique et le changement d'utilisation des terres interagissent pour influencer le changement des populations et des communautés des bourdons d'Amérique du Nord et d'Europe. J'explore également le rôle potentiel des aires protégées dans l'atténuation des déclins. Je constate que le changement climatique a augmenté le risque d'extinction locale pour les bourdons en les exposant à des températures au-delà de leurs tolérances historiques et j'introduis une méthode largement applicable qui améliore la prédiction de ce risque lié au changement climatique (chapitre 2). L'étude des interactions entre le changement climatique et le changement d'utilisation des terres montre que le risque de réchauffement et de températures extrêmes est pire dans les zones historiquement dégradées, et que le changement climatique et le changement d'utilisation des terres peuvent conduire à l'homogénéisation biotique des communautés de bourdons. Pourtant, les modèles à l'échelle du paysage suggèrent que l'utilisation des terres peut être gérée pour avoir des effets minimes, voire positifs, sur les pollinisateurs (chapitre 3). Face à ces pressions mondiales, les aires protégées représentent un moyen de conserver les espèces. Je trouve que l'augmentation du nombre d'aires protégées dans une région, quelle que soit la taille ou la catégorie de gestion des aires protégées, est liée à une réduction du risque d'extinction locale des bourdons en Amérique du Nord et en Europe. Cet avantage est particulièrement fort dans les zones à forte utilisation humaine des terres, soulignant l'importance des aires protégées dans les paysages fortement dominés par l'homme (chapitre 4). Le travail de ma thèse améliore notre compréhension de la façon dont le changement climatique et le changement d'utilisation des terres entraînent des changements dans les espèces et les communautés. Ce travail peut renseigner sur l'efficacité d'actions de conservation spécifiques, des jardins et des espaces verts urbains aux autres mesures de conservation efficaces par zone (chapitre 5).

Acknowledgments

…a.k.a.: "This is my version of a shout-out track"

The shout-out track, or sometimes simply "the outro", is a sacred tradition in hip-hop and rap. From Jay Z's "*My 1st Song*", to Kanye West's *"Last Call",* or "*Note to Self"* by J. Cole, virtually every artist has a song dedicated to expressing gratitude for the people around them who have helped them succeed. In the 5 years since I began the road to a PhD, I've noted a surprising number of parallels between the path to a doctorate and the purported path to hip-hop stardom, but the shout-out track, or "Acknowledgements section", is by far my favorite. Given the enormous privilege and cast of friends and family that have helped me get to this point, it's a special feeling to have one section in this final piece of work where I can express some of the deep gratitude and thanks to all of these people.

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Indigenous affirmation

> *Ni manàdjiyànànig Màmìwininì Anishinàbeg, ogog kà nàgadawàbandadjig iyo akì eko weshkad. Ako nongom ega wìkàd kì mìgiwewàdj.*
>
> *Ni manàdjiyànànig kakina Anishinàbeg ondaje kaye ogog kakina eniyagizidjig enigokamigàg Kanadàng eji ondàpinangig endàwàdjin Odàwàng.*
>
> *Ninisidawinawànànig kenawendamòdjig kije kikenindamàwin; weshkinìgidjig kaye kejeyàdizidjig.*
>
> *Nigijeweninmànànig ogog kà nìgànì sòngideyedjig; weshkad, nongom; kaye àyànikàdj.*

> *We pay respect to the Algonquin people, who are the traditional guardians of this land. We acknowledge their longstanding relationship with this territory, which remains unceded.*
>
> *We pay respect to all Indigenous people in this region, from all nations across Canada, who call Ottawa home.*
>
> *We acknowledge the traditional knowledge keepers, both young and old.*
>
> *And we honour their courageous leaders: past, present, and future.*

With the above affirmation (provided by the University of Ottawa Indigenous Affaires team), I would like to thank and acknowledge the Algonquin Anishinaabe Nation for the many generations of stewardship of the land where I have worked and lived over the last nine years. A land acknowledgement or affirmation is only a small step towards reconciliation and is the least that I can do after living and studying within the traditional territories of the Algonquin Anishinaabe during my PhD.

I also acknowledge my own settler history and the colonial history of the University of Ottawa, which was founded by a Catholic order who ran at least 34% of residential schools in Canada [1]. I also acknowledge that my own field of study (conservation biology and ecology) is often framed in colonial and anti-Indigenous worldviews, and that this needs to change.

My PhD research, which studies climate change and land-use change impacts on bumblebees across Turtle Island (North America) and western Europe, covers the traditional territories of hundreds of Indigenous nations and communities. There are too many to name here, although some can be found here: native-land.ca/ .

[1] - https://nctr.ca/joint-statement-nctr-to-work-with-the-oblates-to-access-residential-school-records/

Official statement of work

Within the following chapters the research ideas, written content, analyses, and figures are my own work, although my co-authors (especially my supervisor) provided invaluable advice, guidance, and support. For all chapters, I led the design, analyses, interpretation, and writing of the work.

Chapter 2 has been published in the peer-reviewed journal *Science*, with the following citation (thanks to subject editor Dr. Sacha Vignieri and several anonymous reviewers for their suggestions and comments that substantially improved the final manuscript):

> Soroye P, Newbold T, Kerr J. 2020. Climate change contributes to widespread declines among bumble bees across continents. Science 367:685–688. Available from https://www.sciencemag.org/lookup/doi/10.1126/science.aax8591.

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> Coristine LE, Soroye P, Soares RN, Robillard C, Kerr JT. 2016. Dispersal Limitation, Climate Change, and Practical Tools for Butterfly Conservation in Intensively Used

Landscapes. Natural Areas Journal 36:440–452. http://www.bioone.org/doi/10.3375/043.036.0410.

Jeanson AL et al. 2019. Twenty actions for a “good Anthropocene”—perspectives from early-career conservation professionals. Environmental Reviews. 28(1): 99-108. https://doi.org/10.1139/er-2019-0021

Cooke SJ et al. 2021. Ten considerations for conservation policy makers for the post-COVID-19 transition. Environmental Reviews. 29(2): 111-118. https://doi.org/10.1139/er-2021-0014

Ethier JP, Fayard A, Soroye P, Choi D, Mazerolle MJ, Trudeau VL. 2021. Life history traits and reproductive ecology of North American chorus frogs of the genus Pseudacris (Hylidae). Frontiers in Zoology 18:1–18. https://doi.org/10.1186/s12983-021-00425-w

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Chapter 1: General introduction

Global biodiversity is changing rapidly due to a combination of factors, and there is little doubt that the world has entered a biodiversity crisis (Dirzo et al. 2014; Ceballos et al. 2017; Ripple et al. 2017). Consistently, studies using long-term temporal monitoring data observe substantial rates of decline across wildlife populations around the globe. The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) estimates that around 1 million species may already be facing extinction from human pressures (IPBES 2019). The World Wildlife Fund's Living Planet Report, which compiles temporal data for more than 20,000 vertebrate populations globally, shows an average ~68% decline in the abundances of globally monitored terrestrial and marine vertebrate populations (WWF 2020), although declines tend to be clustered in certain taxa and regions (Leung et al. 2020). Invertebrates, which comprise the majority of species on Earth, appear to be declining as well, although they are much less studied and trends are consequently less certain (Dirzo et al. 2014; Cardoso et al. 2020; Wagner 2020; Raven & Wagner 2021). Nonetheless, declines consistently appear to be the norm among monitored taxa. Of the invertebrates assessed by the International Union for Conservation of Nature (IUCN), for example, about 40% are considered threatened (Dirzo et al. 2014). While determining the exact level and extent of biodiversity decline is complex (e.g., Dornelas et al. 2013, Vellend et al. 2013, but see Thomas 2013; Newbold et al. 2015; Gonzalez et al. 2016; Wagner 2020), there is no doubt that global rates of extinction are orders of magnitude above the background rate (Pimm et al. 2014; De Vos et al. 2015). Arresting declines and bending the curve of biodiversity loss is possible, and will require a deep understanding of the mechanisms driving biodiversity decline so that we may apply effective, equitable, and integrative conservation solutions (Urban et al. 2016; Mace et al. 2018; Leclère et al. 2020).

Two of the primary drivers of this biodiversity crisis appear to be climate change and land-use change. Climate shapes the distribution of life across the planet (Hawkins et al. 2003; Currie et al. 2004), and rapid anthropogenically-induced climate change has led to widespread and pervasive shifts across species and communities (Parmesan & Yohe 2003; Scheffers et al. 2016; Pecl et al. 2017). Climate change is increasingly implicated in greater extinction risk, and the threat that it presents is expected to grow (Urban 2015; Trisos et al. 2020). Many mechanisms may govern species' responses to climate change, but one consistently supported mechanism is grounded in niche theory.

Niche theory and physiology suggest that species' physiological limits might define whether they persist in some areas and help to inform predictions on climate change effects (Addo-Bediako et al. 2000; Nguyen et al. 2011; Sunday et al. 2012, 2014). Individuals of a species are less likely to persist in or colonize areas where the climate trends surpass their tolerance limits, as in these regions they may be forced to put more energy towards coping with the environment (e.g., through thermoregulation), and less to foraging or reproduction (Deutsch et al. 2008; Scheffers et al. 2014; Sunday et al. 2014). As rapid climate change alters local climatic conditions, some currently inhabited regions may be rendered less suitable, and some unoccupied regions more suitable. Under these conditions, niche theory predicts that species will shift their ranges to track changes (although shifts in phenology may help offset the need for geographic shifts, e.g., Singer 2017). Range shifts consistent with this expectation have been observed across many taxa, particularly in response to temperature (Parmesan & Yohe

2003; Tingley et al. 2009; Sunday et al. 2012; Kerr et al. 2015). Where species are not able to shift with climate, whether because of geographic barriers or dispersal limitations, we expect increasing extinction risk as greater portions of the species' range become less suitable (Sinervo et al. 2010; Kerr 2020).

Land-use change, including conversions to human-dominated land uses and accompanying intensification of this use, is perhaps the greatest threat that biodiversity faces currently (Maxwell et al. 2016), although climate change is expected to surpass it in the near future (Newbold 2018). More than 75% of ice-free land on the planet has been altered by humans (Ellis & Ramankutty 2008), and this land-use change has driven substantial losses of species from local assemblages across the globe (Newbold et al. 2015, 2016; Pfeifer et al. 2017; Di Marco et al. 2018). Changes in land use intensity (e.g., increases in pesticide or fertilizer use) can have distinct additional negative impacts (Kerr & Cihlar 2003; Gibbs et al. 2009; Pekin & Pijanowski 2012; Newbold et al. 2015; Millard et al. 2021). In addition to the direct negative effects of land-use change on biodiversity, it is likely that this pressure interacts with climate change and vice versa (Mantyka-Pringle et al. 2015; Jarzyna et al. 2016; Newbold 2018; Williams & Newbold 2020), although the mechanisms and effects of these potential interactions are not clear (Titeux et al. 2016, 2017).

In the face of these threats, protected areas (and other effective area-based conservation measures) are one of the most critical tools in conservation, especially at continental or global scales (Maxwell et al. 2020). Globally, protected areas contain higher species richness inside than in similar areas outside (Coetzee et al. 2014; Gray et al. 2016), and can improve biodiversity outcomes when properly managed (Geldmann et al. 2018; Boakes et al. 2018). Yet, protected areas are no silver bullet for conservation. Their placement is often chosen for reasons other than biodiversity conservation (Joppa & Pfaff 2009; Venter et al. 2018), and their efficacy at reducing pressures within their boundaries is variable (Joppa & Pfaff 2011; Geldmann et al. 2019). Ultimately, the efficacy of protected areas varies among taxa and species (Coetzee et al. 2014; Gray et al. 2016; Wagner 2020), and some taxa may require alternative or complementary conservation actions to mitigate climate change and land-use change related declines.

Pollinators are especially important when considering the response of fauna to threats like land use and climate change, because of the critical ecological services that they provide (Biesmeijer et al. 2006; Ricketts et al. 2008; Potts et al. 2010; Mallinger & Gratton 2015). Bumblebees (*Bombus*) are an important and beautiful group of pollinators, which have been documented as declining across North America and Europe (Biesmeijer et al. 2006; Williams & Osborne 2009; Potts et al. 2010, 2015; IPBES 2016). About a third of all bumblebee species that have been assessed by the IUCN are listed as threatened with extinction (Arbetman et al. 2017), although a few species have increased in range and abundance in recent decades (Colla & Packer 2008). Unlike most insects, bumblebees are endothermic poikilotherms, and can maintain a surprising control over their body temperature (Heinrich & Esch 1994). Yet, bumblebees remain relatively sensitive to changes in their environment, especially temperature, so climate change may be especially threatening to these species by pushing them near or beyond their thermal tolerance limits (Williams et al. 2007; Iserbyt & Rasmont 2012; Rasmont & Iserbyt 2012; Kerr et al. 2015). Declines in range size and species richness observed for this taxa appear to correlate with recent anthropogenic climate change (Rasmont

& Iserbyt 2012; Kerr et al. 2015; Woodard 2017), and range losses due to climate change are expected to increase in the future (Rasmont et al. 2015; Sirois-Delisle & Kerr 2018). Bumblebees also appear sensitive to land use change and intensification (including pesticide use; Ricketts et al. 2008; De Palma et al. 2017; Woodcock et al. 2017; Millard et al. 2021), but precise mechanisms of decline in this group are still relatively unknown. Given the recent publication of a large temporal occurrence dataset for North American and European bumblebees (Kerr et al. 2015), these pollinators represent an exciting model group with which to investigate large-scale, historic influences of climate change and land-use change.

In this thesis, I investigate the historic effect of climate change and land-use change on bumblebees across North America and Europe, testing for evidence of specific mechanisms of decline and investigating the efficacy of potential conservation solutions. In my first study (Chapter 2) I test whether climate change threatens bumblebee biodiversity by exposing species to climatic conditions beyond their historic tolerances. I also develop and introduce a novel method to measure this risk which appears to improve our ability to predict spatially explicit climate change-related risk across a species' range. In my second study (Chapter 3), I test whether land-use and climate change interactions have shaped historic trends in bumblebee biodiversity, and find that these interactions appear important and consistent with previously described mechanisms of climate change and land-use risk. Next (Chapter 4), I test whether protected areas have mitigated climate change and land-use change risks for species and assemblages, and find that while protected areas appear to offer important benefits, the mechanism for this is unclear. Finally, (Chapter 5), I bring together the conclusions and results gathered through the primary studies of my thesis, and suggest some specific conservation implications arising from each previous chapter.

Throughout, I use a macroecological framework to test hypotheses and predictions (Kerr et al. 2007). Each chapter brings together high resolution, temporally-explicit, cross-continental datasets of environmental change, anthropogenic change, and species occurrence and distribution. While bumblebees are the subject of study here, the hypotheses and predictions I test are more broadly applicable outside of this taxa as well, creating exciting implications for each chapter. Taken together, my thesis contributes both to our understanding of the nature and extent of how climate change and land-use change influence biodiversity, and also to our knowledge of how to protect species in the face of these threats.

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Chapter 2: Climate change contributes to widespread declines among bumblebees across continents

Note: This chapter is a slightly modified version of the following published article:

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Abstract

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

Introduction

Recent climate changes have accelerated range losses among many species (Kerr et al. 2015; Spooner et al. 2018). Variation in species' extinction risk or chances of colonizing a new area determine whether species' ranges expand or decline as new climatic conditions emerge. Understanding how changing climatic conditions alter species' local extinction (extirpation) or colonization probabilities has proven exceptionally challenging, particularly in the presence of other environmental changes, such as habitat loss. Furthermore, identifying which species will most likely be at risk from climate change - and where those risks will be greatest - is critical to the development of conservation strategies (Williams & Jackson 2007; Veloz et al. 2012).

Although many mechanisms could alter how species fare as climate changes, discovering processes that strongly affect species persistence remains among the foremost challenges in conservation (Urban 2015). Climate change could pose risks to species in part by increasing the frequency of environmental conditions that exceed species' tolerances, causing population decline and potentially extirpation (Nguyen et al. 2011; Sunday et al. 2014). Conversely, climate change may render marginal areas more suitable for a species, making colonization of that locale more likely (Kerr et al. 2015). Understanding and predicting spatially explicit colonization and extinction likelihood could identify which species are vulnerable to climate change and where, which species may benefit, and could suggest interventions to mitigate conservation risks. Colonization and extinction dynamics, in combination across a regional species assemblage, determine how species richness changes. Among taxa that contribute critically to ecosystem service provision, including pollinators such as bumblebees (*Bombus*), species richness decline could impair ecosystem services (Potts et al. 2010).

I evaluated changes in bumblebee species extirpation, colonization, occupancy, and regional richness across North America and Europe using a database of ~550,000 georeferenced occurrence records of 66 bumblebee species (Figure S2.1 and S2.2, Table S2.1; Kerr et al. 2015). I estimated species' distributions in quadrats that measured 100 km by 100 km in a baseline (1901-1974) and recent period (2000-2014). Climate across Europe and North America has changed greatly between these time periods (Figure S2.3). Although the baseline period was substantially longer, there were 49% more records in the recent period. Non-detection bias (i.e. a difficulty distinguishing among true and false absences due to imperfect detection) in opportunistic occurrence records can reduce measurement accuracy of species distributions and overall richness (Sadoti et al. 2013). Consequently, I used detection-corrected occupancy models to estimate probability of occurrence for each species in quadrats within each time period. I calculated changes in species' probabilities of occupancy and generated detection-corrected estimates of species richness change between periods (Figure S2.4).

I predict greater declines in bumblebee species occupancy and species richness where changing climatic conditions more frequently exceed individual species' historically-observed tolerances. Conversely, I predict greater occupancy and species richness in areas where climate changes more frequently cause local weather to fall within species' historically-observed tolerances. Temperature and precipitation can affect bumblebee mortality and fecundity directly (e.g. Woodard 2017) and indirectly through changes to floral resources (Ogilvie et al. 2017). For both periods, I calculated proximity of climatic conditions within quadrats across these continents to estimated thermal and precipitation limits of all 66 species. I averaged monthly temperatures and total precipitation in localities where species were observed and rescaled these measures relative to each species' historically observed climatic limits. Those limits were calculated from averages of the five highest monthly maximum and lowest monthly minimum temperatures, or five highest and lowest monthly total precipitation values, from among values for all location-year combinations where that species was observed during the baseline. Although climate limits inferred from observed distributions might not always identify actual physiological tolerances, they can suggest such limits and can prove useful in the absence of more mechanistic data (Kerr et al. 2015). I calculated local changes in this new climatic position index between baseline and recent time periods, and also averaged it across all species present per quadrat to calculate community-averaged climatic position index (Figures 2.1 and S2.5).

Methods

Bumblebee observations, observed distribution, and species richness

I used a dataset comprising 557,622 observations of 66 bumblebee (*Bombus*) species from 1901-2015, from across North America and Europe. The dataset has been previously used in (Kerr et al. 2015), and contains data assembled from a variety of sources including (Potts et al. 2011; Williams et al. 2014; Rasmont et al. 2015; Polce et al. 2018), and other sources acknowledged in Statement of Work. To produce this database from the assembled set of records, potentially unreliable records (e.g., records with missing species, locality, or sampling year information, or disagreement between record georeferencing and stated country of origin) were flagged and removed. Records in the ocean less than 2500m from a high-resolution coastline were assumed to be coastal observations with spatially imprecise georeferences and were reassigned these to the nearest point on land.

Of the 119 species present in the originally assembled data within the study area, I retained 66, which each 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 S2.1). The mean and median species-period sample size was 1887 and 848 unique location-year observations, respectively (Table S2.1). While the baseline period was longer, there were comparable numbers of unique location-year observations in each period (54,446 in the baseline and 61,809 in the recent). I examined the georeferencing for every observation and removed all instances of bee observations that could not be reconciled with lists of countries they inhabit and comparison with range maps from IUCN Red List reports (http://www.iucnredlist.org/; accessed Nov 16, 2017). I merged observations of *Bombus moderatus* with *B. cryptarum*, per IUCN Red List documentation and (Williams et al. 2014), which considers these species to be synonymous. All records included georeferencing and date information. Duplicate collection records of a species for a given location-year were removed to reflect species occurrence rather than sampling or population density.

I mapped presence and absence for each species within 100 km by 100 km equal-area quadrats across the study area in the baseline and recent periods. I inferred absence when there was no observation of the focal species in the quadrats in a period but at least one other species recorded. I tested the robustness of my results to this definition of absence by repeating all analyses after defining absence as no observation of the focal species but at least i) three and ii) five other species. For each species, I estimated the observed distribution as the number of quadrats in the study area where the species was present, and I compared recent and baseline maps of observed distribution to determine extirpation and colonization. I determined mean rates of extirpation or colonization for a species as the proportion of regional extirpation or colonization events relative to the total number of quadrats a species occupied in the baseline. I measured the change in observed distribution for each species. In baseline and recent periods, respectively, species occupied ranges of 17 to 561 and 12 to 338 quadrats (mean = 195.3 and 117.2), respectively. I measured observed distribution uniquely by continent for species that are present in both Europe and North America and did not calculate North American observed distributional change for one species which was only recorded there in the current period (*B. distinguendus*). Differences in sampling effort between periods of different lengths can bias detection of presence and subsequent estimates of change and occupancy, so I accounted for sampling effort in all subsequent analyses. While the baseline period was substantially longer, the recent period had 49% more records, and 13% more unique location-year-species observations (Figure S2.2, Table S2.1). Extirpation and colonization likelihoods showed significant negative relationships with sampling effort, while sampling effort was not significantly related to observed species richness change. This was not surprising as non-detection-corrected richness analyses were restricted to a subset of well-sampled quadrats.

I combined the presence maps of the 66 species to build a map of regional species richness for each period (Figure S2.10). Variation in sampling effort can bias the estimation of observed biodiversity trends (Gotelli & Colwell 2011; Gotelli & Chao 2013), so I excluded quadrats without a minimum of 50 unique location-year observations in the baseline and most recent period. This resulted in 40 North American and 124 European sites, within which I calculated the percent change in species richness from the baseline to the most recent period. While the strict selection protocol limits the number of quadrats in the species richness analysis, a less strict selection (e.g., including quadrats without a minimum of 50 unique location-years observations) fails to account for sampling bias and removes ability to attribute changes in richness to any climatic variables. All data were organized in R 3.4.1 (R Core Team 2017) using packages *tidyverse* (Wickham 2017) and *raster* (Hijmans et al. 2016).

The scale of analysis (100 km by 100 km) 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 my results, I repeated analyses at a i) 50 km by 50 km scale and ii) 200 km by 200 km scale.

Occupancy models

To correct for imperfect detection in the dataset of bumblebee observations, I used single-species occupancy models to estimate occupancy for the 66 species in each period. These models account for the possibility of false-absences within detection/non-detection data by explicitly estimating detection probability (*p*) separately from probability of occurrence (MacKenzie et al. 2006, 2009; Royle & Kéry 2007; Royle & Dorazio 2009; Kéry & Schaub 2012).

Estimating detection probability for a species during a period requires multiple “survey units” or “visits” to sites within that period. I split each of the time periods into three “survey units” (baseline: 1901-1924, 1925-1949, and 1950-1974; recent: 2000-2004, 2005-2009, and 2010-2014). I used observations of a species during a survey unit to inform detection, and marked absence of a species when others were seen as a non-detection. It is likely that there are biases in the species sampled within the dataset, as in most large-scale ecological data. Bumblebees are a charismatic insect species that have been collected by researchers and independent naturalists for hundreds of years, but, as with any taxon, it is possible that agriculturally important species (e.g., *B. terrestris* and *B. impatiens*), common species, and larger or more recognizable species have greater likelihoods of detection. I used total number of records to help inform species-specific detection probabilities in the occupancy models, to account for sampling bias. Unfortunately, reliable inter- and intra-specific data on other traits that may influence detection probability, such as body size, are not available for all species to include in the models. A necessary assumption of occupancy modelling is that there is no change in occupancy (or species turnover) within a survey period or between survey units within the same period: the closure assumption (Rota et al. 2009). Estimates of site occupancy rely on this assumption to calculate a probability of detection from the pattern of detection/non-detections during a period (MacKenzie et al. 2006). Aggregation of occurrence data into periods to estimate species’ presence or absence makes a similar assumption that presence/absence remains static within those periods. Violations of the closure assumption during occupancy modelling are likely to be frequent throughout the literature and within-period colonization or extinction tends to result in overestimates of occupancy probabilities (MacKenzie et al. 2006;

Rota et al. 2009). Since this study focuses on relative change in occupancy probabilities instead of the absolute values themselves, potential violations of the closure assumption are not likely to alter results or conclusions. Change in probability of occupancy for a species was only calculated across the continent(s) it is known to inhabit. Detection-corrected species richness, calculated as the summed probability of species occurrence in a region, was estimated across the study area for each period (this measure is similar to detection-corrected estimates of taxonomic diversity used in (Jarzyna & Jetz 2017)). Using estimates of species-specific site occupancy and detection-corrected species richness for each period, I calculated the percent change in these values between the baseline and recent periods. All data were organized and transformed in R v3.4.1 (R Core Team 2017) using packages *raster* (Hijmans et al. 2016) and *rgdal* (Bivand et al. 2017).

Occupancy models were fit using the Bayesian general-purpose modelling software JAGS (Plummer 2003), with R v3.4.1 (R Core Team 2017) and package *R2jags* (Su & Yajima 2015). Each species- and season-specific model computed season- and site-specific occupancy, using season-specific sampling effort (i.e., the total number of unique location-year observations of any species in a cell) as a covariate for the underlying detection process. I used noninformative Bayesian priors for all parameters and each model ran three Markov chains for at least 100,000 iterations, discarding the first 50,000 as a burn-in and thinning by 10, resulting in 5000 samples from the joint posterior distribution. I ran models until values of the Brooks-Gelman-Rubin statistic suggested convergence had been reached (<1.1) for all parameters (Brooks & Gelman 1998). The JAGS code specifying the model, including the priors used, is available with the rest of the data and materials (Soroye et al. 2020).

Climatic position variables

For each of the 66 bumblebee species, I extracted the average of the five highest monthly maximum and five lowest monthly minimum temperatures from among the values for all location and year combinations within the species' geographic range in the baseline period (1901-1975). These maximum and minimum temperatures were assumed to represent the thermal limits for the species, and previous studies have found that this measure is robust to both variation in the number of records used to calculate it and variation in species sampling effort (Kerr et al. 2015). Maximum and minimum precipitation limits were extracted from the five highest and five lowest monthly total precipitation values from among all location and year combinations within the species' geographic range in the baseline period. Climatic limits were rescaled for each species to equal 0 for the lower climatic (i.e., cold/dry) limit and 1 for the upper climatic (i.e., warm/wet) limit. While these derived environmental limits may not represent the actual critical limits that a species can tolerate, they offer an indication of the species' environmental tolerances and measuring the change in the environment relative to these derived limits enables tests of the main hypotheses here.

For each species, in each cell of the study area in both periods, I rescaled the local maximum and minimum monthly temperatures and precipitations onto the same scale as the climatic limits. These rescaled values were averaged across months to estimate the thermal position index and precipitation position index: values of 1 indicate that temperatures or precipitation across the whole year equals the warm or wet tolerance limits, and values of 0 indicate that temperatures or precipitation across the year approach or meet the cold or dry tolerance limits for the species (values greater than 1 and less than 0 are possible where climate change has caused temperatures or precipitation to exceed species' upper thermal or precipitation limits or to fall below lower thermal or precipitation limits). The change in thermal and precipitation position was calculated by subtracting position in the baseline period from position in the recent.

To calculate the community-averaged estimates of climatic position, I 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 S2.5). I did this for both periods, and then measured the change from the baseline to recent (Figure 2.1).

In addition to these species-specific and community-averaged climatic position variables, I 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 I compare predictions of the climate position indices I developed here. As with climatic position variables, I measured mean/max/min temperature and annual precipitation in each period and then measured the change from baseline to recent (Figure 2.1).

Climate data were obtained from the Climate Research Unit (Harris et al. 2014) at a resolution of 0.5 X 0.5 degrees. After the calculation of the climatic position index, data were projected and resampled to Cylindrical Equal Area projection at 100 km X 100 km resolution to match the bumblebee data, using R 3.4.1 (R Core Team 2017) and packages *raster* (Hijmans et al. 2016) and *rgdal* (Bivand et al. 2017).

Statistical analyses

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

North America and Europe have substantially different histories of land use, human development, and population trends, and different approaches to species conservation, all of which may contribute to differences in rates of species and assemblage change. I included continent as a categorical variable to account for hypothesized differences in rates of change between North America and Europe (Kerr et al. 2015). Species was included as a random effect in the model to account for differences in species’ responses to climate. I ran identical models with separate random intercepts for site and for species and noted qualitatively consistent results between these models and models without site. In cases where models did not clearly converge, I re-ran models using several different optimizers with >10^7 evaluations and found consistent results. I calculated conditional and marginal R^2 using the method proposed by (Nakagawa & Schielzeth 2013).

Observed extirpation/colonization. I ran another series of models separately testing the relationship between local colonization and extinction, and climatic position variables. I used binomial generalized linear mixed models (GLMM), again including species as a random effect. The model structure was identical to change in occupancy models (see previous section) although I included sampling effort, calculated as the total number of observations in each cell in a period (sampling effort was not included in change in occupancy models because it was already used to estimate occupancy). I calculated conditional and marginal R^2 in the same way as in the change in occupancy models. Colonization and extinction models with site included as a separate random effect produced consistent results.

Phylogenetic analyses. To account for phylogeny in the analyses, I repeated the occupancy, extinction, and colonization modelling using a phylogenetic generalized linear mixed model framework, with a comprehensive mitochondrial and nuclear phylogeny (Cameron et al. 2007). I programmed models using the *MCMCglmm* (Hadfield 2010) and *ape* (Paradis & Schliep 2018) packages in R, following the framework from de Villemereuil & Nakagawa (2014). All models used uninformative univariate priors for random effects corresponding to an inverse-Gamma with shape and scale parameters equal to 0.01. Models were run with a minimum of 105,000 iterations with a thinning factor of 20 and while discarding the first 5000, resulting in a minimum of 5000 samples from the joint posterior distribution. Model parameters were visually assessed for convergence, and if all parameters did not appear to converge then were re-ran for more iterations and a longer burn-in. I estimated marginal and conditional R^2, and phylogenetic signal (Pagel's λ) using code from de Villemereuil & Nakagawa (2014). As is common with Bayesian models, I compared them using the Deviance Information Criterion (DIC). *B. magnus* was not present in the phylogeny and so was excluded from these analyses. The structure of fixed model effects tested was identical to the descriptions provided above, and I found that model parameter values using the PGLMMs were very consistent with those from models in *lme4*. I 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 (Kerr et al. 2015; Arbetman et al. 2017).

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

I checked for spatial autocorrelation in the residuals by visually inspecting a correlogram of Moran's I (Figure S2.11A) and found some evidence of spatial autocorrelation. I proceeded by constructing a simultaneous autoregressive (SAR) spatial error model to correct for residual autocorrelation, as suggested by (Kissling & Carl 2008) and (Dormann et al. 2007). This reduced much of the variability in Moran's I (Figure S2.11B). Model results with the SAR model were qualitatively similar to the ANCOVA results that I report here (Tables S2.2 and S2.3). I calculated the Nagelkerke Pseudo-R^2 of the model as a measure of the variance explained.

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

Detection-corrected species richness. I built an ANCOVA model to test the relationship between climatic positioning and detection-corrected species richness. The model structure here was identical to the occupancy PGLMMs but used community-averaged measures of climatic positioning and did not include the random effects of species. As with the observed species richness models, I checked for spatial autocorrelation and used the same procedure to correct for this with SAR models (Figure S2.12). Spatial autocorrelation was significant in the original model, but results were qualitatively similar between SAR and ANCOVA models (Tables S2.2 and S2.3).

The explained variance of the detection-corrected species richness model was substantially lower than the observed species richness model (8% vs 38%). This is likely to be a result of the occupancy modelling process. The occupancy modelling took the binary measures of species detection/non-detection and used a derived detection probability to estimate continuous probabilities of occupancy from these from 1s and 0s, across the entire continent it occupies. In each period, the occupancy models estimate a probability of 1 (or very close) for cells where the species was detected in any one of the survey units, and they estimate some probability between 0 and 1 for cells where a species was never detected. This latter occupancy probability depends on the species-period-specific detection probability and the total sampling effort in that cell. For most species the occupancy probability of cells where they were not detected is between 0 and 0.4. As detection probability and sampling effort vary by period, the same cell can have a different occupancy estimate in the baseline and recent period, even when the species was never observed there or when it has persisted through both periods. This between-period variation reflects the uncertainty within estimates of occupancy probability during a period, and likely drives the lower adjusted R^2 values I see when comparing the detection-corrected and observed species richness models. A similar reasoning likely explains the differences between marginal R^2 of change in occupancy models (0.11) compared to extinction and colonization models (0.87 and 0.53, respectively).

Comparison with mean climate variables. For all models, I created a model identical in structure but with mean climate variables (i.e., mean baseline annual temperature, mean baseline total annual precipitation, and the change in these to the recent period) instead of climatic position variables. I also compared using average annual maximum and minimum temperature variables. All continuous variables in both sets of models were centered and rescaled before modelling, and I used Information Criterion and R^2 to compare between climatic position and mean climate models. I tested models where baseline thermal and precipitation variables were fit as either linear, or quadratic polynomial terms, since I predicted that species would be more likely to decline in occupancy where sites were already closer to an upper or lower limit in the baseline. With the exception of PGLMMs, all models were constructed in R v3.5.1 (R Core Team 2017), using packages *lme4* (Bates et al. 2015) and *spdep* (Bivand & Piras 2015) for simultaneous autoregressive models.

Spatial projection across recent period

Using the detection-corrected species richness model (adjusted $R^2 = 0.14$) and 0.5-degree resolution climate data (Harris et al. 2014), I spatially projected the predicted change in species richness since the baseline across the entire study area (Figure 2.4). I also projected change using the non-detection-corrected species richness model (adjusted $R^2 = 0.44$; Figure

S2.9). I used rescaled climatic position and climatic position change layers at 0.5 × 0.5 degree grid resolution and used the respective model coefficients to predict what percent climate-change-induced change in assemblage richness occurred from the baseline period (1901-1974) to the recent period (2000-2014).

Effects of land-use change

Using high-resolution data on historic land-use from the Global Harmonized Land-use dataset (Hurtt et al. 2011), I calculated the mean proportion of cropland, pasture, and urban land cover (hereafter human-dominated land-use) in each period for cells across the study area. I then measured the mean change in human-dominated land-use between periods. I built PGLMM's of change in probability of occupancy, extinction and colonization, as well as spatial autoregressive error models of detection-corrected species richness, which included the best fitting variables from previous steps of analysis and human-dominated land-use change. I compared these models with land-use to pure climate change models using information criterion values and R^2 and compared the values and estimated significance of fixed effects.

Agricultural species might be declining through increased use of certain pesticides, which could modify relative rates of decline between species. I 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.

Results

Detection-corrected declines and responses to climatic position

My estimates of bumblebee species occupancy over time provide evidence of rapid and widespread declines across Europe and North America. The probability of site occupancy declined on average by 46% (±3.3% SE) in North America and 17% (±4.9% SE) in Europe relative to the baseline period (Figure 2.2). Declines were robust to detection-correction methods (Figures S2.6A and S2.7) and consistent with reductions in detection-corrected species richness (Figure S2.6B).

Declines among bumblebee species relate to the frequency and extent to which climatic conditions approach or exceed species' historically observed climatic limits, particularly for temperature. I modelled change in probability of site occupancy with phylogenetic generalized linear mixed models using thermal position variables (baseline, change since baseline, and the interaction between these), precipitation position variables (baseline, change since baseline, and the interaction between these), the interaction between baseline thermal and precipitation position terms, and the interaction between change in thermal position and change in precipitation position. I controlled for continent. The models support my predictions: Probability of occupancy decreases when temperatures rise above species' upper thermal limits (Figures 2.3A, S2.8A; Table S2.2), whereas warming in regions that were previously near species' cold limits is associated with increasing occupancy. Evidence for precipitation influencing site occupancy was mixed but declines were more likely in sites that became drier (Figures 2.3B, S2.8B; Table S2.2). The model's capacity to predict change in occupancy (marginal coefficient of determination (R^2) = 0.11) was comparable to the predictive ability of other macroecological models of the biological impacts of climate change (Spooner et al. 2018), but similar models predicted extirpation and colonization more capably (marginal R^2 = 0.53-0.87; see methods for details). Whereas there was weak evidence for a phylogenetic signal in the response of occupancy (Pagel's λ = 0.12), modeling extirpation and colonization separately yields a stronger signal (see methods for details). Results were robust to detection correction method for measuring species' presences in quadrats, across spatial scales of analysis, and through a range of thresholds for inferring absences from occurrence data.

Bumblebee species richness declined in areas where increasing frequencies of climatic conditions exceed species' historically observed tolerances in both Europe and North America. An analysis of covariance that modeled the response of detection-corrected richness to community-averaged measures of climatic position revealed that, consistent with observed trends in species-specific occupancy change, richness was more likely to decline in regions experiencing warming, especially when species present were in the warmest parts of their historical ranges (Table S2.2). These models accounted for potential spatial autocorrelation and results were consistent regardless of method to correct for differences in species detection probabilities.

Predicting climate change-related risk

Projections suggest that recent climate change has driven stronger and more widespread bumblebee declines than have been reported previously, especially in Europe (Figure 2.4). 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, which may have contributed to underestimation of recent species richness decline across that continent (Figures S2.6B, S2.9, S2.10). These findings contrast with those for other taxa that predict widespread range expansions and increasing species richness toward warming environments in the north (Deutsch et al. 2008; Sirois-Delisle & Kerr 2018).

Changes in climatic position index predict biologically important changes in bumblebee presence, colonization, extirpation, and richness across two continents. Species-specific changes in climatic position predict bumblebee diversity change as well as or better than mean, maximum, or minimum temperature or precipitation measures (models using climatic position index: marginal R^2 2.6% lower to 23% higher, change in deviance information criterion = 98.7 to 241.9; see methods for details). Including land-use change in the models revealed a significant negative effect but did not influence results for climatic position variables (Table S2.4; see methods for details). At this scale, effects of climate change on bumblebees appear distinct from effects of land-use. Other anthropogenic changes, such as agricultural intensification, pesticide use, and pathogens can also affect occupancy and extirpation risk of bumblebees (Gill et al. 2012; Goulson et al. 2015; Woodcock et al. 2017). Interactions between these factors are expected to accelerate biodiversity loss for bumblebees and other taxa over broad areas (Mantyka-Pringle et al. 2015; Newbold 2018). Understanding how interactions between climate and land use changes alter extinction risk is vital to conservation of pollinator species.

Non-detection corrected declines

Occupancy, extirpation, and colonization. Consistent with measured declines in occupancy (Figure 2.2), 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 S2.6A).

Rates of observed extirpation and colonization were calculated for each species as the proportion of extirpation or colonization events relative to the total number of cells occupied historically. Across all species in North America and Europe there was a 72% (±2.2% SE) and 49% (±2.8% SE) chance, respectively, that a given bumblebee species was lost from a quadrat it occupied historically. Globally, extirpation events were 8 times (±1.7 SE) more likely than colonization events, with ratios being higher in North America (Figure S2.7). Imperfect species detection and patchy sampling mean that extirpation can be overestimated in opportunistic datasets, so observed extirpation rates likely represent the upper bound of true extinction probability.

Non-detection corrected species richness. Since the baseline period, local (non-detection corrected) species richness has declined by about 18.6% (±3.2% SE) in North America, while richness in Europe has stayed relatively constant (2.2% increase since the baseline ±2.6% SE; Figure S2.6B). Species richness declines do not reflect differences in sampling intensity in this subset of well-sampled cells and was not informative or significant in statistical models.

Response of change in occupancy to precipitation position

While the relationship between change in occupancy and proximity to thermal limits was statistically detectable and followed expectations, relationships with precipitation showed more mixed results. Declines in occupancy were stronger in sites that became drier since the baseline but other effects were inconsistent, and I did not see an interaction between baseline precipitation and change in precipitation as I expected if exposure to precipitation limits from climate change was a driver of declines (Figure 2.3, Figure S2.8, Table S2.2). While direct effects of precipitation are undoubtably important for bumblebees at a local scale, especially in terms of moisture availability, I am unable to detect these effects with this analysis. Conflicting indirect effects of precipitation (through changes in floral resources or vegetation structure), may make these effects more difficult to measure and detect than direct effects of temperature.

Response of extirpation and colonization to climatic position

Patterns in extirpation across the 66 bumblebee species display a strong signal of climate change, especially increasing temperature. I used a phylogenetic generalized linear mixed model (PGLMM) with a similar fixed and random effect structure as the site occupancy-climate change model, but here including sampling effort as a covariate. As expected, extirpation probability related to thermal position in the baseline period, change since then, and their interaction (Table S2.2). Increasing thermal position was linked to greater probability of extirpation for species in regions that were already near their upper thermal limit, and lower probability of extirpation for species in regions historically closer to their cold limits (Figure S2.13A). As with occupancy, precipitation position showed more ambiguous associations. While sites that became drier had higher probability of extirpation, the effect of baseline precipitation was not significant and there was no significant interaction between these two effects (Figure S2.13C). The model explained most of the variation in the response of extirpation to climatic position (marginal $R^2 = 0.87$). The strong relationship between temperature warming and extirpation risk among bumblebee species is consistent with previous work demonstrating that extinction risk depends on shifts in the spatial distributions of thermal niches in other taxa (Sinervo et al. 2010; Sunday et al. 2012) and is of particular importance since bumblebee species are being pushed towards their upper thermal limits across most of North America and Europe (Figure 2.1A).

Trends in local colonization also showed a strong association with climate change, providing independent support for a separate prediction of my hypothesis. A PGLMM with similar fixed and random effects to the extirpation models shows that the three thermal position variables appear to significantly drive colonization, with precipitation position showing inconsistent effects (Table S2.2). Species were more likely to colonize regions which were historically near the cold limit and had warmed, and historically hot regions that cooled were more likely to be colonized than historically cool or moderate regions that became colder (Figure S2.13B). Regions that moved towards species' wet limits were more likely to be colonized (Figure S2.13D). Regions that were simultaneously hot and dry historically had higher rates of colonization, as did regions that got simultaneously hotter and drier. Models explained a large part of the variation in local colonization (marginal $R^2 = 0.53$). The difference in explained variance between the extirpation and colonization models (marginal R^2 0.87 vs 0.53) could suggest that the process of colonization is less tied to physiological climate limits than extirpation. In regions that were historically moderate or near species' hot limits, rates of extirpation greatly exceeded rates of colonization following warming. Given that species and communities appear to have been moderately situated with respect to their climatic limits in many northern regions across North America and Europe that warmed (Figures 2.1A and

S2.5A), this finding may help explain why most bumblebees are not generally expanding their ranges at poleward limits of their distributions to track climate change (Kerr et al. 2015; Sirois-Delisle & Kerr 2018).

The models revealed a significantly detectable phylogenetic signal in the response to both extirpation and colonization to climatic position, with the signal for extirpation (Pagel's λ= 0.88) being stronger than the signal for colonization (Pagel's λ= 0.70). Previous work has also detected significant phylogenetic signal in patterns of declines across bumblebees (Arbetman et al. 2017) and found that traits can influence the sensitivity of bumblebees to land-use and agricultural pressures (De Palma et al. 2015). More data on inter- and intra-specific variation on traits should be gathered to test questions about how traits and evolutionary change may mediate responses to climate change at this scale.

Comparing climatic position models to mean climate variables

While measures of climate like mean annual temperature or mean annual precipitation are easy to gather, inter-specific variation in physiological tolerances mean that how these conditions influence species depends on proximity to species physiological limits. A regional measure of climatic position directly measures whether climatic conditions are near or outside species' tolerances to test whether changing exposure to such conditions drives persistence and colonization. Predictions from this hypothesis are consistent with recent trends in North American and European bumblebees (Figures 2.3 and S2.13) and using thermal and precipitation position variables instead of mean climate variables produces models that better predict extinction, colonization, and change in occupancy (marginal R^2 7% lower to 12.5% higher) and are more informative (ΔDIC ~ 202.4, ΔDIC ~ 102.8 and ΔDIC ~ 164.9 respectively). This increase in explanatory power was consistent when comparing to models using average annual maximum (marginal R^2 1.6% to 23% higher; ΔDIC = 98.7-157.5) or minimum temperatures (marginal R^2 2.6% lower to 21.3% higher; ΔDIC = 128.2-241.9). I show that accounting for inter-specific variation significantly improves detection of relatively local-scale climate impacts on bumblebees. Regardless of technique used, there is a biologically meaningful signal of climate change within patterns of bumblebee decline.

Climatic sampling across continents

I tested whether the most well-sampled quadrats in my analysis (which were used for the non-detection-corrected species richness analysis) presented a representative sample of historic climate and climatic patterns across North America and Europe, and found that well-sampled regions in Europe tended to be cooler in the baseline and experience less warming between periods (Welch's two-sample t-test results: t-statistics = 2.72 and 4.16, p-values = 7.0x10-3 and 4.8 x10-5, df = 227 and 206, respectively). Previous estimates of European bumblebee richness change extrapolating from well-sampled areas may have systematically underestimated recent richness declines. Well-sampled quadrats in North America appeared representative of the general temperature trends experienced over the continent as a whole, but tended to be historically wetter and have gotten wetter than the continental average (Welch's two-sample t-test results: t-statistics = 2.95 and 2.30, p-values = $5.1\text{x}10^{-3}$ and 0.03, df = 41.5 and 40.2, respectively).

Land-use change

Human land-use has also been associated with pollinator declines (Potts et al. 2010). I 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 S2.4).

I did not find any statistically significant relationship between percent of species' geographical range covered by cropland and unique location-year observations (t-value= -0.79, p-value= 0.43, d.f.= 64), mean change in probability of occupancy (t-value= 0.07, p-value= 0.94, d.f.= 64), or mean change in observed distribution (t-value= 1.24, p-value= 0.22, d.f.= 64). It appears that rates of species decline do not appear to strongly differ between species more associated with agricultural areas, although I note that the subset of well-sampled species is likely already biased toward species more associated with agricultural and urban areas. This is consistent with previous work that concluded latitudinal range shifts in bumblebees appeared strongly sensitive to climate change but not especially sensitive to agriculture (Kerr et al. 2015).

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 (Nadeau et al. 2017a, 2017b), but reasonably chosen spatial scales can still reveal valuable macroecological patterns (Blackburn & Gaston 2002). Here, I selected 100 km by 100 km cells as the spatial scale of the analysis, which represented a balance between having adequate sampling density across my study area and a high resolution to detect "local" effects of climate and climate change. Repeating analyses in 50 km by 50 km cells and 200 km by 200 km cells produced results that were qualitatively similar (Tables S2.5 and S2.6), suggesting analyses were robust to the scale used.

Absence threshold. When converting occurrence records into presence absence data, I inferred absence of a species when the focal species was not seen but at least one other species was (absence threshold of one). A liberal absence threshold could result in overestimating absences (and ultimately detection ability), which could lead to overestimates of extirpation and local colonization. I tested the sensitivity of the results to my definition of "absence" by repeating analyses using an absence threshold of three and five, and found that all results were qualitatively similar (Tables S2.7 and S2.8).

Conclusion

Climate is expected to warm rapidly in the future (IPCC 2014). Using a spatially explicit method of measuring climatic position and its change over time, I show that risks of bumblebee extirpation rise in areas where local temperatures more frequently exceed species' historical tolerances, whereas colonization probabilities in other areas rise as climate changes cause conditions to more frequently fall within species' thermal limits. Nevertheless, overall rates of climate change-related extirpation among species greatly exceed those of colonization, contributing to pronounced bumblebee species declines across both Europe and North America with unknown consequences for the provision of ecosystem services. Mitigating climate change-driven extinction risk among bumblebees requires efforts to manage habitats to reduce exposure to growing frequency of temperatures that are extreme relative to species' historical tolerances.

Figures 2.1-2.4

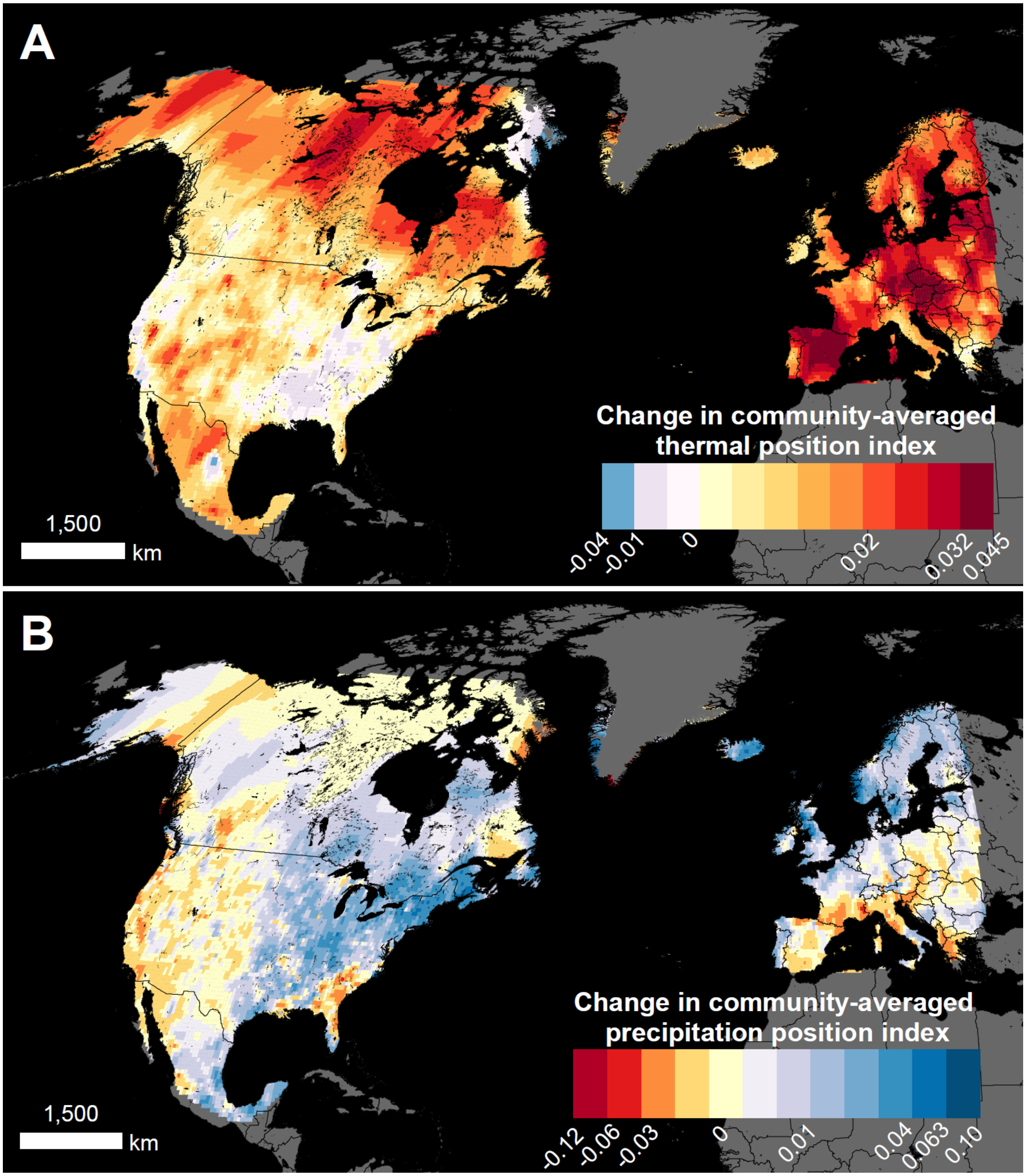

Figure 2.1. Change in community-averaged thermal (A) and precipitation position (B) from the baseline (1901-1974) to the recent period (2000-2015). Increases indicate warmer or wetter regions and that on average, species in that assemblage are closer to their hot/wet limits than historically. Declines indicate cooling or drying regions and that on average, species in that assemblage are closer to their cold/wet limits than historically.

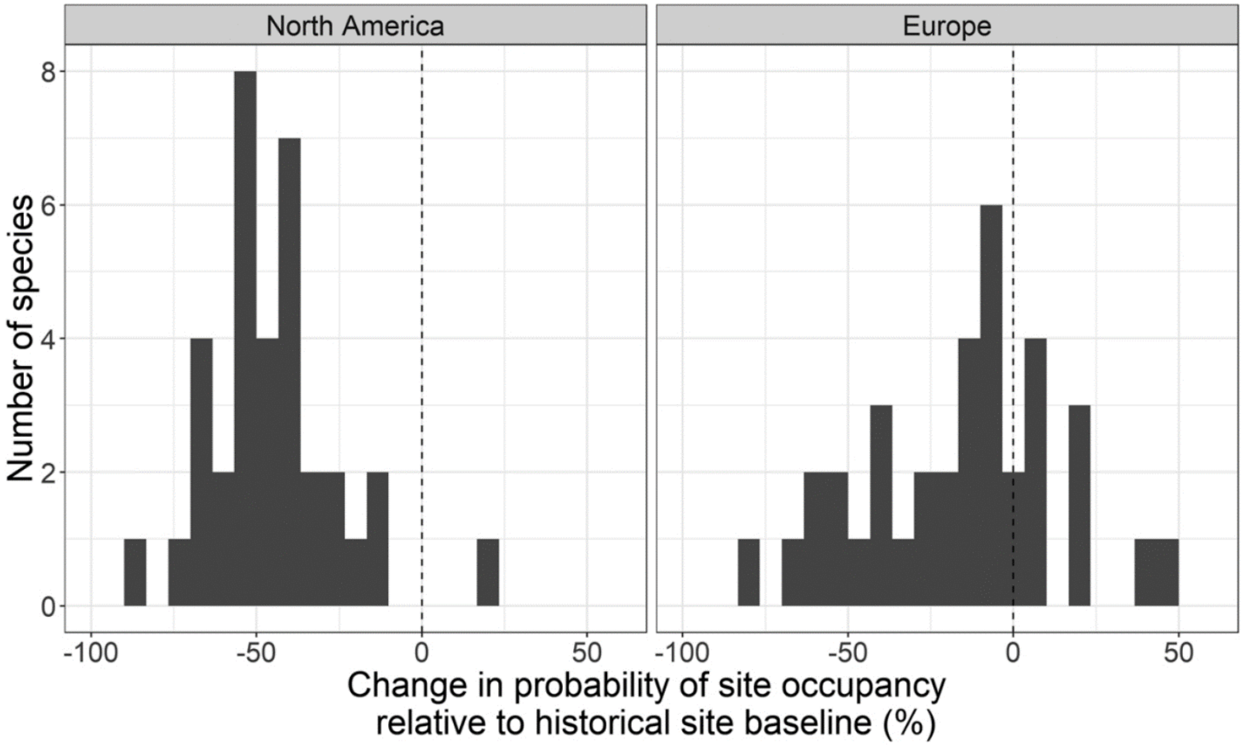

Figure 2.2. Percent change in site occupancy since a baseline period (1901-1974) for 35 North American and 36 European bumblebee species.

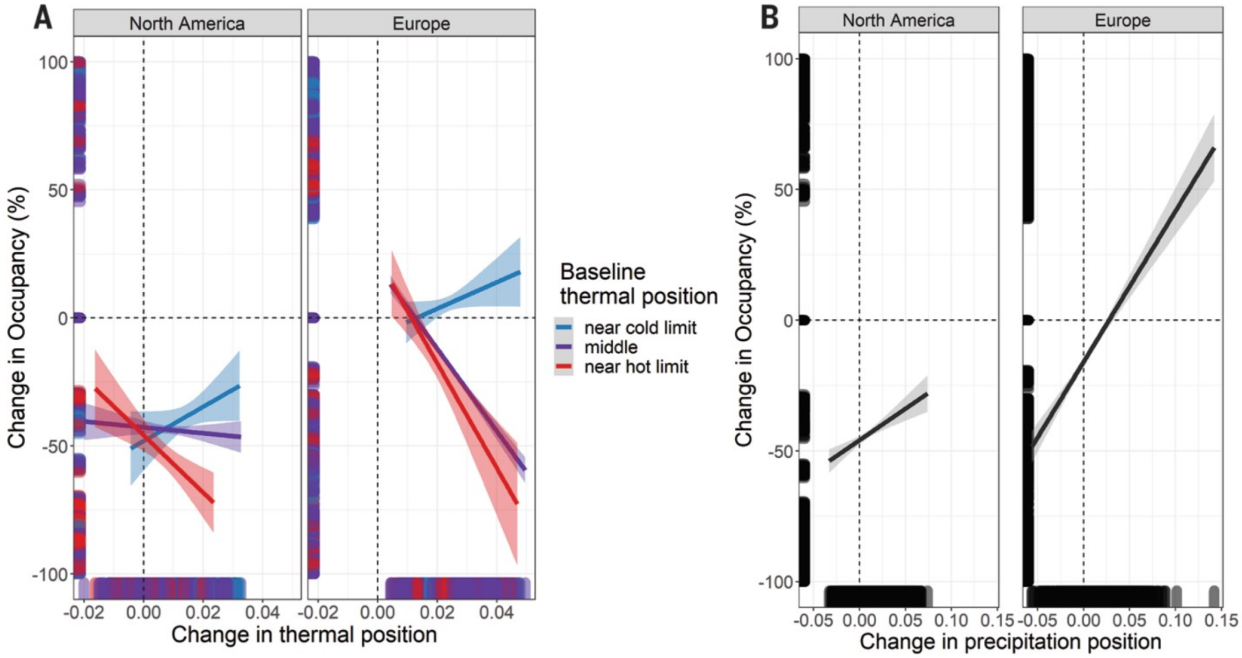

Figure 2.3. Change in probability of occupancy in response to change in thermal (A) and precipitation (B) position from the baseline (1901-1974) to the recent period (2000-2014). Thermal and precipitation position ranges from 0 to 1, with 1 indicating conditions at a site are at a species' hot or wet limit for the entire year, and zero meaning conditions are at a species' cold or dry limit for the entire year during the historic period. For ease of visualizing the significant interaction between baseline thermal position and change in thermal position, the continuous baseline thermal position variable has been split at the 1st and 3rd quantile to show sites that were historically close to species' hot limits (red; n=969), cold limits (blue; n=2,244), and middle of their observed climatic limits (purple; n=11,793). Rug plot shows the distribution of observations. Confidence intervals (±95%) are shown around linear trendlines.

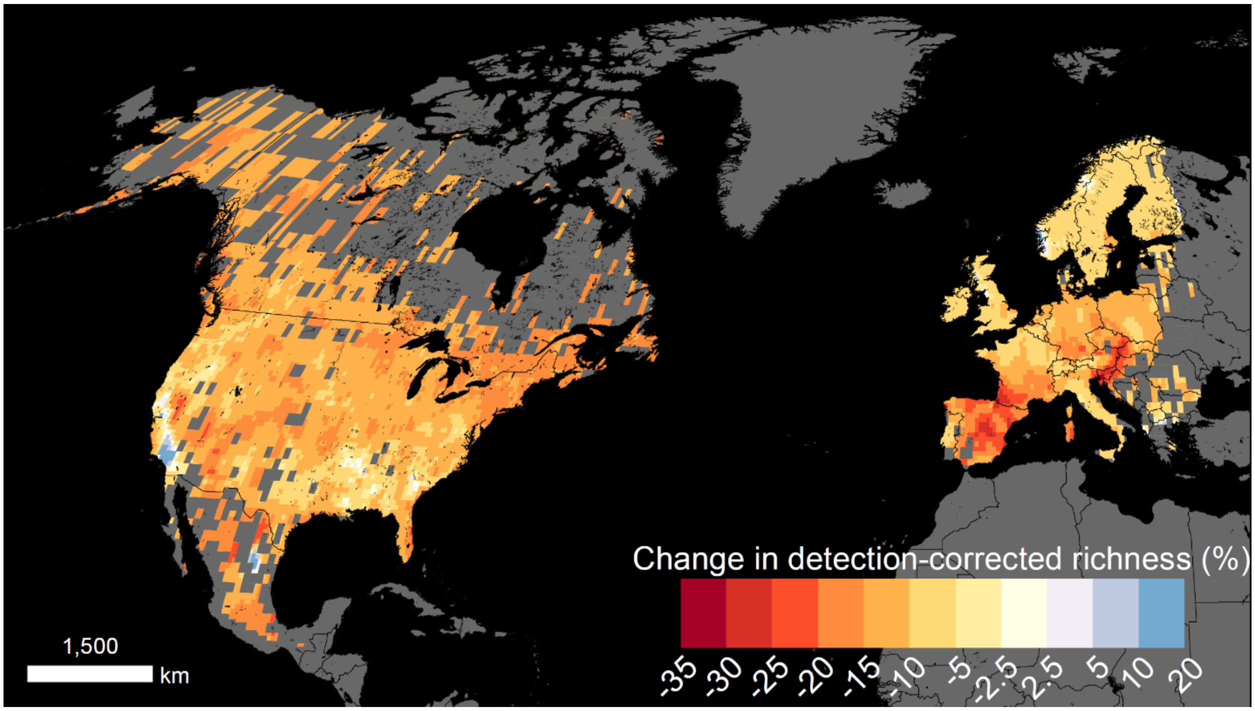

Figure 2.4. Climate change-related change in bumblebee species richness from a baseline (1901-1974) to a recent period (2000-2014). Predictions from a model predicting percent change in detection-corrected bumblebee species richness as a function of mean community-averaged thermal and precipitation position.

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Supplemental Materials

Supplemental Figures S2.1-S2.13

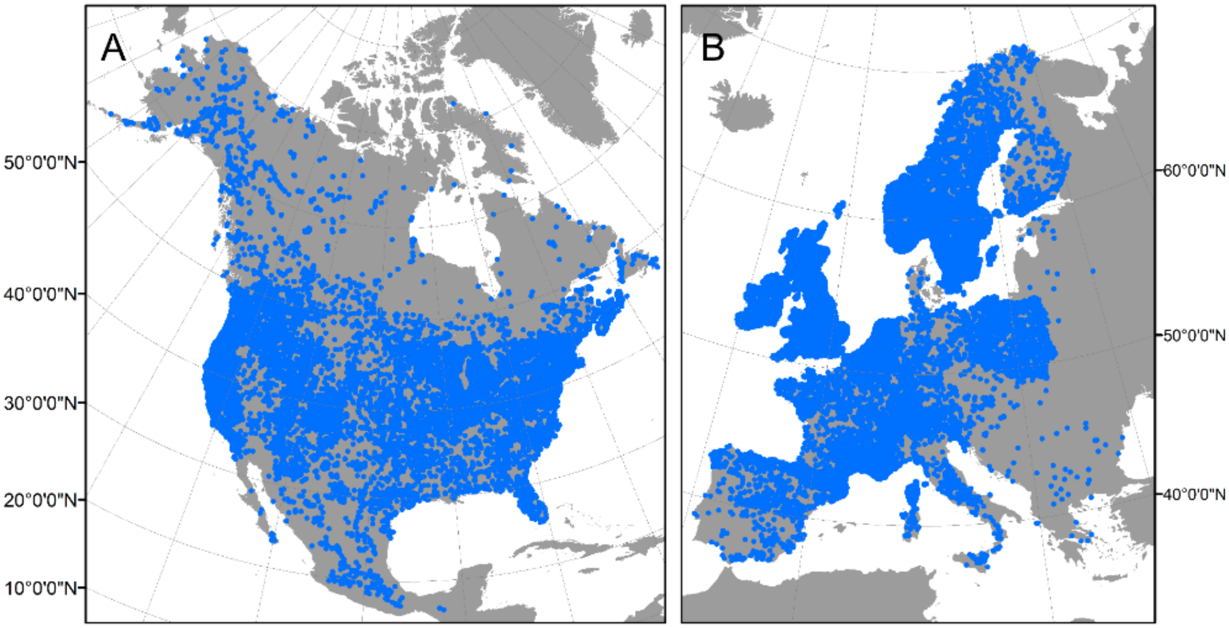

Figure S2.1. Distribution of unique species-location-year sampling locations from North America (A) and Europe (B).

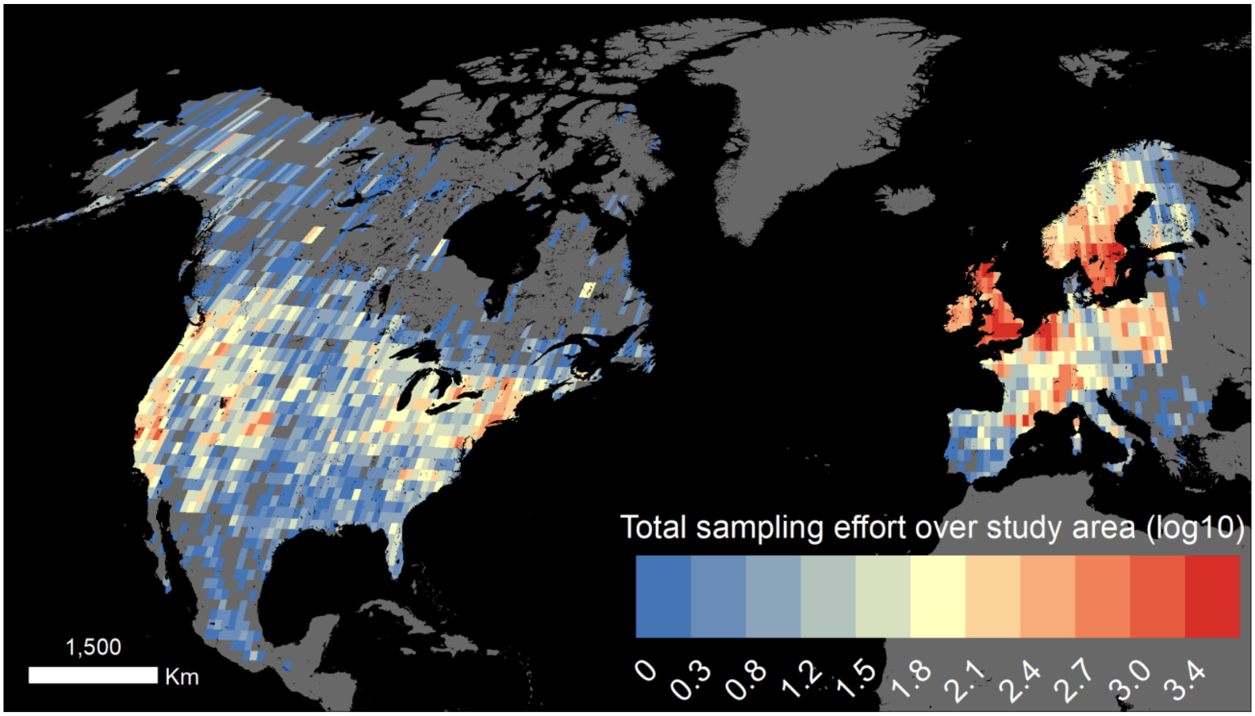

Figure S2.2. Density of unique location-year observations per 100 km by 100 km grid cell across North America and Europe.

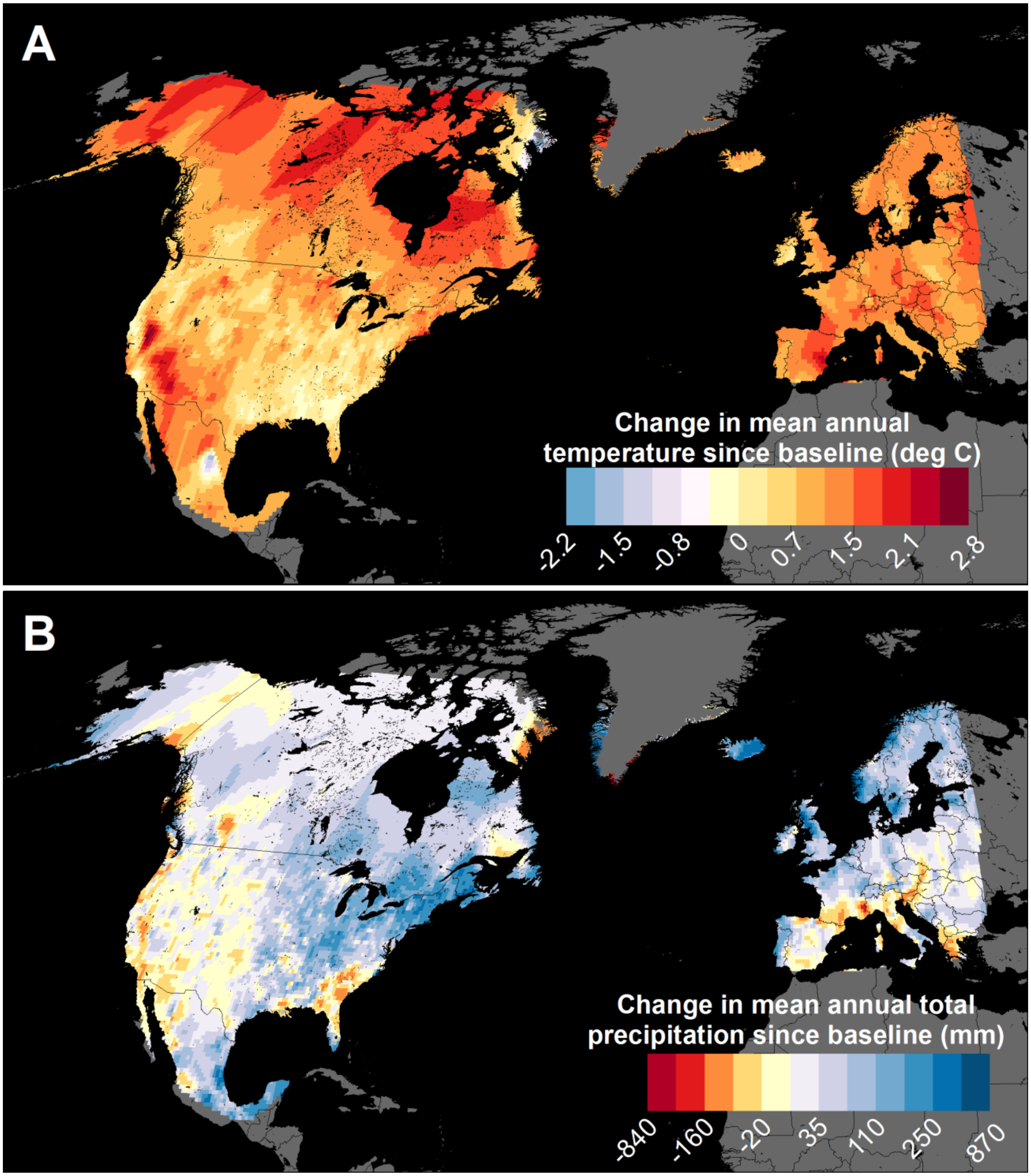

Figure S2.3. Change in mean annual mean temperature (A) and mean total precipitation (B) from the baseline (1901-1974) to the recent period (2000-2015) across North America and Europe.

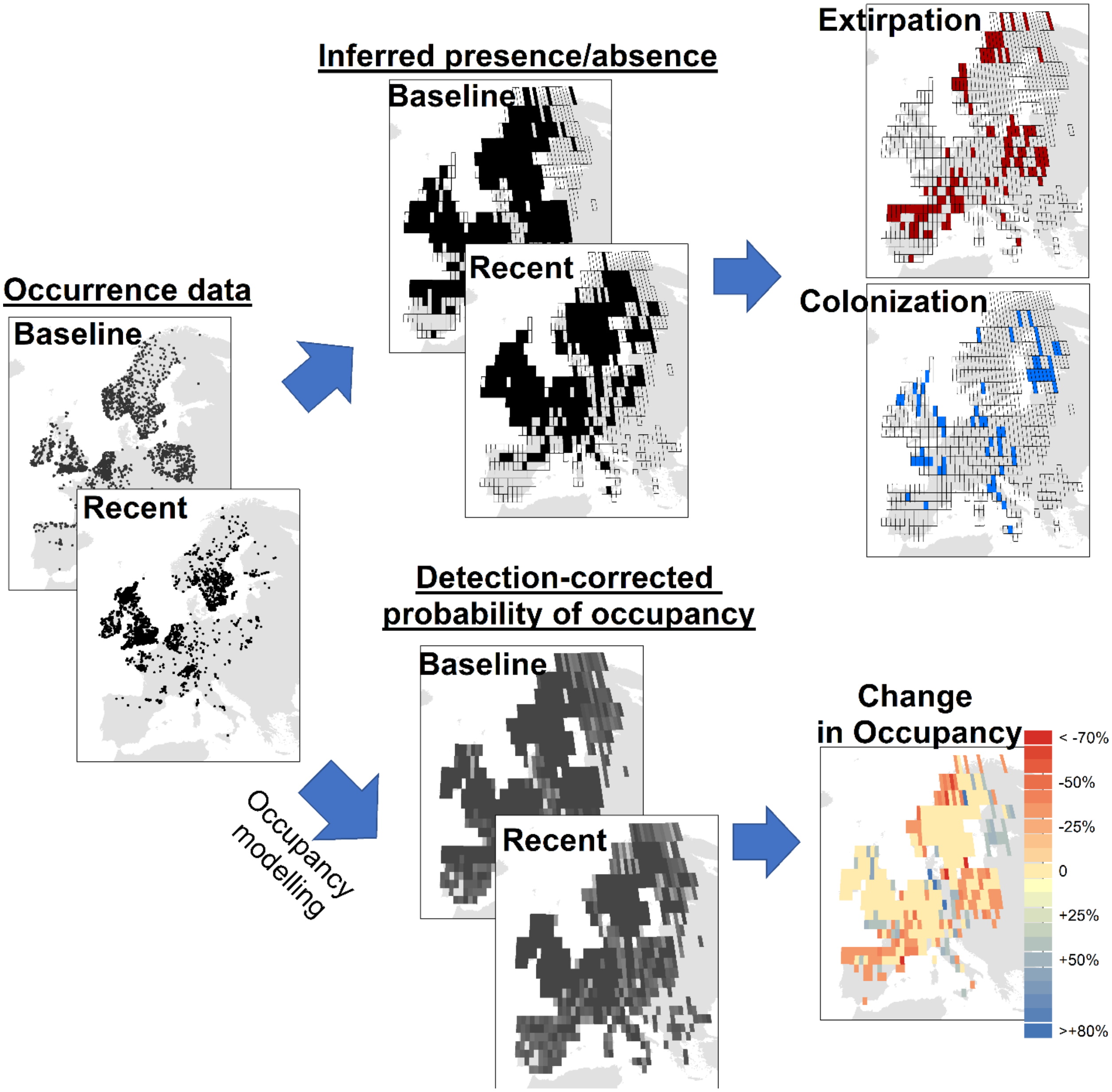

Figure S2.4. Graphical description of methods visualizing relation between occurrence records and eventual measures of detection-corrected change in occupancy, extirpation, and colonization for an example species, Bombus hortorum.

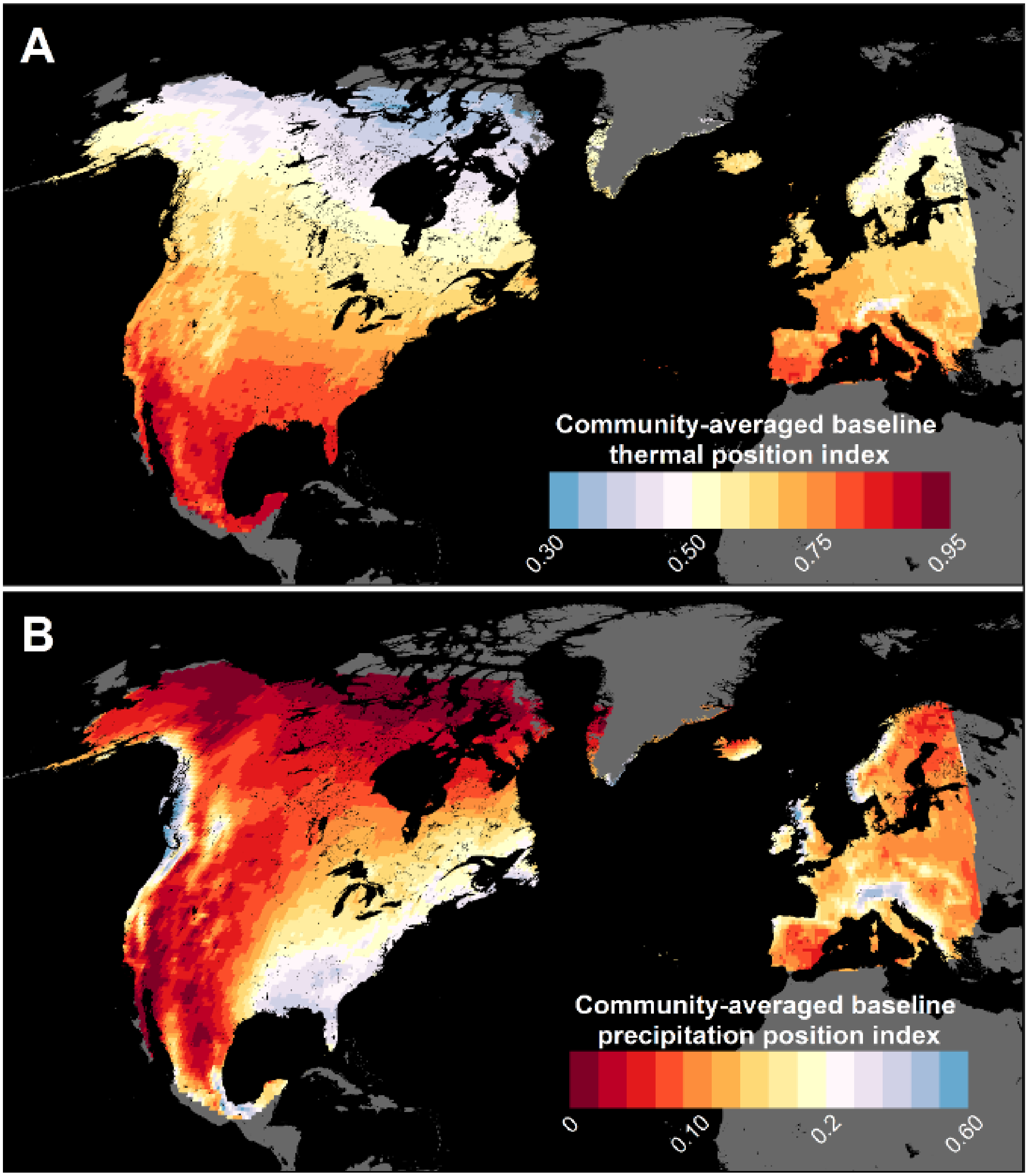

Figure S2.5. Community-averaged thermal (A) and precipitation position (B) in the baseline period (1901-1974) across North America and Europe. Both thermal and precipitation position indices have a potential range of 0 to 1. Zero indicates that species in the assemblage are on average at their cold/dry tolerance limit for the entirety of the year in the period. One indicates that species in the assemblage are on average at their hot/wet tolerance limit for the entirety of the year in the period.

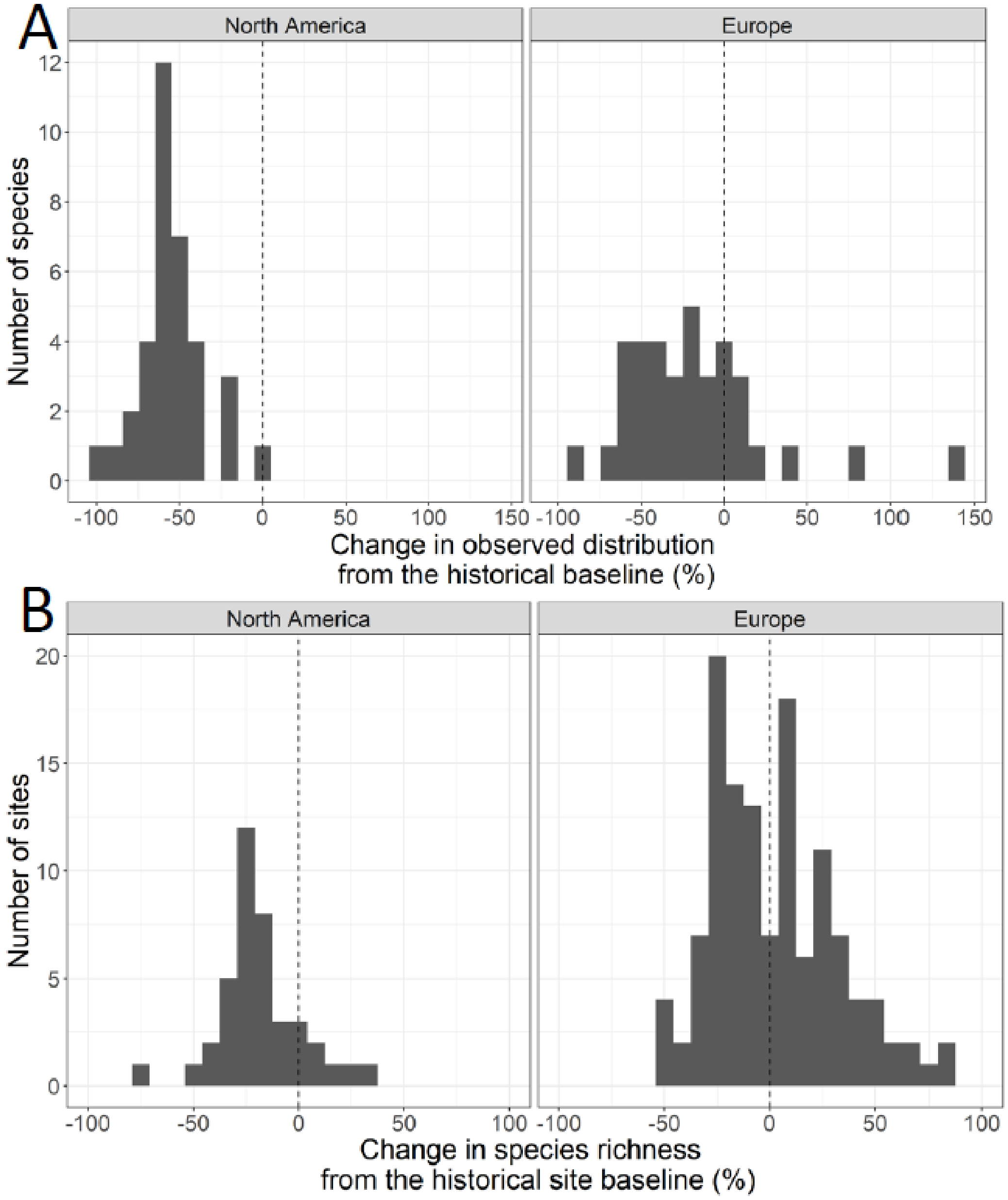

Figure S2.6. Change in species' observed distribution (A) and observed species richness (B) from the baseline (1901-1974) to recent period (2000-2014) in sites across the study area. Observed species richness was only measured in sites with a minimum of 50 unique location-year-species observations in the baseline and most recent period. N= 164.

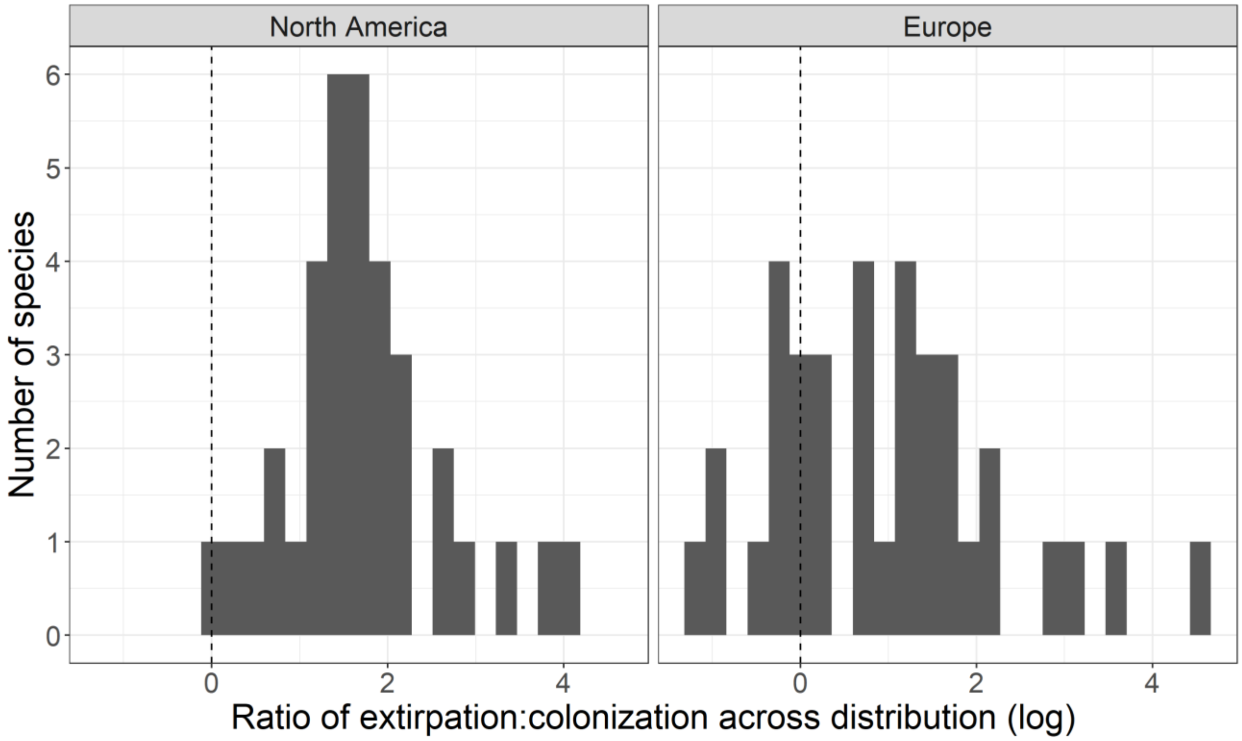

Figure S2.7. Ratio of local extirpation to colonization across species' observed distributions between the baseline (1900-1975) and recent period (2000-2015).

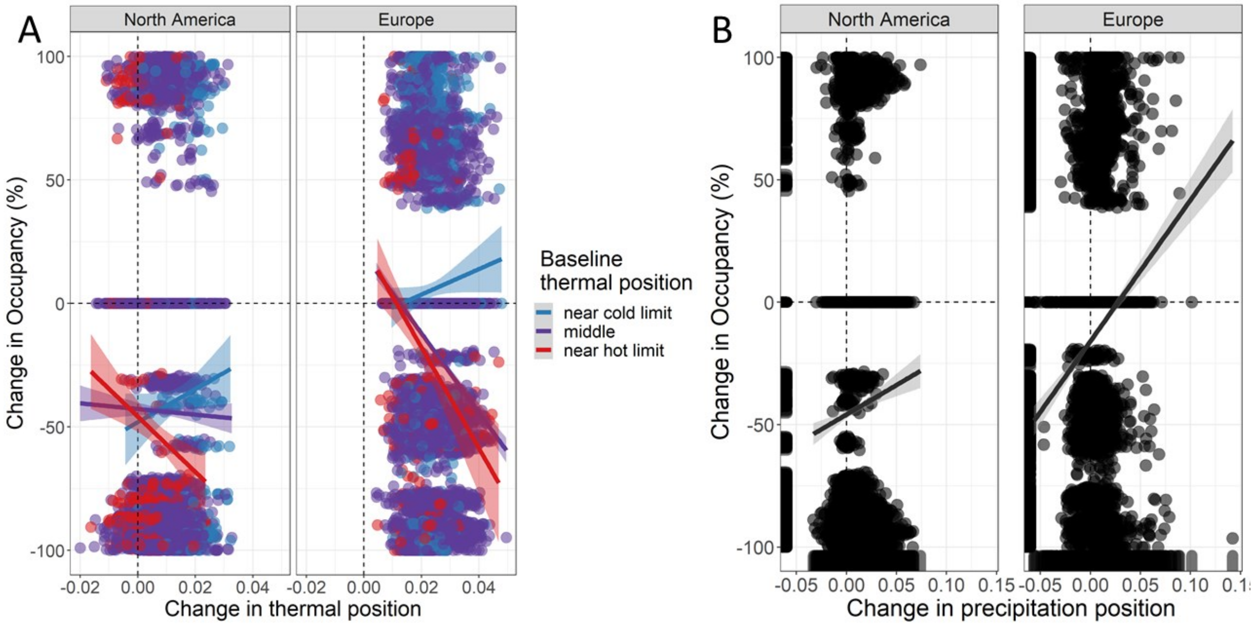

Figure S2.8. Change in probability of occupancy in response to change in thermal (A) and precipitation (B) position from the baseline (1901-1974) to recent period (2000-2014). Note that this figure is identical to Figure 3 in the main text but shows raw data points. Thermal and precipitation position ranges from 0 to 1, with 1 indicating conditions at a site are at a species' hot or wet limit for the entire year, and zero meaning conditions are at a species' cold or dry limit for the entire year during the historic period. For ease of visualizing the significant interaction between baseline thermal position and change in thermal position, the continuous baseline thermal position variable has been split at the 1st and 3rd quantile to show sites that were historically close to species' hot limits (red; n=969), cold limits (blue; n=2,244), and middle of their observed climatic limits (purple; n=11,793). Rug plot shows the distribution of observations. Confidence intervals (±95%) are shown around linear trendlines.

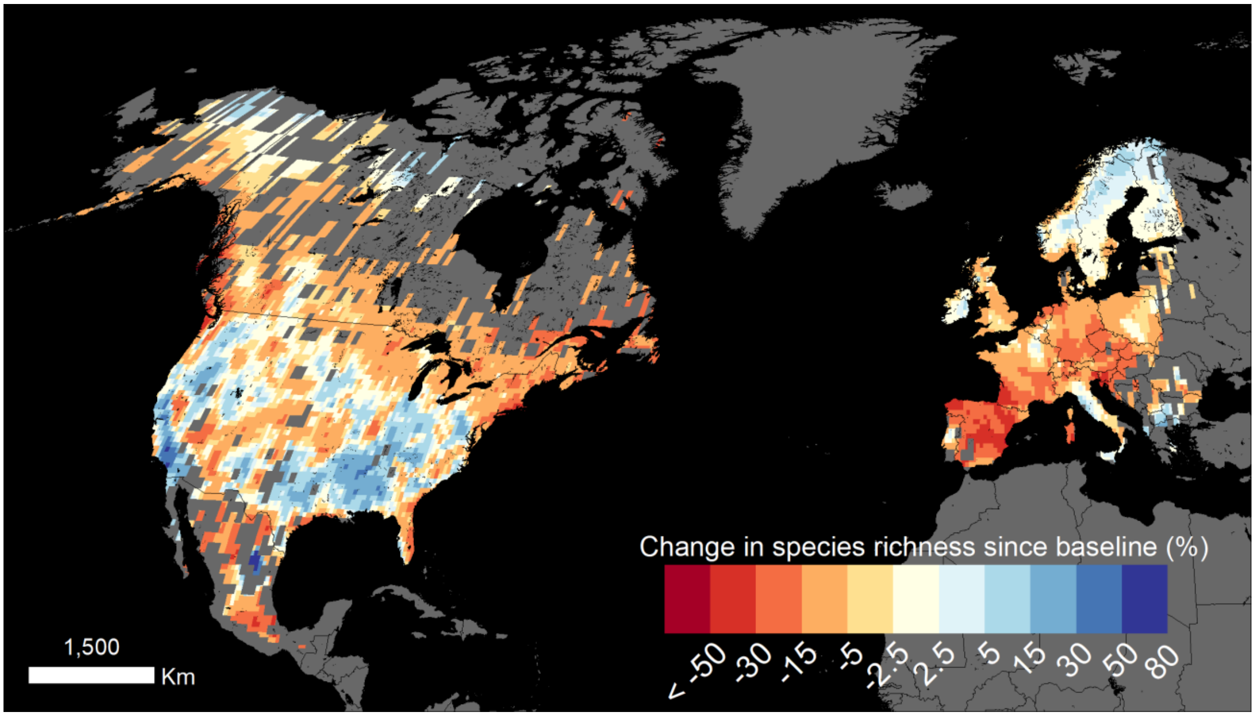

Figure S2.9. Spatial projections of climate change-related change in non-detection-corrected bumblebee species richness from a baseline period (1901-1974) to a recent period (2000-2014). Made using a model predicting percent change in non-detection-corrected bumblebee species richness as a function of mean community thermal and precipitation position (R^2= 0.44; see Materials and Methods for model details).

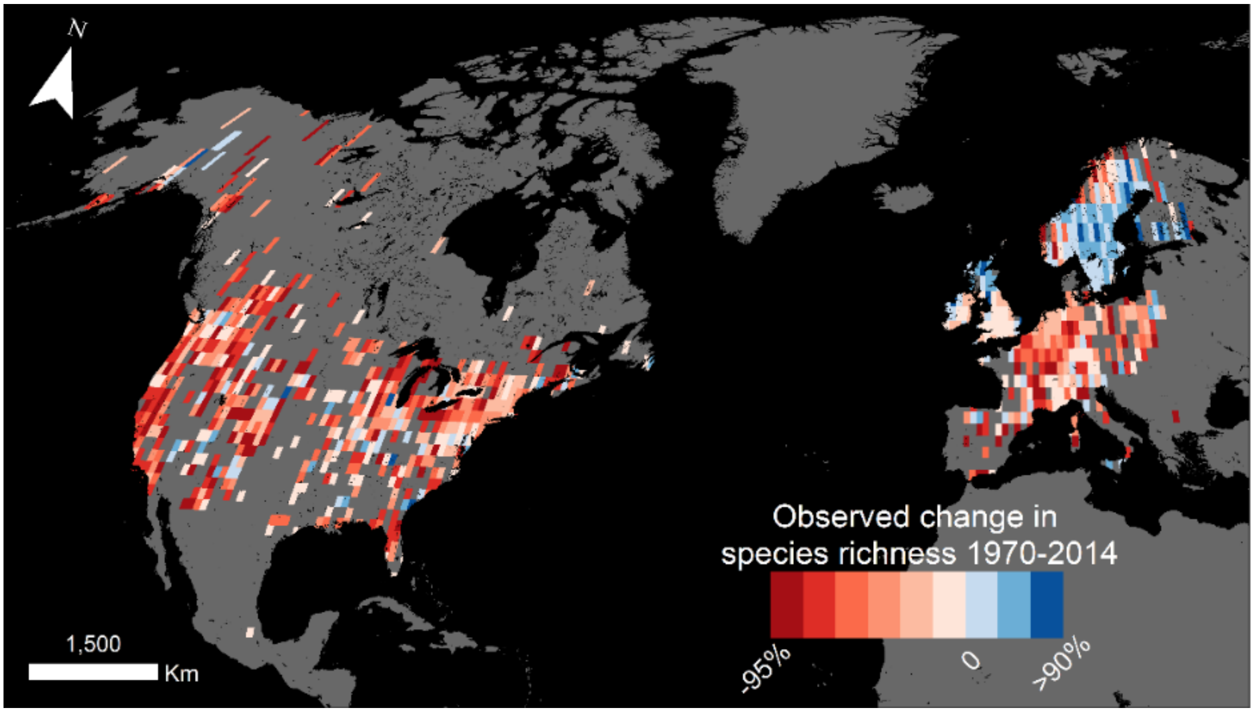

Figure S2.10. Percent change in observed bumblebee species richness across North America from the baseline (1901-1974) to recent period (2000-2014). Grid cells shown are 100 km by 100 km, in an equal area projection. No sampling-based selection (see methods) applied here.

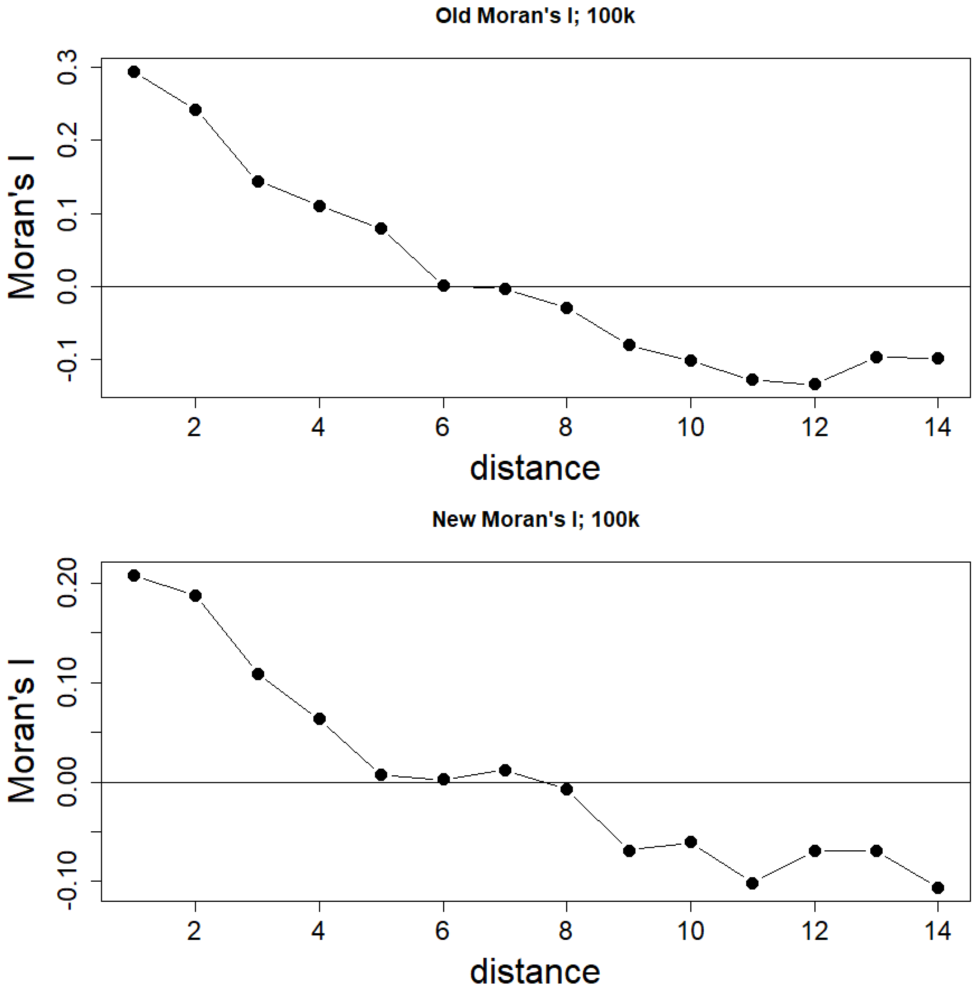

Figure S2.11. Correlogram of Moran’s I for non-detection corrected species richness model. Moran’s I calculated from ordinary least squares regression model (top) and simultaneous autoregressive (SAR) error model (bottom). SAR model was a significantly better fit (according to log likelihood). Model coefficients were qualitatively similar between both models.

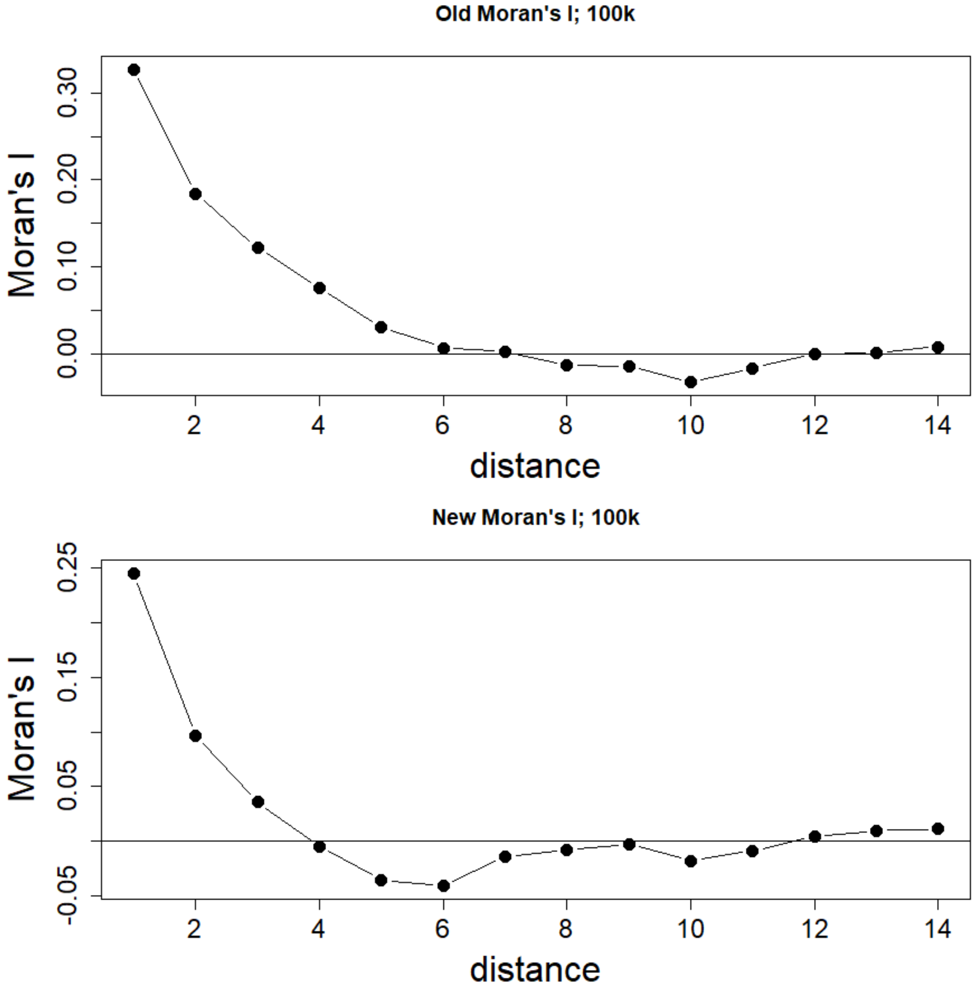

Figure S2.12. Correlogram of Moran’s I for detection-corrected species richness response model. Moran’s I calculated from ordinary least squares regression model (top) and simultaneous autoregressive (SAR) error model (bottom). SAR model was a significantly better fit (according to log likelihood). Model coefficients were qualitatively similar between both models.

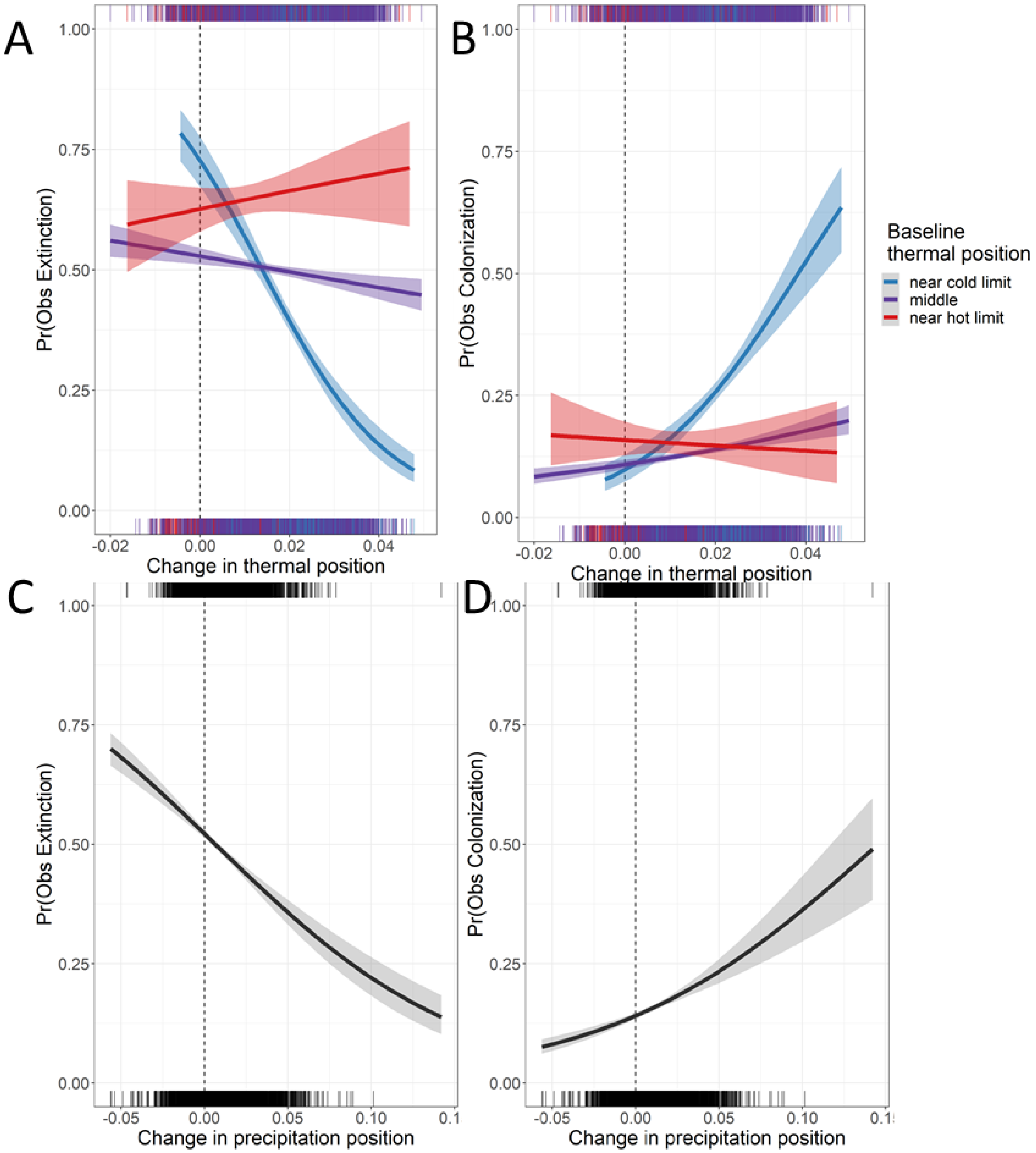

Figure S2.13. Probability of local extinction (A, C) and colonization (B, D) in response to change in thermal (A, B) and precipitation (C, D) position from the baseline (1901-1974) to recent period (2000-2014). Thermal and precipitation position ranges from 0 to 1, with 1 indicating conditions at a site are at a species' hot or wet limit for the entire year, and zero meaning conditions are at a species' cold or dry limit for the entire year during the historic period. For ease of visualizing the significant interaction between baseline thermal position and change in thermal position, the continuous baseline thermal position variable has been split at the 1st and 3rd quantile to show sites that were historically close to species' hot limits (red; n=969), cold limits (blue; n=2,244), and middle of their observed climatic limits (purple; n=11,793). Rug plot shows the distribution of observations. Confidence intervals (±95%) are shown around linear trendlines.

Supplementary Tables S2.1-S2.8

Table S2.1. 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 S2.2. Estimated model coefficients for the five main models. Posterior means and 95% Bayesian credible intervals are shown for PGLMM models. t-values (for analysis of covariance models, ANCOVA) are included as a measure of significance. Generally, coefficients with t-values < -2 and > 2 are considered significant, these and coefficients where the 95% CI does not overlap zero are in bold text in the table. Variance explained is expressed in terms of marginal R^2 (for PGLMM) and adjusted-R^2 (for ANCOVA models).

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

Precipitation position variables										
Baseline (1st order polynomial)	**-1.63**	**-3.04 - -0.25**	-0.89	-7.39 - 6.14	**-30.56**	**-39.56 - -21.29**	**-5.57 (2.09)**	**-2.67**	-0.73 (0.44)	-1.64
Baseline (2nd order polynomial)	--	--	-2.56	-8.56 - 2.96	**13.56**	**6.53 - 20.55**	--	--	--	--
Change since baseline	**3.9**	**2.55 - 5.13**	**-0.14**	**-0.21 - -0.09**	**0.21**	**0.13 - 0.29**	-1.27 (2.47)	-0.51	0.26 (0.5)	0.53
Baseline:Change interaction	-0.11	-0.81 - 0.69	0.02	-0.02 - 0.05	-0.03	-0.08 - 0.02	**-9.74 (4.31)**	**-2.26**	0.47 (0.34)	1.38
Climatic position interactions										
Baseline thermal:Baseline precipitation interaction	-0.05	-1.82 - 1.69	0.02	-0.05 - 0.1	**0.12**	**0.03 - 0.21**	--	--	-0.39 (0.39)	-1.01
Change in thermal:Change in precipitation interaction	-0.15	-1.17 - 0.85	0.02	-0.02 - 0.06	0.06	0 - 0.12	--	--	**2.04 (0.39)**	**5.26**
Covariates										

Continent (Europe)	**39.35**	**32.95 - 45.45**	**-1.98**	**-2.22 - -1.71**	**1.27**	**0.96 - 1.56**	**12.2 (5.13)**	**2.38**	**7.87 (1.13)**	**6.95**
Sampling Effort	--	--	**-0.59**	**-0.65 - -0.55**	**-0.17**	**-0.21 - -0.13**	--	--	--	--
Random effects	Variance (95% CI)		Variance (95% CI)		Variance (95% CI)					
Species	**181.4**	**117 - 256.2**	**0.3**	**0.19 - 0.44**	**0.26**	**0.15 - 0.39**	--		--	
Model summary										
Number observations (n)	4617-5264		30.8-1035.5		118.5-1730.1		164		1849	
Variation explained (R2)	0.11		0.87		0.53		0.38		0.07	

Table S2.3. 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^2.

	Species richness SAR		Detection-corrected species richness SAR	
	Estimate	z value	Estimate	z value
Intercept	-12.64 (11.27)	-1.12	**-14.19 (1.98)**	**-7.16**
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
Climatic position interactions				
Baseline thermal:Baseline precipitation interaction	--	--	0.36 (0.55)	0.65
Change in thermal:Change in precipitation interaction	--	--	0.7 (0.43)	1.63
Covariates				

Continent (Europe)	14.47 (12.99)	1.11	7.1 (3.72)	1.91
<u>Model summary</u>				
Number observations (n)	164		1849	
Variation explained (R2)	0.44		0.14	

Table S2.4. 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^2 (for ANCOVA models), and Nagelkerke pseudo-R^2.

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

Baseline:Change interaction	**-11.06**	**-13.09 - -8.93**	**0.52**	**0.43 - 0.61**	**-0.5**	**-0.68 - -0.34**	**-2.7 (0.45)**	**-6**	**-1.18 (0.56)**	**-2.1**
Precipitation position variables										
Baseline (1st order polynomial)	**-2**	**-3.44 - -0.58**	1.9	-4.63 - 7.57	**-35.49**	**-47.78 - -23.32**	-0.59 (0.46)	-1.28	0.12 (0.62)	0.19
Baseline (2nd order polynomial)	--	--	-4.05	-10.46 - 2.35	**15.95**	**6.79 - 25.15**	--	--	--	--
Change since baseline	**3.78**	**2.46 - 5.03**	**-0.14**	**-0.2 - -0.09**	**0.24**	**0.14 - 0.34**	0.25 (0.5)	0.5	0.32 (0.64)	0.5
Baseline:Change interaction	-0.02	-0.76 - 0.74	0.02	-0.02 - 0.05	-0.03	-0.08 - 0.02	0.48 (0.34)	1.4	-0.04 (0.38)	-0.1
Climatic position interactions										
Baseline thermal:Baseline precipitation interaction	-0.3	-2.02 - 1.4	0.04	-0.04 - 0.11	0.13	0.03 - 0.25	-0.32 (0.4)	-0.81	0.36 (0.55)	0.65
Change in thermal:Change in precipitation interaction	-0.1	-1.08 - 0.95	0.02	-0.02 - 0.06	0.07	0 - 0.14	**2.01 (0.39)**	**5.14**	0.7 (0.43)	1.63
Human dominated land-use										

Land-use change	**-16.4**	**-27.33 - -6.46**	**0.92**	**0.44 - 1.39**	-0.61	-1.3 - 0.15	3.72 (3.73)	1	0.11 (4.35)	0.03
Covariates										
Continent (Europe)	**38.78**	**33.03 - 45.31**	**-1.96**	**-2.25 - -1.67**	**1.43**	**1 - 1.91**	**8.21 (1.18)**	**6.94**	7.11 (3.74)	1.9
Sampling Effort	--	--	**-0.57**	**-0.64 - -0.53**	**-0.19**	**-0.25 - -0.14**	--	--	--	--
Random effects	Variance (Std.dev.)		Variance (Std.dev.)		Variance (Std.dev.)					
Species	**181.6**	**118.1 - 256.8**	**0.31**	**0.19 - 0.43**	**1.32**	**0.14 - 3.66**	--		--	
Model summary										
Number observations (n)	7235-7500		18.4-1464.9		57.9-1551.6		164		1849	
Variation explained (R2)	0.11		0.87		0.27		0.07		0.14	

Table S2.5. Estimated model coefficients for the change in occupancy, extirpation, colonization, and detection-corrected species richness models at a 50 km by 50 km 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.

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

Baseline:Change interaction	**-7.12**	**-8.45 - -5.58**	**0.47**	**0.4 - 0.53**	**-0.32**	**-0.39 - -0.24**	**-1.41 (0.22)**	**-6.29**	**-0.68 (0.28)**	**-2.38**
Precipitation position variables										
Baseline (1st order polynomial)	-0.88	-2.02 - 0.19	0.73	-5.91 - 7.46	**-23.4**	**-30.61 - -15.15**	-0.26 (0.21)	-1.23	0.13 (0.31)	0.44
Baseline (2nd order polynomial)	--	--	**-10.36**	**-15.67 - -5.18**	**13.49**	**6.85 - 20.92**	--	--	--	--
Change since baseline	**4.99**	**4.01 - 6.04**	**-0.26**	**-0.3 - -0.22**	**0.22**	**0.17 - 0.27**	0.25 (0.24)	1.03	0.25 (0.33)	0.76
Baseline:Change interaction	-0.31	-0.97 - 0.38	**0.08**	**0.05 - 0.11**	-0.02	-0.05 - 0.02	0.3 (0.17)	1.81	-0.01 (0.19)	-0.04
Climatic position interactions										
Baseline thermal:Baseline precipitation interaction	0.71	-0.62 - 1.9	-0.06	-0.11 - 0	**0.12**	**0.07 - 0.18**	-0.21 (0.18)	-1.2	0.01 (0.25)	0.05
Change in thermal:Change in precipitation interaction	-0.3	-1.09 - 0.46	**-0.05**	**-0.09 - -0.02**	0.01	-0.03 - 0.05	**1.04 (0.2)**	**5.25**	0.4 (0.23)	1.79
Covariates										
Continent (Europe)	**37.1**	**31.46 - 42.32**	**-1.87**	**-2.09 - -1.65**	**1.46**	**1.23 - 1.69**	**3.96 (0.57)**	**6.95**	3.06 (1.97)	1.55

Sampling Effort	--	--	**-0.53**	**-0.56 - -0.5**	**-0.09**	**-0.11 - -0.07**	--	--	--	--
Random effects	Variance (Std.dev.)		Variance (Std.dev.)		Variance (Std.dev.)					
Species	238.8	160.1 - 334	0.37	0.23 - 0.52	0.25	0.16 - 0.36	--		--	
Model summary										
Number observations (n)	5000-5490		40.3-5608		58.8-2410.7		4856		4856	
Variation explained (R2)	0.1		0.84		0.61		0.03		0.06	

Table S2.6. Estimated model coefficients for the change in occupancy, extirpation, colonization, and detection-corrected species richness models at a 200 km by 200 km scale. Posterior means and 95% Bayesian credible intervals presented for PGLMM models, model coefficients (and standard error) presented for analysis of covariance (ANCOVA) and spatial autoregressive (SAR) error models. t-values (for analysis of covariance models) and z-values (for SAR error models) are included as a measure of significance. Generally, coefficients with t-values < -2 and > 2 are considered significant, these and coefficients where the 95% CI does not overlap zero are in bold text in the table. Variance explained is expressed in terms of marginal R2 (for PGLMM), adjusted-R2 (for ANCOVA models), and Nagelkerke pseudo-R2.

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

Baseline:Change interaction	**-9.96**	**-12.87 - -6.94**	**0.54**	**0.33 - 0.81**	**-0.47**	**-1.16 - -0.08**	**-5.5 (0.99)**	**-5.55**	**-2.97 (1.11)**	**-2.69**
<u>Precipitation position variables</u>										
Baseline (1st order polynomial)	**-2.89**	**-4.89 - -0.91**	0.07	-7.03 - 7.34	**-37.24**	**-83.9 - -14.07**	-1.04 (1.05)	-0.99	0.31 (1.26)	0.24
Baseline (2nd order polynomial)	--	--	3.68	-4.3 - 11.65	11.72	-6.28 - 38.02	--	--	--	--
Change since baseline	**4.33**	**2.59 - 6.08**	**-0.13**	**-0.25 - -0.02**	**0.49**	**0.17 - 1.15**	0.26 (1.16)	0.23	0.48 (1.33)	0.36
Baseline:Change interaction	0.26	-0.72 - 1.16	-0.05	-0.12 - 0.02	-0.12	-0.34 - 0.03	0.77 (0.94)	0.83	0.48 (0.99)	0.49
<u>Climatic position interactions</u>										
Baseline thermal:Baseline precipitation interaction	1.07	-1.54 - 3.83	0.05	-0.07 - 0.2	0.28	-0.01 - 0.74	1.1 (0.89)	1.23	1.28 (1.09)	1.18
Change in thermal:Change in precipitation interaction	0.57	-0.88 - 1.92	0.02	-0.06 - 0.09	**0.25**	**0.05 - 0.59**	2.42 (0.9)	2.68	1.2 (0.93)	1.29
<u>Covariates</u>										
Continent (Europe)	**38.47**	**31 - 45.34**	**-2.13**	**-3.18 - -1.46**	**1.55**	**0.55 - 3.55**	-1.5 (2.52)	-0.6	-0.52 (5.76)	-0.09

Sampling Effort	--	--	**-0.72**	**-0.93 - -0.54**	**-0.34**	**-0.79 - -0.14**	--	--	--	--
Random effects	Variance (Std.dev.)		Variance (Std.dev.)		Variance (Std.dev.)					
Species	133.8	75.62 - 193.4	0.41	0.16 - 0.82	0.66	0.09 - 2.47	--		--	
Model summary										
Number observations (n)	4181-5284		10.5-1428.2		6.5-382.6		584		584	
Variation explained (R2)	0.1		0.71		0.14		0.08		0.19	

Table S2.7. 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)		Colonization (PGLMM)		Species richness (ANCOVA)		Detection-corrected species richness (SAR error model)	
	Posterior mean	95% CI	Posterior mean	95% CI	Posterior mean	95% CI	Estimate (SE)	t value	Estimate (SE)	z value
Intercept	-45.15	-102.49 - 11.21	0.89	-1.41 - 3.21	**-2.52**	**-4.73 - -0.33**	**-15.36 (0.74)**	**-20.69**	**-14.85 (1.47)**	**-10.09**
Thermal position variables										
Baseline (1st order polynomial)	**-5.4**	**-7.18 - -3.58**	**20.67**	**15.2 - 25.93**	**-7.69**	**-14.72 - -0.65**	-0.08 (0.56)	-0.15	0.52 (0.72)	0.72
Baseline (2nd order polynomial)	--	--	**13.85**	**9.03 - 19.04**	**14.45**	**8.32 - 20.34**	--	--	--	--
Change since baseline	**-3.69**	**-5.23 - -2.17**	**0.27**	**0.21 - 0.34**	-0.05	-0.14 - 0.03	**-2.85 (0.78)**	**-3.66**	**-3.12 (0.8)**	**-3.88**

Baseline:Change interaction	**-9.51**	**-11.24 - -7.75**	**0.44**	**0.35 - 0.52**	**-0.36**	**-0.47 - -0.26**	**-3.97 (0.59)**	**-6.71**	**-2.94 (0.66)**	**-4.46**
Precipitation position variables										
Baseline (1st order polynomial)	**-1.93**	**-3.34 - -0.5**	0.63	-6 - 6.94	**-33.81**	**-42.7 - -25.37**	-1 (0.58)	-1.74	-0.61 (0.67)	-0.91
Baseline (2nd order polynomial)	--	--	-5.52	-11.5 - 0.4	**15.51**	**8.38 - 22.84**	--	--	--	--
Change since baseline	**4.63**	**3.21 - 6.01**	**-0.19**	**-0.25 - -0.13**	**0.25**	**0.16 - 0.33**	0.4 (0.65)	0.61	1.11 (0.76)	1.46
Baseline:Change interaction	-0.25	-1.05 - 0.55	0.04	0 - 0.08	-0.04	-0.08 - 0.01	0.39 (0.44)	0.9	0.06 (0.46)	0.13
Climatic position interactions										
Baseline thermal:Baseline precipitation interaction	0.13	-1.41 - 1.58	0.01	-0.06 - 0.08	**0.11**	**0.03 - 0.18**	-0.36 (0.46)	-0.78	-0.19 (0.54)	-0.35
Change in thermal:Change in precipitation interaction	-0.24	-1.29 - 0.84	0.02	-0.02 - 0.07	0.05	-0.01 - 0.11	**2.29 (0.52)**	**4.42**	**1.63 (0.54)**	**3.04**

Covariates										
Continent (Europe)	**38.03**	**31.62 - 44.05**	**-1.99**	**-2.29 - -1.7**	**1.26**	**0.93 - 1.59**	**9.48 (1.51)**	**6.29**	**10.17 (2.63)**	**3.87**
Sampling Effort	--	--	**-0.56**	**-0.62 - -0.51**	**-0.17**	**-0.21 - -0.13**	--	--	--	--
Random effects	Variance (Std.dev.)		Variance (Std.dev.)		Variance (Std.dev.)					
Species	185.1	115.6 - 256	0.3	0.18 - 0.43	0.27	0.16 - 0.4	--		--	
Model summary										
Number observations (n)	4596-5481		69.4-2453.7		201.6-4627.8		1374		1374	
Variation explained (R2)	0.1		0.85		0.56		0.09		0.1	

Table S2.8. 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.

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

Baseline:Change interaction	**-9.07**	**-10.73 - -7.5**	**0.42**	**0.34 - 0.5**	**-0.32**	**-0.42 - -0.22**	**-4.66 (0.66)**	**-7.05**	**-2.43 (0.83)**	**-2.92**
Precipitation position variables										
Baseline (1st order polynomial)	**-1.99**	**-3.47 - -0.59**	-0.14	-6.21 - 6.16	**-36.96**	**-45.96 - -28.29**	-0.94 (0.65)	-1.45	-0.04 (0.87)	-0.05
Baseline (2nd order polynomial)	--	--	**-7.41**	**-12.94 - -1.84**	**16.85**	**9.68 - 23.69**	--	--	--	--
Change since baseline	**4.7**	**3.39 - 6.19**	**-0.19**	**-0.26 - -0.11**	**0.26**	**0.18 - 0.35**	0.62 (0.76)	0.82	0.73 (0.98)	0.74
Baseline:Change interaction	-0.16	-1.03 - 0.65	0.03	-0.01 - 0.07	-0.03	-0.08 - 0.02	0.37 (0.49)	0.75	-0.38 (0.53)	-0.72
Climatic position interactions										
Baseline thermal:Baseline precipitation interaction	0.31	-1.11 - 1.65	-0.02	-0.07 - 0.04	**0.08**	**0.02 - 0.16**	-0.17 (0.51)	-0.34	0.17 (0.69)	0.25
Change in thermal:Change in precipitation interaction	-0.66	-1.75 - 0.38	0.05	-0.01 - 0.1	0.04	-0.02 - 0.11	**2.16 (0.61)**	**3.56**	0.74 (0.69)	1.07
Covariates										
Continent (Europe)	**38.09**	**31.68 - 44.28**	**-1.97**	**-2.27 - -1.67**	**1.34**	**0.99 - 1.67**	**9.44 (1.74)**	**5.42**	**8.44 (3.63)**	**2.32**

Sampling Effort	--	--	**-0.54**	**-0.6 - -0.48**	**-0.17**	**-0.21 - -0.13**	--	--	--	--
Random effects	Variance (Std.dev.)		Variance (Std.dev.)		Variance (Std.dev.)					
Species	185.9	120.9 - 265.9	0.3	0.18 - 0.43	0.31	0.17 - 0.46	--		--	
Model summary										
Number observations (n)	5000-5324		25.3-2121.9		175.4-3736.8		1133		1133	
Variation explained (R2)	0.1		0.86		0.53		0.1		0.18	

Chapter 3: Complex interactions between land-use and climate change influence extinction risk and assemblage shifts in bumblebees

Abstract

Climate change and human land-use both modify local climates, potentially interacting to alter biodiversity responses. These two pressures also tend to favour similar species, leaving communities more similar than historically. Using long-term occurrence data for 74 bumblebee species across North America and Europe from 1900-2018, I tested whether land-use and climate change interactions have contributed to changes in extirpation risk, colonization, site occupancy, and species richness. I find that recent climate change and land-use change have driven historic trends in biodiversity. Declines related to increasing temperatures and thermal extremes are more severe in areas with historically high proportions of human-dominated land-use, but species respond better to increasing human land-use in places where they were historically near their hot tolerance limits. Many assemblages experienced positive biodiversity outcomes concurrent with land-use change, suggesting that human-dominated landscapes can be managed to benefit species. Finally, I find that biotic homogenization is occurring across North America and Europe, suggesting a focus on the composition of assemblages will also be required for conserving diverse wild pollinator communities.

Introduction

Land-use and climate change are driving changes in biodiversity globally, and understanding the interactions between these two drivers of change is critical for preventing the loss of species (Titeux et al. 2017; Leclère et al. 2020). Maintaining biodiversity and bending the curve of biodiversity loss requires tools that predict how climatic and land-use changes will alter local extinction (extirpation) and colonization probabilities, but development of these tools has remained challenging (e.g. De Palma et al. 2018). Identifying the species and regions which are likely to be most at risk from climate change and land-use change can inform conservation, and elucidating potential mechanisms driving change is also critical for developing conservation solutions (Urban et al. 2016).

Recent climate change has altered the distribution of many species, forcing them to move to track habitable environmental conditions or adapt to new conditions, and causing the loss of species from historically occupied areas (Parmesan & Yohe 2003; Scheffers et al. 2016; IPBES 2019). Climate change also poses a risk to species by increasing the frequency and severity of extreme events, such as heat waves, that may exceed species' tolerances or challenge their thermoregulatory capacities (Sunday et al. 2014; Erenler et al. 2020; Soroye et al. 2020). The resulting costs to species are likely to cause population declines in affected regions. Conversely, climate change may render some regions more suitable for a species, increasing the likelihood of successful colonization by dispersing individuals (Deutsch et al. 2008; Sunday et al. 2012). Measures such as the thermal position index, which estimate the ratio of time a species spends close to or beyond their historical temperature tolerance limits in a region (or the change in this ratio over time), allow for species-specific, spatially-explicit measures of climate change-risk which incorporate risk from both gradual warming and extreme events (Soroye et al. 2020; Williams & Newbold 2021).

Land-use change alters extinction risk in a variety of ways and is currently the most important cause of biodiversity decline globally (Maxwell et al. 2016; Di Marco et al. 2018; IPBES 2019; Schipper et al. 2020). Land-use changes cause habitat loss for species (i.e., eliminating areas species require to fulfill basic life history needs) and contribute strongly to extinction risks for many species. Land-use intensification, including increased use of pesticides and fertilizers, can exert effects on species abundances and distributions that are distinct from land-use change (Kerr & Cihlar 2003; Gibbs et al. 2009; Millard et al. 2021).

Climate change and land-use change can interact to accelerate potential biodiversity responses (Mantyka-Pringle et al. 2012; Williams & Newbold 2020). In addition to the direct destruction of species' habitats or resources, land-use changes (including intensification) can also alter local climatic conditions, for example by modifying vegetation cover, creating hotter and more extreme local conditions that exacerbate the effects of global climate change (Frishkoff et al. 2015a; Findell et al. 2017; Senior et al. 2017; Williams & Newbold 2020; Lembrechts & Nijs 2020). Land-use changes can also remove the microrefugia which are critical for species' thermoregulation in the face of increasing temperatures, and fragmentation of habitats from land-use changes may impede species' distributional shifts in response to climate change (Kearney et al. 2009; Tuff et al. 2016). These two pressures can both favour species which tolerate extremes and hotter or drier temperatures better, which can influence the composition of communities and potentially drive biotic homogenisation (Frishkoff et al. 2016; Piano et al. 2017; Nowakowski et al. 2018; Williams et al. 2020). The nature and relative importance of land use-climate change interactions are still being tested (Frishkoff et al. 2015a; Oliver et al. 2015, 2017; Merckx et al. 2018; Srinivasan et al. 2019; Williams & Newbold 2020; Srinivasan & Wilcove 2021), but understanding mechanisms for their potential impacts on species will inform management activities to mitigate biodiversity loss. This becomes increasingly important as the potential for interactions grows (Mantyka-Pringle et al. 2015).

Elevated extinction risks confront many taxa, but declines and losses of wild pollinator species are particularly likely to include practical consequences given the ecosystem services they provide (Potts et al. 2010; IPBES 2016). Diverse and abundant wild pollinator communities are linked with benefits for wild lands and agriculture (Garibaldi et al. 2013; Mallinger & Gratton 2015). Climate change, especially warming temperatures and growing frequencies of extreme conditions, is linked to extirpation and shrinking ranges in pollinator taxa like bumblebees (*Bombus*) (Kerr et al. 2015; Soroye et al. 2020), but habitat loss and land-use intensification (including pesticide use) are also linked to recent declines (Ricketts et al. 2008; Winfree et al. 2009; Millard et al. 2021). Other threats, such as the introduction of novel pathogens or parasites, and competition with invasive species also contribute to pollinator losses in some areas (Goulson et al. 2015). Responses to land use are variable, and in some cases low levels of human-dominated land use are associated with positive effects (Winfree et al. 2009; Millard et al. 2021).

Here, I present a cross-continental study investigating effects of historic interactions between climate change and land-use change on species distributions. I test whether changes among several biodiversity metrics from a historic period (1900-1974) to a more recent period (2000-2018) in 100 km by 100 km sites across North America and Europe are related to concurrent changes in land use and thermal position. I use a large dataset of >330,000 unique spatiotemporal occurrences of 74 species (Table S3.1), high-resolution temporal climate data (Figure S3.1), and landscape-level, temporal data on human-dominated land use data (including cropland, grazing, and urban land uses; Figure S3.2). I hypothesize that climate change and land-use change will interact to increase extirpation risk in historically occupied areas and reduce colonization in new areas, decreasing probabilities of site occupancy, and reducing species richness. Specifically, I predict greater declines in biodiversity in areas where both human-dominated land uses and thermal position have increased simultaneously, and in areas where both were high historically. I also expect to see direct effects of climate change and land-use change, and that differences in land-use change-related relationships may exist between continents given the different histories of land use in North America and Europe. As human-dominated land use has historically been higher in Europe than North America (Goldewijk et al. 2016), I suspect that the species and assemblages there may be less negatively impacted by current land-use change.

Methods

Bumblebee data

I used a dataset of 333,423 spatiotemporally unique occurrence observations of North America and European bumblebees (*Bombus*). The dataset is similar to one used previously (see Kerr et al. 2015; Soroye et al. 2020) and contains North American data from the Bumblebees of North America dataset (Williams et al. 2014) and Williams et al. (2019), and European data from Williams et al. (2019) and the Global Biodiversity Information Facility (GBIF.org 2020).

From a larger initial dataset, I removed records with incomplete species, location, or sampling-year information. Records in bodies of water but less than 5000m from a high-resolution coastline were assumed to be coastal observations with spatially imprecise coordinates and were subsequently reassigned to the nearest point on land. Records more than 5000m from coastline were removed. I removed duplicate location-year-species observations to reflect species occurrence rather than sampling or population density, and kept observations within a historic period (1900-1974; inclusive) and a recent period (2000-2018; inclusive). This historic period represents a baseline of relatively low anthropogenic climate change (Walther et al. 2002), and climate between these two periods have changed sufficiently to detect biological impacts (e.g. Kerr et al. 2015; Lewthwaite et al. 2017; Soroye et al. 2020). While the baseline period was substantially longer, there were about 3 times more observations in the recent period. In North America, the final dataset included 43 species, with 48,588 observations in the historic period and 68,098 in the recent period. In Europe, the dataset contained 36 species, and contained 21,309 historic records and 195,428 recent records.

The 74 species retained in the final dataset represent over half of the approximately 123 known bumblebee species across this study area. I selected all species that appeared reasonably well-sampled, so that observed changes would be less likely to be the result of changing sampling intensity. All 74 species in the final dataset had >50 spatiotemporally unique observations in each period, except for *B. suckleyi*, *B. pomorum*, and *B. confusus* (Table S3.1). These three species had >50 observations in the historic period and only 20-34 observations in the recent period, but have been assessed as by the IUCN Red List as decreasing and either Critically Endangered (*B. suckleyi;* Hatfield et al. 2015) or Vulnerable (*B. pomorum*, and *B.*

confusus; Rasmont et al. 2015b, 2015c). Given this strong expectation for decline in these species, they were included. The mean (and median) number of spatiotemporally unique observations per species was 944.6 (569.5) in the historic period and 3561.2 (1193.5) in the recent period.

Biodiversity change

I mapped presence and absence for each species within 100 km by 100 km equal-area quadrats (sites) across the study area in the historic and recent periods, inferring absence of a species when there was no observation of the focal species in a site during a period, but at least one other species recorded. Previous work with a similar occurrence dataset has shown that biodiversity change relationships are robust to the definition of absence (e.g., defining absence as places where a focal species was not seen but 3 or 5 other species were; Soroye et al. 2020). Spatial aggregation of the data is necessary, and the 100 km by 100 km equal-area quadrats strikes a balance between achieving reasonable sampling across North America and Europe, and still maintaining relevance for conservation at local scales. Previous work with a similar occurrence dataset demonstrates that biodiversity change and global change relationships are robust to quadrat size (Soroye et al. 2020).

Using the presence-absence maps, I measured observed extirpation, colonization, and species richness change between the two time periods across 1,258 sites with data for at least one species in each period (Figures 3.1 and S3.4). I calculated percentage change in observed species richness from the historic to recent period. Using the identity of species present in each site and the R package *vegan* (Oksanen et al. 2016), I calculated the mean pairwise Jaccard dissimilarity from each focal site to all others in its continent for each period and subtracted this from one to estimate community similarity (Jaccard's similarity). In each period, similarity of 0 indicates no species in common on average between a focal site and all other on its continent, and 1 represents identical assemblage composition to all other sites on the continent. I calculated the change in this between periods, with increases indicating biotic homogenization (Figure S3.3).

I calculated change in the probability of site occupancy to provide an alternate measure of biodiversity change that reflected extinction-colonization dynamics at a site and that accounted for non-detection bias. Accounting for non-detection bias (i.e. a difficulty distinguishing among true and false absences due to imperfect detection) is a well-known challenge of working with occurrence data, and a growing literature surrounds how to account for this in opportunistic data through the use of occupancy models (e.g. van Strien et al. 2010, 2013; Molinari-Jobin et al. 2017).

I used single-species occupancy models to estimate occupancy for the 74 species in each period. I modelled probability of occupancy within the range of the focal species and a 200-km buffer in sites where a species was seen in either the historic or recent period. These models account for the possibility of false-absences within detection/non-detection data by explicitly estimating detection probability (p) separately from probability of occurrence (MacKenzie et al. 2006, 2009; Royle & Kéry 2007; Royle & Dorazio 2009; Kéry & Schaub 2012). Estimating detection probability for a species during a period requires multiple "survey units" or "visits" to sites within that period. I split each of the time periods into three "survey units" (historic: 1901-

1924 (12,759 observations), 1925-1949 (16,580 observations), and 1950-1974 (40,549 observations); recent: 2000-2006 (32,652 observations), 2007-2013 (95,575 observations), and 2014-2018 (135,299 observations)). There is much variation in sampling among visits here, but others have shown that occupancy models using opportunistic data which varies greatly across time still produces similar results to structured monitoring data (e.g., van Strien et al. 2013). I used observations of a species during a survey unit to inform detection, and absence of a species where others were seen as a non-detection. Occupancy models using opportunistic data are sensitive to parameterization decisions (e.g., Guzman et al. 2021), so I use change in probability of occupancy as an additional metric of biodiversity change for hypothesis-testing purposes (Soroye et al. 2021).

It is likely that there are biases in the species sampled within the dataset, as in most large-scale ecological datasets. Bumblebees are charismatic insect species that have been collected by researchers and independent naturalists for hundreds of years, but agriculturally important species (e.g., *B. terrestris* and *B. impatiens*), common species, and larger or more recognizable species may have greater likelihoods of detection. Conversely, common species may be less likely to be digitized in museum collections. I used total number of records at a site to help inform species-specific detection probabilities in the occupancy models and account for variation in sampling intensity. Unfortunately, reliable inter- and intra-specific data on other traits that may influence detection probability are not available for all species to include in the models. A necessary assumption of occupancy modelling is that there is no change in occupancy (or species turnover) within a survey period or between survey units within the same period: the closure assumption (Rota et al. 2009). Estimates of site occupancy rely on this assumption to calculate a probability of detection from the pattern of detection/non-detections during a period (MacKenzie et al. 2006). Aggregation of occurrence data into periods to estimate species' presence or absence makes a similar assumption that presence/absence remains static within those periods. Violations of the closure assumption during occupancy modelling are likely to be frequent throughout the literature but recent work suggests that spatially or temporally aggregating opportunistically collected data is not likely to have large effects on model performance (Jönsson et al. 2021).

Occupancy models were fit using the Bayesian general-purpose modelling software JAGS (Plummer 2003) and package R2jags (Su & Yajima 2015). Each species- and season-specific model computed season- and site-specific occupancy, using season-specific sampling effort (i.e., the total number of unique location-year observations of any species in a cell) as a covariate for the underlying detection process. I used noninformative Bayesian priors for all parameters and each model ran four Markov chains for 200,000 iterations, discarding the first 5,000 as a burn-in and thinning by 10, resulting in 195,000 samples from the joint posterior distribution. I ran models until values of the Brooks-Gelman-Rubin statistic suggested convergence had been reached (<1.1) for all parameters (Brooks & Gelman 1998). The JAGS code specifying the model, including the priors used, is available in Appendix 3.1.

I calculated a measure of detection-corrected species richness, measured as the summed probability of site occupancy for all species in a site, across the study area for each period (this is similar to detection-corrected estimates of taxonomic diversity used elsewhere e.g., Jarzyna & Jetz 2017). I calculated the percent change in this measure between the historic and recent periods (Figure S3.5).

Thermal position data

I calculated thermal position for each species as described previously (e.g., Kerr 2020; Soroye et al. 2020), using global climate data obtained from Harris et al. (2020). For each of the 74 bumblebee species, I extracted the average of the five highest monthly maximum and five lowest monthly minimum temperatures from among the values for all location and year combinations within the species' geographic range in the historic period (1901-1974). These maximum and minimum temperatures were assumed to represent the thermal limits for the species. Thermal limits were rescaled for each species to equal 0 for the lower thermal (i.e., cold) limit and 1 for the upper thermal (i.e., warm) limit. These derived environmental limits measure species' realized niche limits or tolerances. Realized niche limits likely differ from lab-based measurements of upper and lower critical temperatures, but lab-based measures are not available for more than a handful of the 74 bumblebee species in the study. Past work has shown that measuring the change in the environment relative to these derived realized niche limits relates to biodiversity change (Soroye et al. 2020; Williams & Newbold 2021).

For each species, in each cell of the study area in both periods, I rescaled the local maximum and minimum monthly temperatures onto the same scale as the realized climatic limits. These rescaled values were averaged across months to estimate the thermal position index: a value of 1 indicates that average temperatures across the year are at the warm tolerance limit of a species, and values of 0 indicate that average temperatures across the year are at the cold tolerance limit for the species (values greater than 1 and less than 0 are possible where climate change has caused annual-average temperatures to exceed species' upper thermal limits or to fall below lower thermal limits). The change in thermal position from the baseline to the recent period was calculated by subtracting position in the recent period from position in the baseline.

To calculate the community-averaged estimates of thermal position, I clipped each species' thermal 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 position for the entire estimated assemblage of species in that region (Figure S3.1). I did this for both periods, and then measured the change from the baseline to recent (Figure S3.1). These estimates of community-averaged thermal position were used in the species richness analyses.

Climate data were obtained from the Climate Research Unit (Harris et al. 2020) at a resolution of 0.5 X 0.5 degrees. After the calculation of the climatic position index, data were projected and resampled to Cylindrical Equal Area projection at 100 km X 100 km resolution to match the biodiversity data.

Land-use change data

Using the temporal, high-resolution HYDE 3.2.1 dataset (Goldewijk et al. 2016, 2017), I calculated the average cover of human-dominated land uses in the historic and recent periods across North America and Europe. The HYDE dataset provides global estimates of total area (km^2) used for pasture, grazing, and urban land uses at a 5-arcminute resolution (~8.3 km X 8.3 km at the equator), from 10,000 BCE to 2017. I averaged the data available for the two time periods (1900-1974 and 2000-2018) and calculated the proportion of land area in each site covered by human-dominated land uses (summed cropland, grazing, and urban) across the study area. I resampled the data to 100 km by 100 km equal area grids to match the biodiversity data, and used the proportion of human-dominated land use and change between periods for analyses (Figure S3.2).

Statistical analyses

Extirpation and colonization models. I tested the relationship between thermal position, land-use change, and extirpation or colonization by constructing a series of binomial generalized linear mixed models (GLMM). Models included the thermal position variables (historic, change since historic, interaction between these), human-dominated land use variables (historic, change since historic, interaction between these), and the interactions between historic land use and historic thermal position, historic land use and change in thermal position, historic thermal position and change in land use, and change in land use and change in thermal position. The models included species as a random effect, and I included continent as a categorical variable to account for potential differences between North America and Europe. I also included sampling intensity into the model, as the number of unique spatiotemporal occurrence observations within a site in a period. I ran all models to convergence, and visually assessed model assumptions. I calculated conditional and marginal R^2 for these models (Nakagawa & Schielzeth 2013).

Change in probability of occupancy. I ran another series of linear mixed models to test the relationship between climate change, land-use change, and change in probability of site occupancy. Change in probability of site occupancy was the difference in occupancy probability between the historic and recent periods, and could range continuously from -100% to 100%, with negative values indicating a decrease in probability of site occupancy and positive values indicating an increase in probability of site occupancy. The model structure was identical to extirpation and colonization models, although I did not include sampling effort, as it was already used to estimate occupancy. I calculated conditional and marginal R^2 in the same way as in the change in occupancy models.

Phylogenetic models. To account for phylogeny in the analyses, I repeated the extirpation, colonization, and change in occupancy modelling using a phylogenetic generalized linear mixed model framework, with a comprehensive mitochondrial and nuclear phylogeny (Cameron et al. 2007). I programmed models using the *MCMCglmm* (Hadfield 2010) and *ape* (Paradis & Schliep 2018) packages in R, following the framework from de Villemereuil & Nakagawa (2014). All models used uninformative univariate priors for random effects corresponding to an inverse-Gamma with shape and scale parameters equal to 0.01. Models were run with a minimum of 105,000 iterations with a thinning factor of 20 and discard the first 5,000, resulting in a minimum of 5,000 samples from the joint posterior distribution. Model parameters were visually assessed for convergence, and if all parameters did not appear to converge then I reran the models with more iterations and a longer burn-in. I estimated marginal and conditional R^2, and phylogenetic signal (Pagel's λ) using code adapted from de Villemereuil & Nakagawa (2014). As is common with Bayesian models, I compared them using the Deviance Information Criterion (DIC). *B. magnus* and *B. kirbiellus* were not present in the phylogeny and were excluded from these analyses. The structure of fixed model effects tested was identical to the descriptions provided above, and I found that model parameter values using the PGLMMs were very consistent with non-phylogenetic models (Tables 3.1 and S3.1). I present results from the PGLMMs in the main text because while DIC was very similar (ΔDIC= 4.7 lower for extirpation model, 1.2 higher for colonization model, 3.8 lower for the change in site occupancy model), the PGLMMs explained greater variation (25.7% more for extirpation model, 5.2% more for colonization model, 20.4% more for change in site occupancy model).

Assemblage richness. I built an analysis of covariance model (ANCOVA) model to test the relationship between climate change, land-use change, and detection-corrected species richness (Table 1). The model structure here was identical to the change in occupancy PGLMM, but used community-averaged measures of thermal positioning and did not include a random effect of species. I used a similar ANCOVA to model observed (non-detection corrected) species richness, which was the same as the above model, but also included a covariate accounting for sampling intensity (Table S3.4).

I checked for spatial autocorrelation in the residuals of both assemblage richness models by visually inspecting a correlogram of Moran's I (Figures S3.6 and S3.7). I found evidence of spatial autocorrelation and proceeded by constructing a simultaneous autoregressive spatial error (SAR) model to correct for residual autocorrelation, as suggested by (Kissling & Carl 2008) and (Dormann et al. 2007). This reduced much of the variability in Moran's I (Figures S3.6 and S3.7). While model results with the SAR models were qualitatively similar to the ANCOVA results (Tables S3.3 and S3.4), incorporating spatial autocorrelation removed the statistical significance of some terms. Shifts in coefficient strength and significance are a common phenomenon when accounting for spatial autocorrelation with SAR and other common methods of accounting for spatial autocorrelation (Bini et al. 2009). Given that the relative coefficient strength and z-values of terms in the SAR models confirm the importance of the significant ANCOVA effects, I present those results in Table 3.1. I calculated the Nagelkerke Pseudo-R^2 as a measure of the variance explained. Results from the models appeared robust to the presence of outliers, and aside from violations of spatial autocorrelation in the residuals, appeared to satisfy all other assumptions.

Change in similarity. To test whether increases in assemblage richness relate to increasing assemblage similarity, I used an ANCOVA model predicting change in similarity as a function of change in richness (running separate models for detection-corrected richness and observed richness; Table S3.5). I included continent and sampling intensity as covariates, and also included an interaction between continent and richness, to test whether richness might be related to similarity on one continent but not the other.

Increasing similarity (or decreasing similarity) in a site may arise either from extirpation of species, new species arriving, or a combination of both of these. To investigate the potential cause of increasing similarity, I used an ANCOVA model predicting change in site similarity with total extirpation and colonization events (Table S3.6). The model also included sampling intensity and continent as covariates, and interactions between continent and extirpation, and continent and colonization.

All analyses were performed in R version 3.6.1 (R Core Team 2017), primarily with the *raster* (Hijmans et al. 2016) and *tidyverse* (Wickham 2017) packages, and others specifically mentioned. Continuous variables in all statistical models were re-scaled and centered. Mapping and visualization of data was done in ArcGIS Pro (ESRI 2021), using a Winkel Tripel projection.

Results

Extirpation and colonization trends across the 74 North American and European bumblebee species showed a relatively strong signal of climate change and land-use change, including consistently appearing interactions. Using binomial generalized linear mixed effects models, which controlled for continent and sampling intensity, I modelled observed extirpation and colonization of species across the study area using thermal position variables (historic, change since historic, interaction between these), human-dominated land use variables (proportion of human-dominated land use historically, change in human-dominated land use since historic, interaction between these), and the interactions between historic land use and historic thermal position, historic land use and change in thermal position, historic thermal position and change in land use, and change in land use and change in thermal position. As expected, higher thermal position was associated with higher extirpation risks and reduced colonization likelihoods, independent of land-use change (though there was a weak positive relationship between changing thermal position and colonization; Table 3.1). Extirpation risk and colonization were both higher in areas with higher proportions of human-dominated land uses historically (Figure 3.1). Conversely, increasing landscape-level human-dominated land uses at a site did not appear related to extirpation risk, but was linked to reduced colonization, especially when increases occurred in areas with historically low human land-use (Table 3.1).

As predicted, climate change and land-use change interactions appeared to influence extirpation and colonization, although the effect and importance of interactions differed for each process. Increasing thermal position was related to increased extirpation risk for species in areas where human land-uses historically dominated, suggesting that landscapes with little remaining natural habitat put species at higher risk of climate change. Yet, not all interactions were associated with negative outcomes for species. Species which were already near their historic upper thermal tolerance limit experienced lower land-use change-related extirpation risk and had higher colonization in sites with historically high human-dominated land uses (Table 3.1), consistent with species in these hotter areas being better equipped to take advantage of human-dominated land uses (Frishkoff et al. 2016; Williams et al. 2020).

Probability of site occupancy, particularly near species' range boundaries, should relate to relative extinction and colonization rates. Generalized linear mixed models with the same fixed and random effects as the extirpation and colonization models revealed a negative effect of thermal position, but no clear direct effect of broad-scale land use (Table 3.1). Statistically significant interactions in the model further support that declines in probability of site occupancy were lower in sites with historically high thermal position and high proportions of human-dominated land-uses (Table 3.1). Together with the observed trends in extirpation and colonization, this could suggest that bumblebee populations which are better able to withstand increased temperatures and extremes can also better withstand challenges associated with human-dominated land-uses, as has been observed in other taxa (Frishkoff et al. 2015b; Piano et al. 2017; Williams et al. 2020).

Responses of extirpation risk, colonization, and change in probability of site occupancy to climate and landscape-scale land-use change appeared only weakly related to phylogeny. The inclusion of phylogeny into extirpation, colonization, and change in probability of occupancy models improved the fit only slightly according to DIC (ΔDIC ranged from 4.7 lower to 1.2 higher) but increased the variation in the response variable explained by 5-26% compared to non-phylogenetic models. Results were otherwise qualitatively consistent between phylogenetic models (presented in here) and non-phylogenetic models (Table S3.2). Pagel's λ indicated a moderate phylogenetic signal in the response of extirpation and change in probability of site occupancy (Pagel's $\lambda = 0.13$ and 0.10, respectively), with a substantially weaker signal in the response of colonization (Pagel's $\lambda = 0.06$).

Increasing thermal position and increasing land-use change appear to also influence changes in assemblage richness. An analysis of covariance model predicting change in detection-corrected species richness using community-averaged climatic position variables and site-level land-use measures indicated that, consistent with species-level trends, richness was significantly more likely to decline where assemblages were already close to their thermal limits, and where human-dominated land uses were increasing (although this latter trend bordered statistical significance; Table 3.1; Figure 3.2). Consistent with trends in extirpation, the negative effects of increasing thermal position were stronger in sites historically dominated by human land-uses (Figure 3.3). Accounting for spatial autocorrelation of residuals in the model removed the statistical significance of most terms (i.e., $p > 0.05$; Table S3.3), but relative strength of coefficients and t-values confirmed that the effects mentioned above were among the strongest influences on past changes in richness. Modelling observed species richness (i.e., without correcting for potential non-detection) highlighted the negative effect of thermal position (Table S3.4). Models predicting change in assemblage richness explained about 15-20% of variation in the response (Table 3.1, Tables S3.3 and S3.4).

While thermal position and land-use change were broadly related to declines in richness, there were large amounts of unexplained variation in these models (Table 3.1), and many sites experienced increases in assemblage richness concurrent with increasing thermal position or human-dominated land uses (e.g., Figure 3.3). Climate change and land-use change often favour the same species, which may alter assemblages and can lead to biotic homogenization (Frishkoff et al. 2016; Newbold et al. 2018, 2019; Williams et al. 2020). To test whether observed changes in local richness were related to increasing biotic homogenisation across study regions, I modelled the relationship between change in assemblage richness and change in site similarity (similarity here being the mean pairwise similarity of a focal site to all others on its continent, where 0 indicates no species in common and 1 represents identical assemblage composition). Assemblage similarity has increased on average in both North America (0.0048 ± 0016 SE) and Europe (0.17 ± 0.007 SE), and there was a strongly positive and statistically significant association with increasing richness, especially in Europe (Figures 3.4 and S3.3; Table S3.5). Increasing similarity can be driven by either increasing colonization of certain species, selective extirpation of others, or some combination of both processes. Here, similarity was highest when extirpation was low and colonization was high (Figure 3.5; Table S3.6), suggesting that range expansions of common species into areas with low extinction rates is a driver of biotic homogenization over broad areas. Among the 74 species in this dataset, the highest colonization rates were observed in species known to thrive in human-dominated landscapes (e.g., *B. terrestris* and *B. hypnorum*), but also species which are hard to identify and have historically been confused with other species (e.g., *B. norvegicus, B. cryptarum, B. sporadicus,* and *B. magnus)* (Rasmont et al. 2015a).

Conclusion

Climate change has driven declines in North American and European bumblebee species and assemblages independently of land-use change (Soroye et al. 2020), and here I find that broad-scale interactions between these drivers of change further shape bumblebee biodiversity. Patterns of interactions across species and assemblage-level change suggest that effects of climate change are exacerbated in historically human-dominated areas (Figure 3.3), and that populations used to temperatures near their historic upper thermal tolerance are better able to withstand land-use pressures (Table 3.1). While the correlative hypothesis-testing approach here cannot imply specific mechanisms driving these effects, human land uses and land-use change directly increase the risk of climate change by driving local climatic changes, including hotter local temperatures and increased exposure to temperature extremes (Medvigy et al. 2012; Findell et al. 2017; Senior et al. 2017). Habitat modification can also destroy critical microrefugia that insects and ectotherms use to thermoregulate (Kearney et al. 2009), and habitat fragmentation can limit species' ability to shift in response to changing climates, increasing the risk from climate change (Oliver et al. 2015). Yet, where species were able to withstand warm temperatures and extremes historically, they appeared better able to respond to increasing land-use. Thermal niche has previously been shown to predict tolerance to deforestation for ectotherms, suggesting that climate and land-use change favor the same species (Frishkoff et al. 2015a, 2016).

The results here have particular relevance for global conservation, which is especially pertinent as nations look towards post-2020 conservation frameworks and targets. At species and assemblage levels, sites with more natural habitat historically appeared to buffer against effects of climate change (Figure 3.2; Table 3.1), pointing to the importance of maintaining wilderness or other natural areas to reduce biodiversity loss (Di Marco et al. 2019) and to the potential value for habitat restoration in areas where habitat losses are significant. I find that bumblebee species richness can be high in managed landscapes that have experienced warming (Figure 3.3), suggesting that these species can persist or thrive in human-dominated areas under some conditions or types of land-use management (Tscharntke et al. 2005; Carvell et al. 2017). Yet, recent increases in bumblebee assemblage richness are linked to biotic homogenization, which appears driven by increasing colonization of some species into areas of low extirpation risk. Biotic homogenization would be a particularly grave indication of conservation threat if range expansions of common species were associated with losses among rarer species. While bumblebee diversity across continents shows strong patterns of biotic homogenization, that trend is not directly dependent on range losses among rare species here. Nonetheless, community composition in addition to richness will be important to consider for conservation. Protecting wild spaces and managing landscapes for climate change, for example by protecting and creating microrefugia and maintaining diverse habitat types that may reduce species’ exposure to temperature extremes (Scheffers et al. 2014), appears to be a strong path forward for protecting species in a future of increasing climatic and anthropogenic pressures.

Figures 3.1-3.5

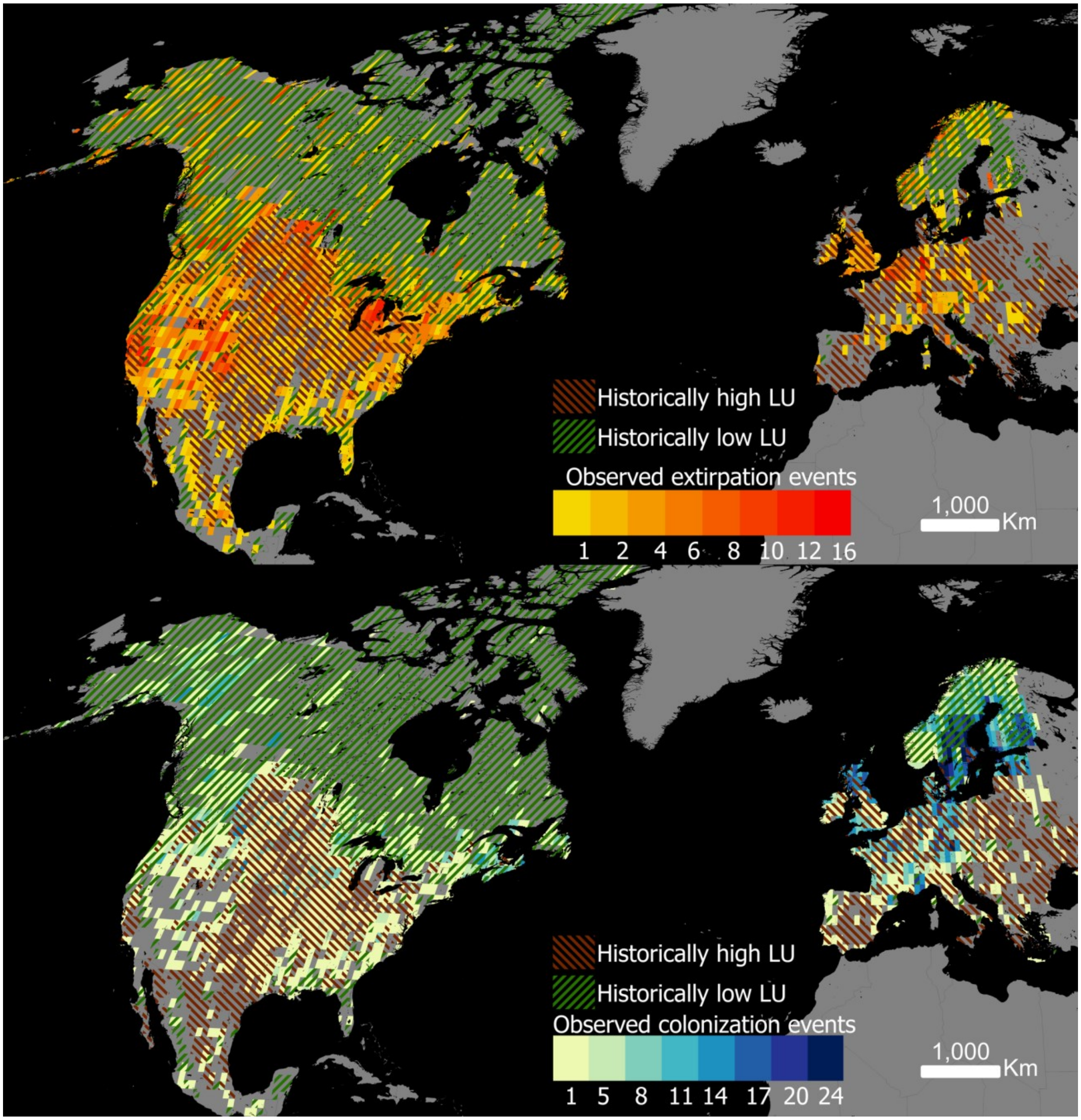

Figure 3.1. Patterns of human-dominated land use (cropland, grazing, and urban) and observed extirpation (A) and colonization (B) of 74 bumblebee species across North America and Europe between the historic (1900-1974) and recent (2000-2018) periods. Yellow-Red scale (A) shows number of observed extirpation events per cell; yellow-blue scale (B) show number of observed colonization events per cell. Hatched brown and green lines indicate areas of historically very high (>50%) and very low (<10%) coverage of human-dominated land uses.

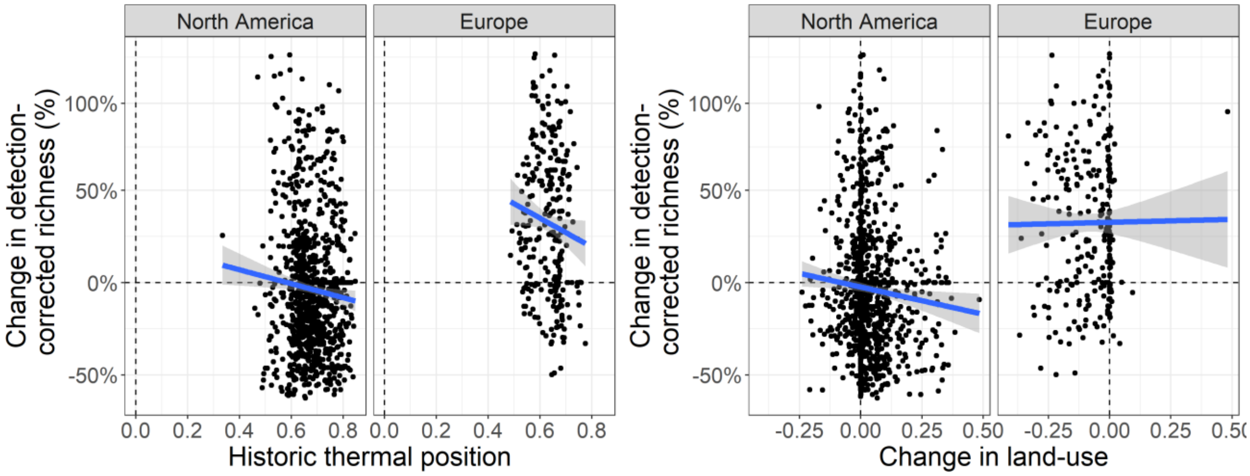

Figure 3.2. Change in detection-corrected species richness in response to historic thermal position and change in land use across North America (991 sites) and Europe (267 sites) between a historic period (1900-1974) and recent (2000-2018). Historic thermal position has a potential range of 0 to 1 where zero indicates that a species is on average at their historic cold tolerance limit for the entirety of the year in the period at that site, and one indicates that a species is on average at their historic hot tolerance limit for the entirety of the year in the period at that site. Change in land use indicates the overall increase or decrease in proportion of the site now covered with human-dominated land uses (cropland, pasture, and urban). Confidence intervals (±95%) are shown around linear trendlines.

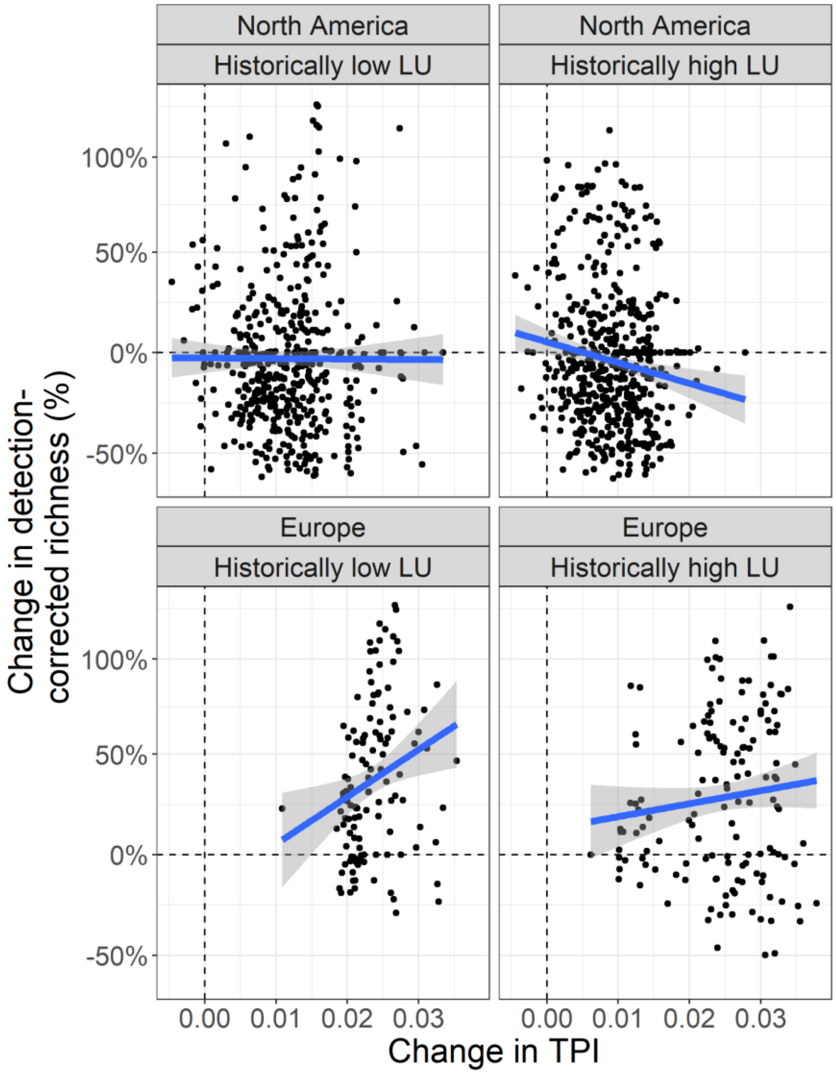

Figure 3.3. Response of change in detection-corrected to changing thermal position in sites with historically low, and high human-dominated land use across North America and Europe between historic period (1900-1974) and recent (2000-2018). For visualization of the significant interaction between changing thermal position and historic land use, the continuous land-use variable has been split to group responses at sites with historically low (<33% human-dominated land use in the historic period; n= 736 in North America, n=173 in Europe), and high land use (>33% human-dominated land use in the historic period; n= 685 in North America, n=247 in Europe). Linear trendlines and confidence intervals (±95%) show the average across sites in each panel. Note that European sites with low historic land-use are largely >58° latitude where species are generally near their cold limits (e.g., see Figure 1), likely contributing to an extremely positive effect of increasing thermal position at these sites.

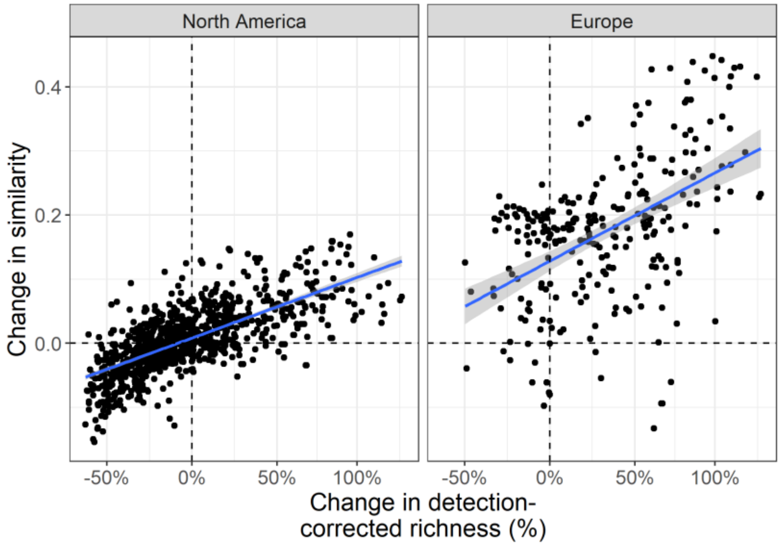

Figure 3.4. Association between change in detection-corrected richness and change in similarity for North American and European bumblebee assemblages between a historic (1900-1974) and recent period (2000-2018). Similarity is the mean pairwise similarity of a focal site to all other sites on its continent, where 0 indicates no species in common and 1 represents identical assemblage composition. n = 991 for North America, and 267 for Europe. Confidence intervals (±95%) are shown around linear trendlines.

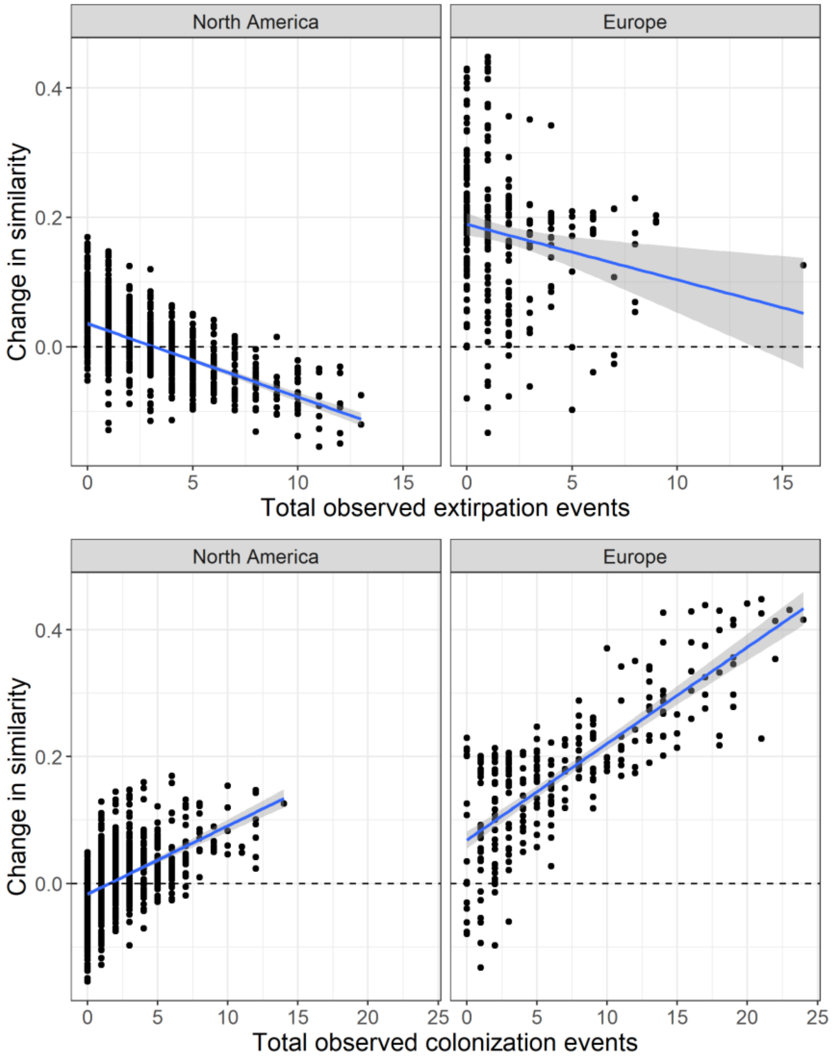

Figure 3.5. Change in similarity and observed extirpation and colonization events within North American and European bumblebee assemblages between a historic (1900-1974) and recent (2000-2018) period. Similarity is the mean pairwise similarity of a focal site to all other sites on its continent, where 0 indicates no species in common and 1 represents identical assemblage composition. n = 991 for North America, and 267 for Europe. Confidence intervals (±95%) are shown around linear trendlines.

Table 3.1

Table 3.1. Estimated model coefficients for extirpation, colonization, change in probability of occupancy, and percent change in detection-corrected species richness models. Posterior means and 95% Bayesian credible intervals are shown for phylogenetic generalized linear mixed models (PGLMM). For analysis of covariance models (ANCOVA), t-values are included as a measure of significance. Generally, coefficients with t-values < -1.96 or > 1.96 are considered statistically significant, these and coefficients where the 95% CI does not overlap zero are in bold text in the table. Variance explained is expressed in terms of marginal R^2 (for PGLMM) and Adjusted R^2 (ANCOVA).

	Extirpation (PGLMM)		Colonization (PGLMM)		Change in probability of site occupancy (PGLMM)		Detection-corrected assemblage richness (ANCOVA)	
	Posterior mean	95% CI	Posterior mean	95% CI	Posterior mean	95% CI	Estimate (SE)	t-value
Intercept	95.7	-172.86 - 373.78	-168.3	-354.1 - 13.94	-37.72	-100.29 - 23.51	**-0.03 (0.02)**	**-2.13**
<u>Thermal position (TPI) variables</u>								
Historic (1st order polynomial)	**1201.72**	**437.82 - 1968.14**	**-1615**	**-2410 - -799.8**	**-361.22**	**-505.66 - -221.78**	**-1.38 (0.54)**	**-2.55**
Historic (2nd order polynomial)	**4192.11**	**3255.49 - 5155.95**	295	-371.9 - 972.1	**-488.07**	**-614.01 - -355.63**	0.13 (0.54)	0.23
Change since historic	**42.1**	**26.98 - 58.33**	**25.75**	**11.51 - 40.1**	-2.07	-4.56 - 0.77	-0.005 (0.019)	-0.29
Historic:Change interaction	**65.32**	**39.69 - 90.96**	-8.04	-30.5 - 12.73	**-11.07**	**-15.46 - -6.7**	**-0.031 (0.015)**	**-2.08**
<u>Land-use (LU) variables</u>								
Historic	**17.87**	**5.6 - 29.83**	**27.34**	**14.29 - 39.77**	0.79	-1.32 - 3.12	0.017 (0.013)	1.25
Change since historic	-10.01	-24.71 - 5.01	**-22.83**	**-38.24 - -8.02**	-0.64	-3.34 - 2.01	**-0.035 (0.018)**	**-1.96**
Historic:Change interaction	8.16	-2.77 - 19	**19.42**	**9.14 - 29.98**	1.25	-0.7 - 3.07	0.02 (0.02)	0.98
<u>Climate and land-use interactions</u>								
Historic TPI:Historic LU	17.2	-2.54 - 37.56	**29.11**	**9.48 - 48.52**	**4.08**	**0.48 - 7.68**	-0.022 (0.016)	-1.41
Change in TPI:Change in LU	-1.3	-9.57 - 7.06	0.06	-7.28 - 7.7	-0.75	-2.2 - 0.7	-0.0082 (0.013)	-0.63

Historic LU:Change in TPI	**11.14**	**4.48 - 18.06**	-3.2	-9.16 - 2.87	-0.96	-2.12 - 0.21	**-0.028 (0.014)**	**-2.07**
Historic TPI:Change in LU	**-34.93**	**-59.96 - -8.78**	-16.1	-41.47 - 7.15	0.46	-4.18 - 5.26	0.012 (0.013)	0.9
Covariates								
Continent (Europe)	**-263.51**	**-315.53 - -210.76**	**155.1**	**117.6 - 191.4**	**44.09**	**38.61 - 49.68**	**0.32 (0.04)**	**7.63**
Sampling intensity	**-11.54**	**-15.75 - -7.62**	**-28.31**	**-34.08 - -22.08**	--	--	--	--
Random effects	Variance (95% CI)		Variance (95% CI)		Variance (95% CI)			
Species	4651	2481 - 7026	2052	940.7 - 3223	253.7	167.7 - 344.3	--	--
Model summary								
Effective sampling	184.4 - 19515		136.2 - 16384.6		3678 - 5315		1258	
Variation explained (R2)	0.33		0.19		0.18		0.16	

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Supplemental Materials

Supplemental Figures S3.1-S3.8

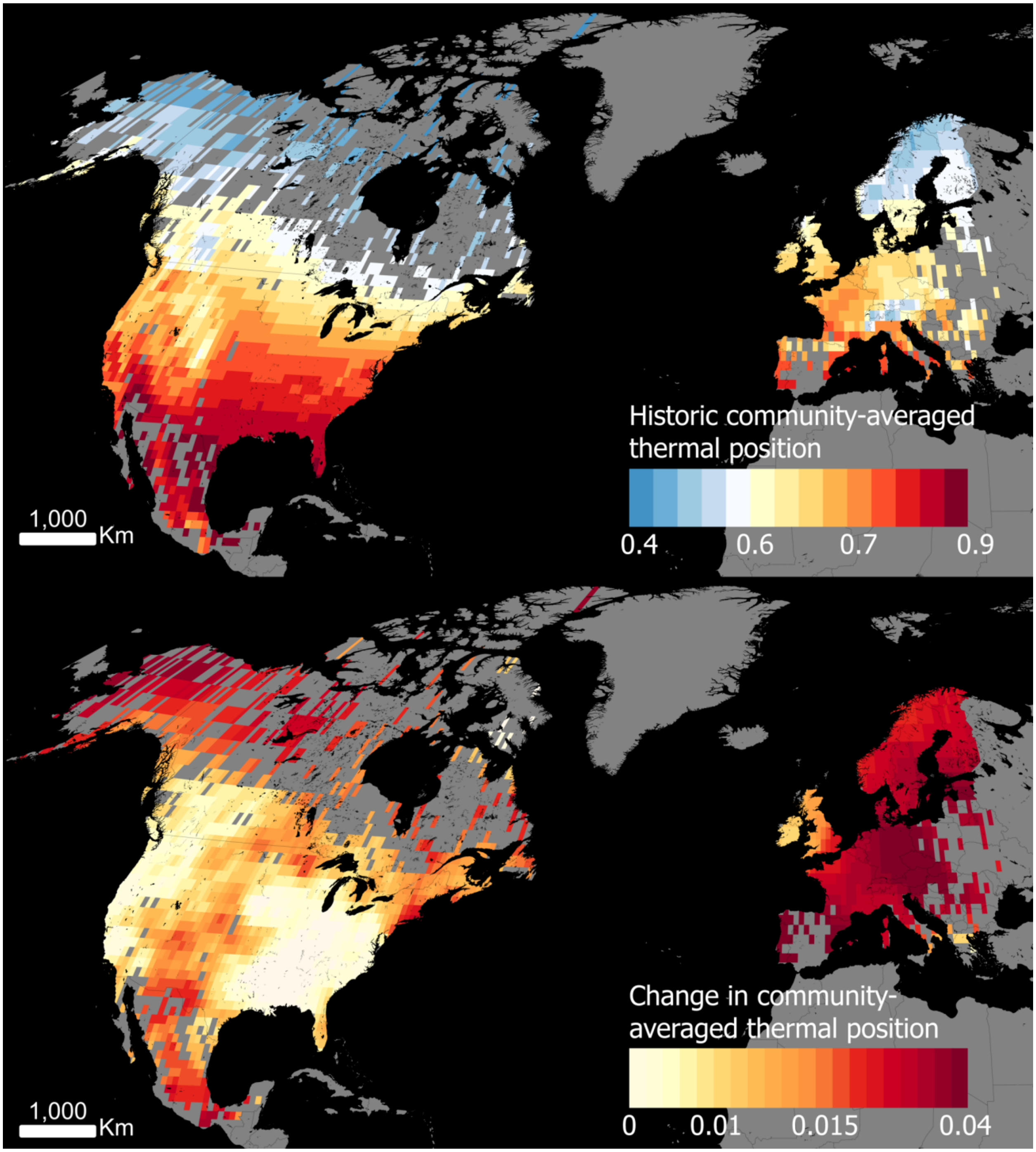


Figure S3.1. Historic community-averaged thermal position across the study area (A) and change in thermal position between historic period (1900-1974) to recent period (2000-2018) (B). Historic thermal position has a potential range of 0 to 1. Zero indicates that species in the assemblage are on average at their historic cold tolerance limit for the entirety of the year in the period. One indicates that species in the assemblage are on average at their historic hot tolerance limit for the entirety of the year in the period. Recent thermal position can exceed 1 or go below zero if local climate change means species are exceeding their historic tolerance limits.

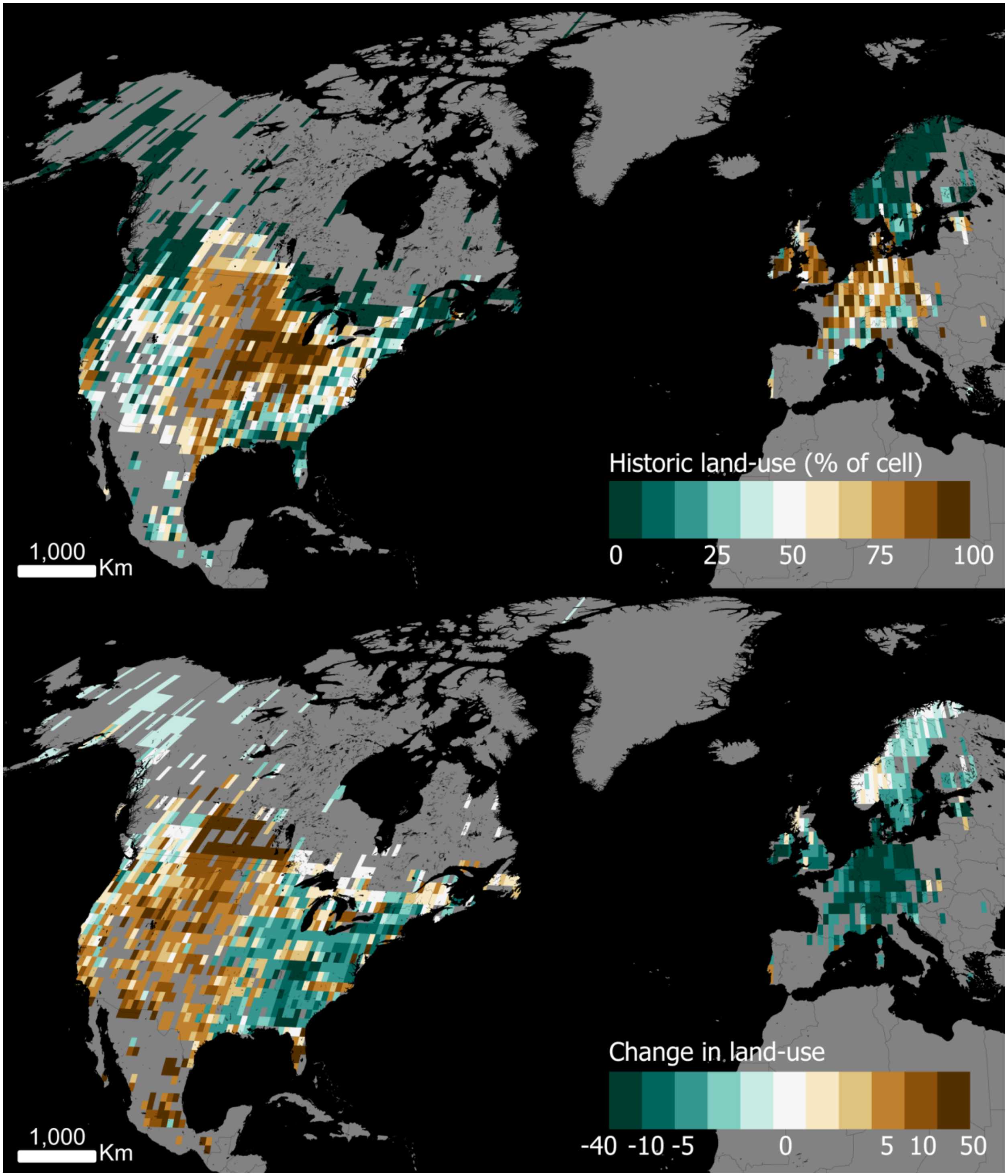


Figure S3.2. Historic human-dominated land use across the study area (A; percentage per cell), and change in land use between the historic period (1900-1974) and recent period (2000-2018) (B). Human-dominated land use is estimated from the HYDE 3.2.1 dataset (Goldewijk et al. 2016), and is the summed proportion of land area in a cell used by pasture, grazing, or urban land-use.

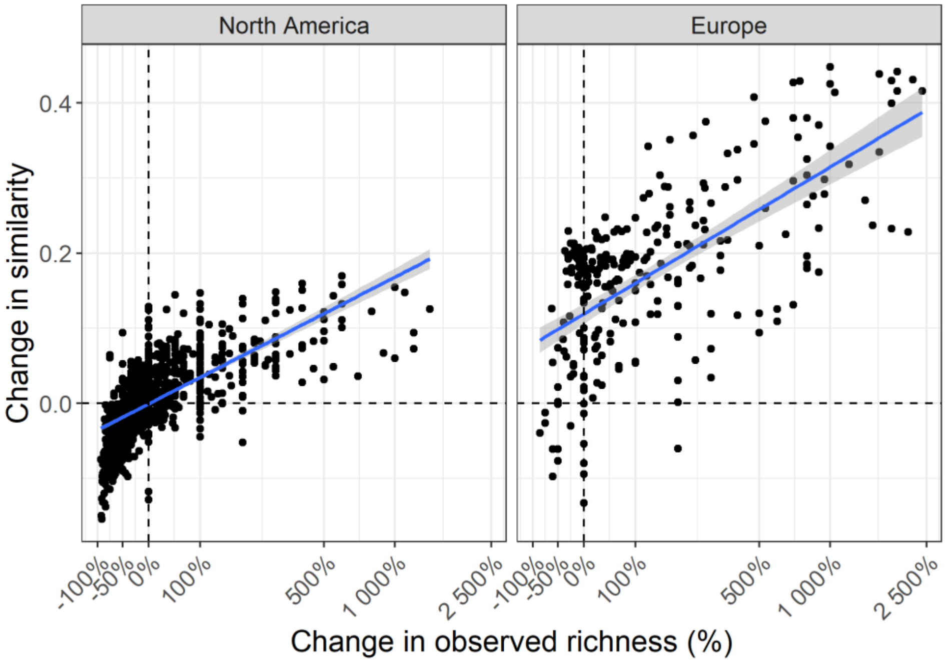


Figure S3.3. Association between change in observed assemblage richness (not corrected for non-detection) and change in similarity for North American and European bumblebee assemblages between a historic (1900-1974) and recent period (2000-2018). Similarity is the mean pairwise similarity of a focal site to all other sites on its continent, where 0 indicates no species in common and 1 represents identical assemblage composition. n = 991 for North America, and 267 for Europe. Confidence intervals (±95%) are shown around linear trendlines.

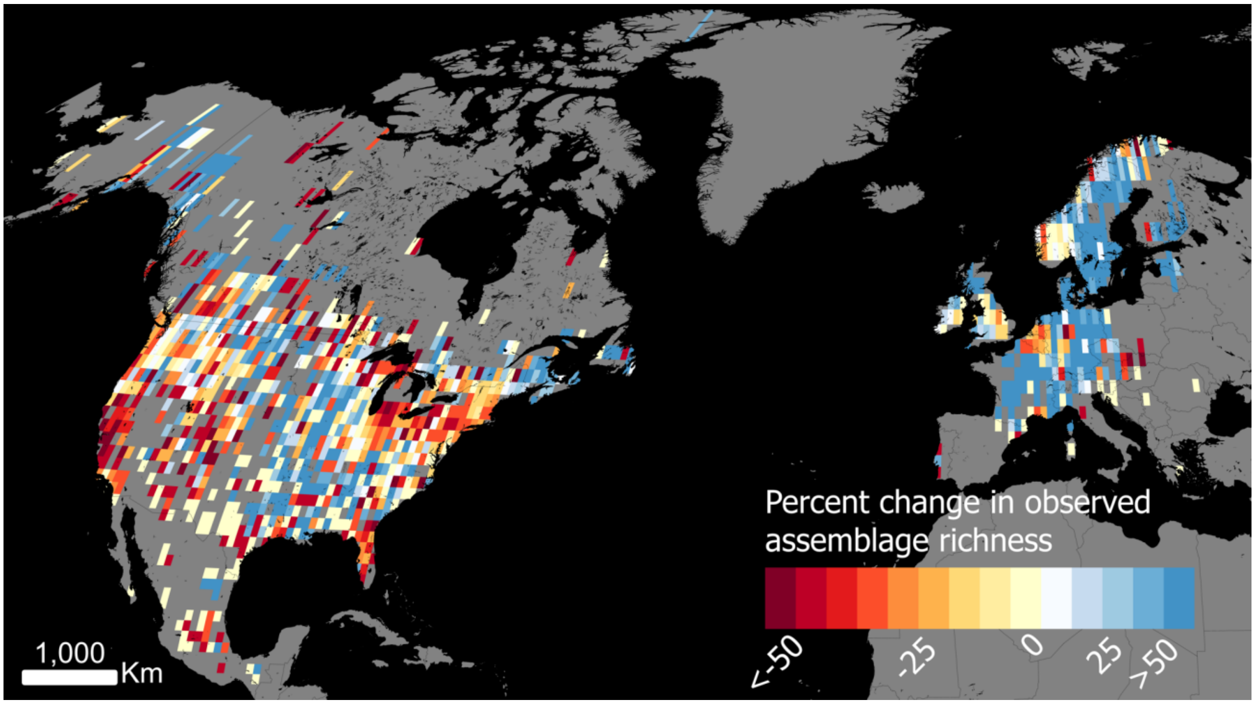


Figure S3.4. Percent change in observed assemblage richness between historic (1900-1974) and recent period (2000-2018). Grid cells shown are equal-area 100 km by 100 km. No detection or sampling correction applied.

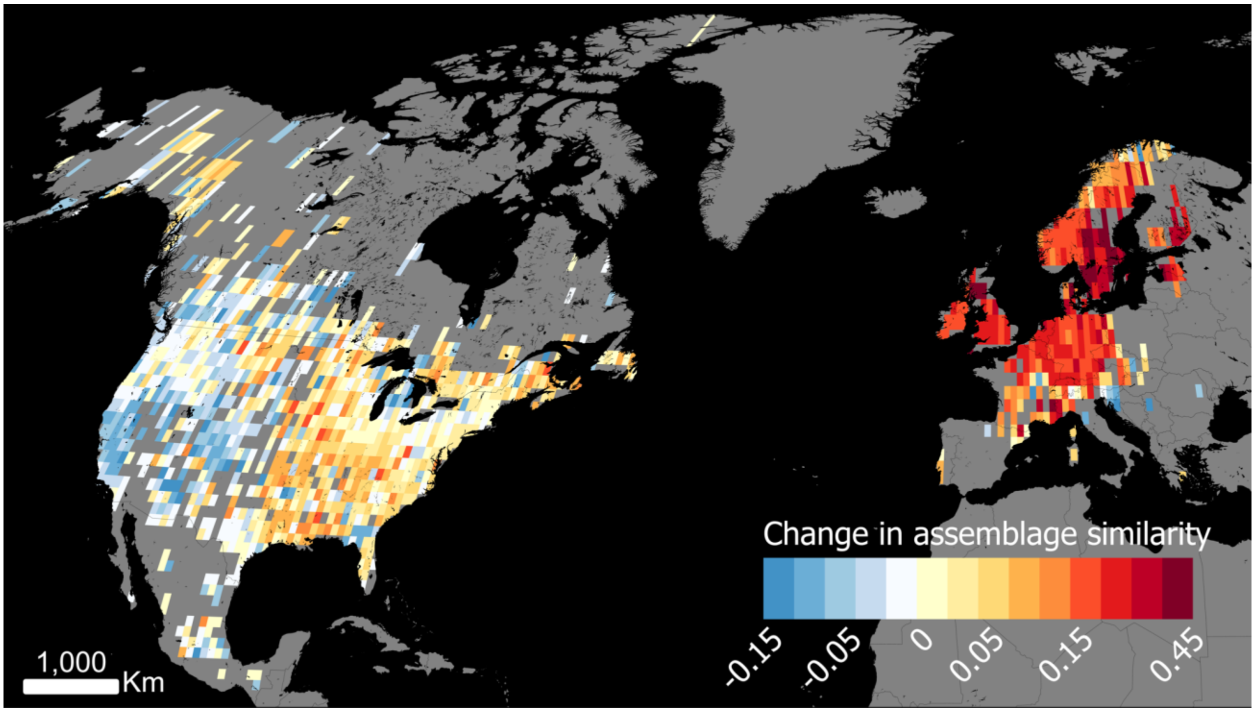


Figure S3.5. Change in assemblage similarity from historic (1900-1974) to recent (2000-2018) period. Similarity is the mean pairwise similarity of a focal site to all other sites on its continent, where 0 indicates no species in common and 1 represents identical assemblage composition.

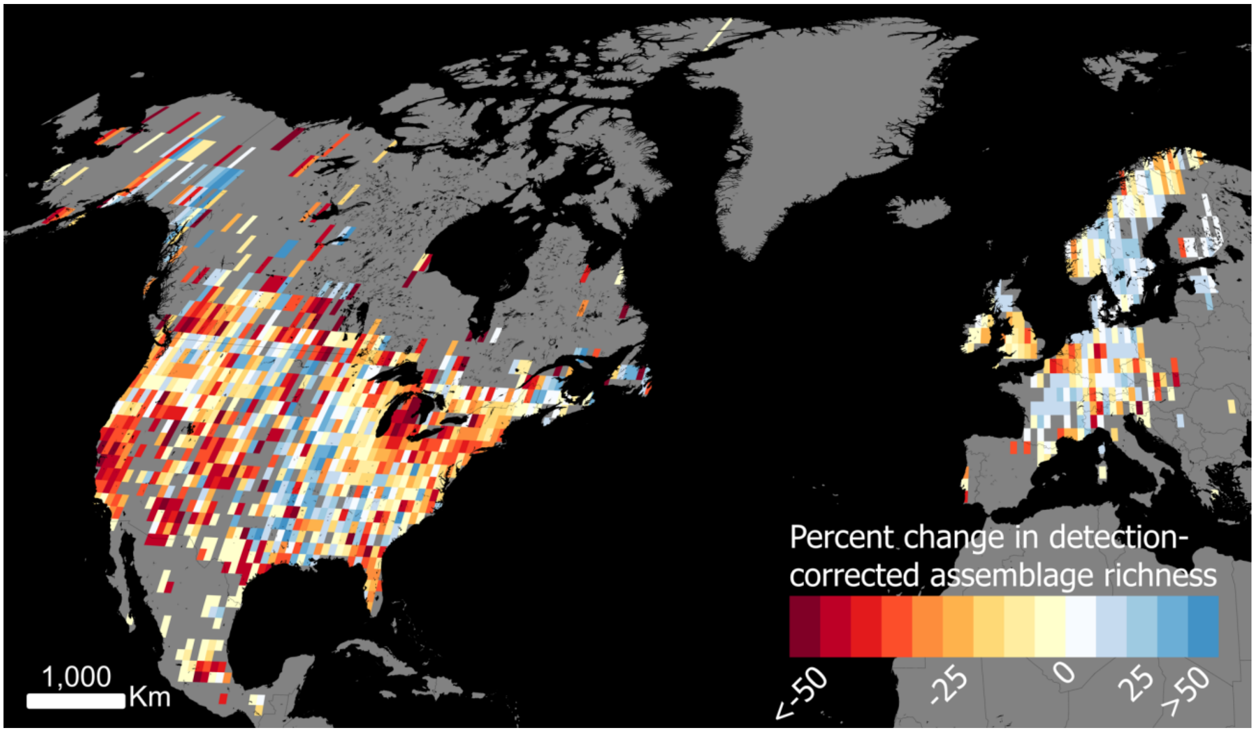
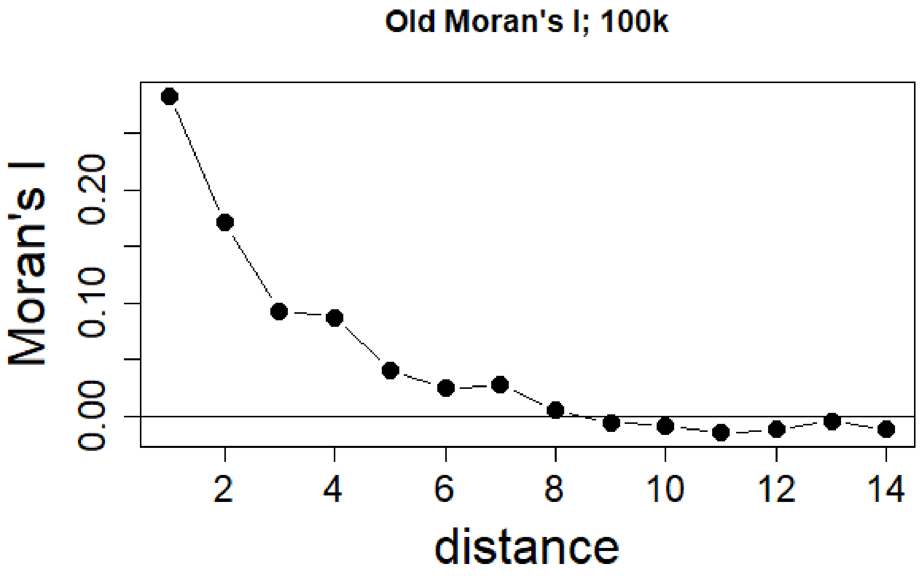


Figure S3.6. Percent change in detection-corrected assemblage richness between historic (1900-1974) and recent period (2000-2018). Grid cells shown are equal-area 100 km by 100 km.



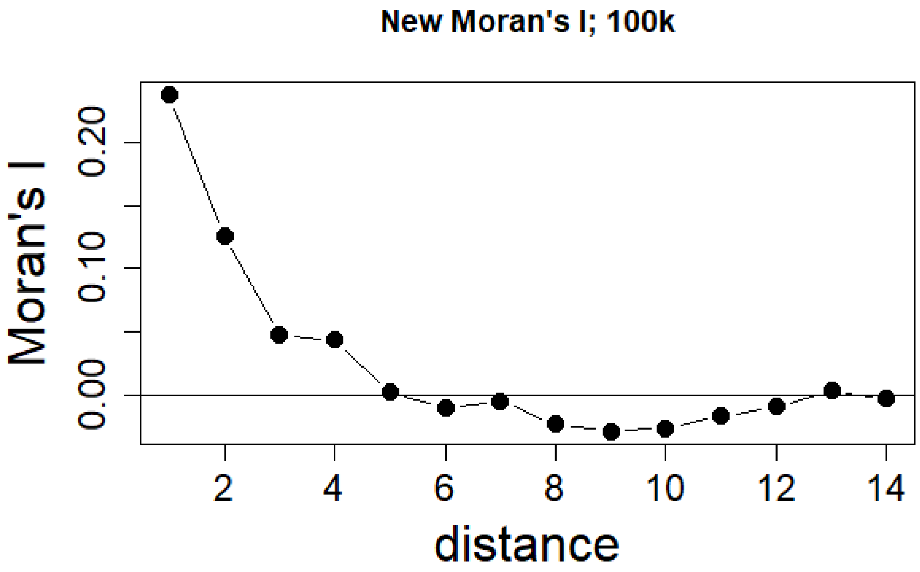


Figure S3.7 - Correlogram of Moran's I for detection-corrected species richness model. Moran's I calculated from ANCOVA model (top) and simultaneous autoregressive (SAR) error model (bottom). SAR model was a significantly better fit (according to log likelihood). Model coefficients were qualitatively similar between both models.

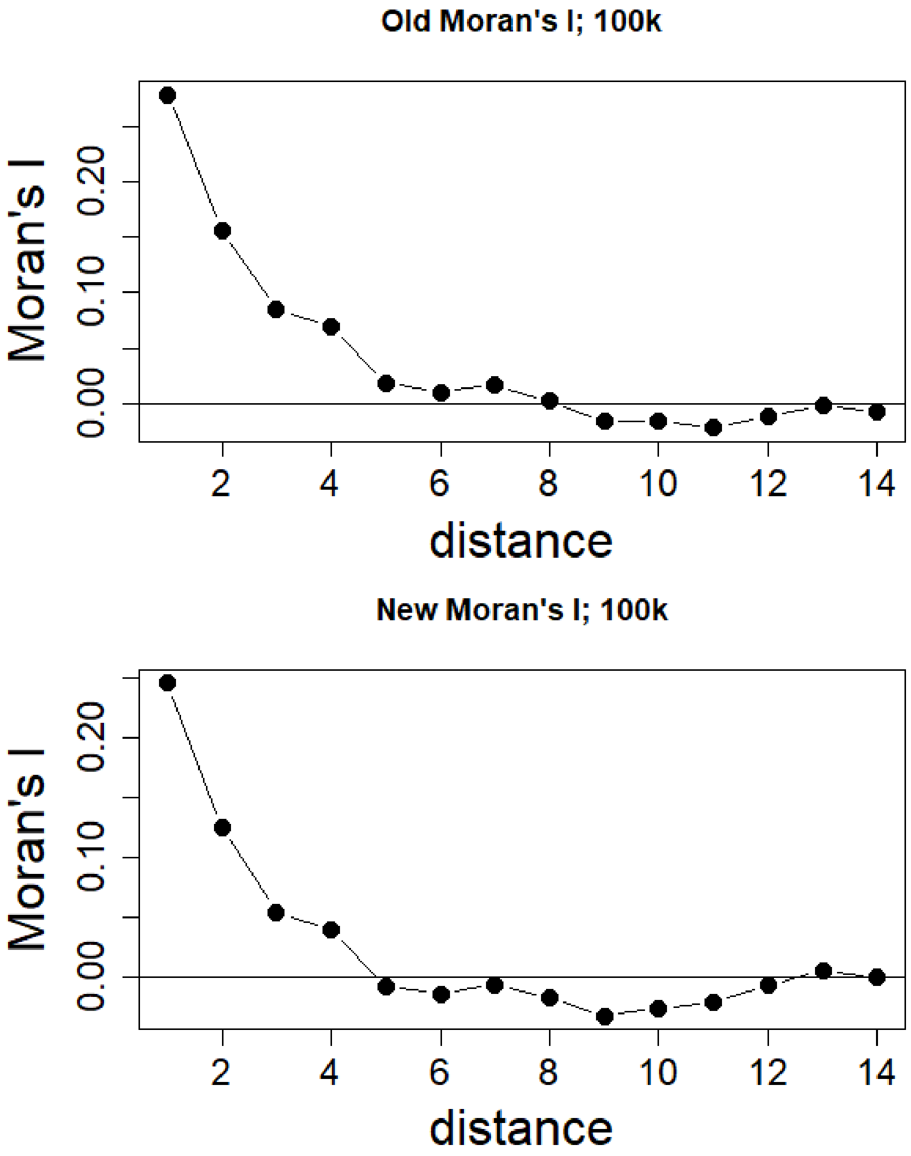


Figure S3.8 - Correlogram of Moran's I for non-detection-corrected species richness model. Moran's I calculated from ANCOVA model (top) and simultaneous autoregressive (SAR) error model (bottom). SAR model was a significantly better fit (according to log likelihood). Model coefficients were qualitatively similar between both models.

Supplemental Tables S3.1-S3.6

Table S3.1. Number of unique spatiotemporal occurrence observations of bumblebee species in the historic (1900-1974; inclusive) and recent (2000-2018; inclusive) period.

Species	Historic (1900-1974)	Recent (2000-2018)
B. affinis	1432	760
B. appositus	792	476
B. auricomus	527	1178
B. barbutellus	281	408
B. bifarius	2987	1429
B. bimaculatus	1163	4891
B. bohemicus	1079	3949
B. borealis	600	1274
B. caliginosus	448	69
B. campestris	480	2267
B. centralis	1084	710
B. cingulatus	69	228
B. citrinus	580	946
B. confusus	56	20
B. consobrinus	242	345
B. crotchii	359	70
B. cryptarum	222	788
B. distinguendus	325	1070
B. ephippiatus	97	127
B. fervidus	3737	2761
B. flavidus	473	575
B. flavifrons	1388	1209
B. fraternus	440	314
B. frigidus	395	467

B. griseocollis	1733	6745
B. hortorum	1501	11162
B. humilis	329	2238
B. huntii	1428	1558
B. hypnorum	1114	13045
B. impatiens	3155	16108
B. insularis	950	515
B. jonellus	1233	3787
B. kirbiellus	242	196
B. lapidarius	1198	27352
B. lapponicus	514	393
B. lucorum	1732	18394
B. magnus	262	980
B. medius	53	63
B. melanopygus	1632	1664
B. mixtus	983	1261
B. monticola	149	1415
B. morrisoni	1032	174
B. muscorum	454	2271
B. nevadensis	602	794
B. norvegicus	69	677
B. occidentalis	3351	1068
B. pascuorum	3660	39319
B. pensylvanicus	4409	4708
B. perplexus	738	1751
B. polaris	63	72
B. pomorum	80	34
B. pratorum	2022	19130
B. ruderarius	559	1908
B. ruderatus	329	157
B. rufocinctus	1260	1895

B. rupestris	321	2339
B. sandersoni	182	366
B. sitkensis	380	218
B. soroeensis	623	3401
B. sporadicus	125	542
B. subterraneus	212	1513
B. suckleyi	527	34
B. sylvarum	457	3758
B. sylvestris	539	2917
B. sylvicola	605	532
B. ternarius	910	3880
B. terrestris	682	27141
B. terricola	2136	1339
B. vagans	1483	3324
B. vandykei	185	107
B. vestalis	245	1982
B. veteranus	236	269
B. vosnesenskii	3346	2152
B. wurflenii	611	547

Table S3.2. Estimated non-phylogenetic model coefficients for extirpation, colonization, and change in probability of site occupancy. Posterior means and 95% Bayesian credible intervals are shown for generalized linear mixed models. 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.

	Extirpation (GLMM)		Colonization (GLMM)		Change in probability of site occupancy (GLMM)	
	Posterior mean	95% CI	Posterior mean	95% CI	Posterior mean	95% CI
Intercept	-5.9	-37.8 - 24.76	**-149.46**	**-181.64 - -115.5**	**-20.08**	**-26.5 - -13.82**
Thermal position (TPI) variables						
Historic (1st order polynomial)	**1098.58**	**335.34 - 1885.11**	**-1569.93**	**-2383.39 - -776.62**	**-346.52**	**-496.62 - -212.58**
Historic (2nd order polynomial)	**4087.87**	**2973.37 - 5217.84**	284.54	-391.42 - 948.22	**-478.26**	**-605.81 - -350.21**
Change since historic	**39.33**	**21.99 - 55.66**	**25.97**	**11.66 - 40.25**	-1.76	-4.48 - 0.8
Historic: Change interaction	**57.69**	**31.81 - 85.3**	-4.4	-26.1 - 16.89	**-9.97**	**-14.41 - -5.54**
Land-use (LU) variables						
Historic	**19.14**	**7.13 - 32.25**	**26.73**	**14.21 - 39.46**	0.64	-1.72 - 2.79
Change since historic	-10.43	-25.06 - 5.15	**-22.48**	**-37.83 - -7.64**	-0.51	-3.19 - 2.32
Historic: Change interaction	8.69	-2 - 20.05	**19.02**	**8.66 - 29.55**	1.13	-0.79 - 3.06
Climate and land-use interactions						
Historic TPI: Historic LU	17.03	-3.05 - 36.87	**30.76**	**10.83 - 50.28**	**4.23**	**0.82 - 8.36**
Change in TPI: Change in LU	-1.65	-10.05 - 6.49	-0.45	-8.16 - 6.9	-0.72	-2.14 - 0.8

Historic LU: Change in TPI	**12.44**	**5.48 - 19.71**	-3.93	-10.04 - 1.96	-1.1	-2.24 - 0.07
Historic TPI: Change in LU	**-33.27**	**-59.84 - -7.22**	-16.79	-42.48 - 6.45	0.31	-4.32 - 4.9
Covariates						
Continent (Europe)	**-249.07**	**-310.92 - -182.18**	**154.75**	**118.16 - 190.18**	**41.77**	**36.41 - 47.32**
Sampling intensity	**-11.31**	**-15.78 - -6.75**	**-28.43**	**-34.14 - -22.27**	--	--
Random effects	Variance (95% CI)		Variance (95% CI)		Variance (95% CI)	
Species	12872	5297 - 20679	3989	1945 - 6206	566.5	381.9 - 777.8
Model summary						
Effective sampling	85.55 - 14206.5		160.5 - 16552.5		4846 - 5000	
Variation explained	0.26		0.18		0.15	

Table S3.3. Estimated model coefficients for the simultaneous autoregressive error model (SAR error) for percent change in detection-corrected species richness. t-values, for analysis of covariance (ANCOVA) models, and z-values, for simultaneous autoregressive error model (SAR error), are included as measures of significance. Generally, coefficients with t-values or z-values < -1.96 or > 1.96 are considered statistically significant, and these are in bold text in the table. Variance explained is expressed in terms of adjusted R^2 (ANCOVA) and Nagelkerke pseudo-R^2 (SAR error).

	Detection-corrected assemblage richness (ANCOVA)		Detection-corrected assemblage richness (SAR error)	
	Estimate (SE)	t-value	Estimate (SE)	z-value
Intercept	**-0.03 (0.02)**	**-2.13**	-0.04 (0.05)	-0.85
Thermal position (TPI) variables				
Historic (1st order polynomial)	**-1.38 (0.54)**	**-2.55**	-0.41 (0.72)	-0.56
Historic (2nd order polynomial)	0.13 (0.54)	0.23	-0.85 (0.59)	-1.45
Change since historic	-0.005 (0.019)	-0.29	-0.006 (0.024)	-0.25
Historic: Change interaction	**-0.031 (0.015)**	**-2.08**	-0.028 (0.017)	-1.6
Land-use (LU) variables				
Historic	0.017 (0.013)	1.25	0.003 (0.015)	0.23
Change since historic	**-0.035 (0.018)**	**-1.96**	-0.024 (0.018)	-1.31
Historic: Change interaction	0.02 (0.02)	0.98	0.009 (0.02)	0.44
Climate and land-use interactions				
Historic TPI: Historic LU	-0.022 (0.016)	-1.41	-0.029 (0.016)	-1.74
Change in TPI: Change in LU	-0.0082 (0.013)	-0.63	0.0009 (0.013)	0.06
Historic LU: Change in TPI	**-0.028 (0.014)**	**-2.07**	-0.022 (0.014)	-1.59
Historic TPI: Change in LU	0.012 (0.013)	0.9	0.02 (0.014)	1.43
Covariates				
Continent (Europe)	**0.32 (0.04)**	**7.63**	**0.32 (0.1)**	**3.06**
Model summary				
n	1258		1258	
Variation explained	0.16		0.2	

Table S3.4. Estimated model coefficients for the observed species richness models. t-values, for analysis of covariance (ANCOVA) models, and z-values, for simultaneous autoregressive error model (SAR error), are included as measures of significance. Generally, coefficients with t-values or z-values < -1.96 or > 1.96 are considered statistically significant, and these are in bold text in the table. Variance explained is expressed in terms of adjusted R^2 (ANCOVA) and Nagelkerke pseudo-R^2 (SAR error).

	Observed assemblage richness (ANCOVA)		Observed assemblage richness (SAR error)	
	Estimate (SE)	t-value	Estimate (SE)	z-value
Intercept	**-0.1 (0.03)**	**-3.03**	-0.11 (0.09)	-1.31
Thermal position (TPI) variables				
Historic (1st order polynomial)	**-3.05 (1.2)**	**-2.54**	-0.98 (1.57)	-0.62
Historic (2nd order polynomial)	-0.25 (1.21)	-0.21	-2.17 (1.31)	-1.66
Change since historic	-0.03 (0.04)	-0.76	-0.02 (0.05)	-0.42
Historic: Change interaction	-0.05 (0.03)	-1.56	-0.05 (0.04)	-1.4
Land-use (LU) variables				
Historic	0.051 (0.03)	1.72	0.047 (0.033)	1.42
Change since historic	**-0.082 (0.04)**	**-2.08**	-0.059 (0.041)	-1.42
Historic: Change interaction	0.02 (0.02)	0.98	0.015 (0.046)	0.34
Climate and land-use interactions				
Historic TPI: Historic LU	**-0.07 (0.035)**	**-2.02**	**-0.089 (0.037)**	**-2.44**
Change in TPI: Change in LU	0.001 (0.029)	0.05	0.015 (0.03)	0.5
Historic LU: Change in TPI	**-0.061 (0.03)**	**-2.01**	-0.051 (0.031)	-1.66
Historic TPI: Change in LU	0.035 (0.03)	1.18	0.047 (0.031)	1.54
Covariates				
Continent (Europe)	**0.8 (0.1)**	**8.4**	**0.76 (0.2)**	**3.86**
Sampling intensity	**-0.06 (0.02)**	**-2.45**	**-0.06 (0.02)**	**-2.49**
Model summary				
n	1258		1258	
Variation explained	0.15		0.19	

Table S3.5. Estimated model coefficients for analysis of covariance (ANCOVA) models predicting change in similarity. t-values are included as measures of significance. Generally, coefficients with t-values or z-values < -1.96 or > 1.96 are considered statistically significant, and these are in bold text in the table. Variance explained is expressed in terms of adjusted R^2 (ANCOVA).

	Detection-corrected assemblage richness (ANCOVA)		Observed assemblage richness (ANCOVA)	
	Estimate (SE)	t-value	Estimate (SE)	z-value
Intercept	**0.012 (0.002)**	**6.8**	0.002 (0.002)	1.4
Change in richness	**0.098 (0.005)**	**20.94**	**0.02 (0.001)**	**17.02**
Continent (Europe)	**0.098 (0.005)**	**20.26**	**0.123 (0.004)**	**27.97**
Sampling intensity	**0.019 (0.002)**	**11.91**	**0.016 (0.002)**	**9.6**
Continent: Change in richness interaction	**0.058 (0.009)**	**6.17**	**-0.005 (0.001)**	**-3.37**
Model summary				
n	1258		1258	
Variation explained	0.71		0.7	

Table S3.6. Estimated model coefficients for analysis of covariance (ANCOVA) models predicting change in similarity using extirpation and colonization. t-values are included as measures of significance. Generally, coefficients with t-values or z-values < -1.96 or > 1.96 are considered statistically significant, and these are in bold text in the table. Variance explained is expressed in terms of adjusted R^2 (ANCOVA).

	Change in similarity	
	Estimate (SE)	t-value
Intercept	**0.018 (0.003)**	**6.99**
Continent (Europe)	**0.022 (0.006)**	**3.56**
sc_sampling	**0.012 (0.001)**	**9.14**
sum_extinct	**-0.0098 (0.0005)**	**-18.41**
sum_coloniz	**0.0081 (0.0006)**	**13.1**
continentEurope:sum_extinct	**0.017 (0.0014)**	**11.65**
continentEurope:sum_coloniz	**0.0083 (0.0008)**	**10.42**
Model summary		
n	1258	
Variation explained	0.81	

Appendix 3.1

JAGS code specifying occupancy model

```
" model {


  ### specify priors
  # overall intercepts
  alpha_p ~ dnorm(0, 0.01)


  # covar effects
  b_lp_samp ~ dnorm(0, 0.1)


  for (k in 1:nyears){ # repeat for each year (with distinct priors)
   alpha_psi[k] ~ dnorm(0, 0.01)


   # Ecological submodel: Define state conditional on parameters
   for (i in 1:nsites){


    z[i,k] ~ dbern(psi[i,k]) # true occurrence z at site i
    psi[i,k] <- 1 / (1 + exp(-lpsi.lim[i,k]))
    lpsi.lim[i,k] <- min(999, max(-999, lpsi[i,k])) #stabilize logit to avoid numerical under or overflow
    lpsi[i,k] <- alpha_psi[k]




    for (j in 1:nsurveys){   # Observation model
```

```
    y[i,j,k] ~ dbern(mu_p[i,j,k]) # Detection-nondetection at i and j


    mu_p[i,j,k] <- z[i,k] * p[i,j,k]

    p[i,j,k] <- 1 / (1 + exp(-lp.lim[i,j,k]))

    lp.lim[i,j,k] <- min(999, max(-999, lp[i,j,k]))

    lp[i,j,k] <- alpha_p + b_lp_samp * sampmat[i,j,k]



   }#j

  }#i

  # extra tings

  # Derived quantities

  n_occ[k] <- sum(z[,k]) # Number of occupied sites

  mean_p[k] <- exp(alpha_p) / (1 + exp(alpha_p)) # Average detection

}#k

}"
```

Chapter 4: Extent of protected areas in a landscape related to decreased extirpation risk for North American and European bumblebees

Abstract

Protected areas represent an important tool for conservation, and understanding their efficacy for mitigating biodiversity loss is important for determining whether alternative conservation measures should be prioritized for certain taxa. This is especially true for pollinators like bumblebees, which are declining across North America and Europe primarily due to climate change and land-use change. Using a large occurrence dataset including 74 bumblebee species across North America and Europe, I test whether the extent of protected areas across these continents is related to biodiversity change, and whether it influences biodiversity responses to climate change or land-use change. I find that across species, increasing extent of protected area in a landscape is related to lower extirpation risk and increasing probability of occupancy over time. This effect is even stronger in highly human-dominated landscapes, suggesting that protected areas are useful conservation tools for bumblebees in these places regardless of size or IUCN management category. At the landscape scale, geographic and location effects (i.e., where protected areas are distributed) are more important than the local effects of protected areas in mitigating climate or land-use change related risks. Future studies with smaller geographic scopes may be able to reveal the precise mechanisms of how protected areas mitigate against these pressures. This study demonstrates the value of protected areas for an important group of pollinators, especially relevant as countries look toward post-2020 conservation goals.

Introduction

Biodiversity is declining across the globe, and conservation action is required to mitigate declines and "bend the curve" of this loss (Mace et al. 2018; IPBES 2019). Habitat loss and land-use change frequently appear as the dominant forces behind these changes, endangering species by removing resources and areas required for species' persistence (Foley et al. 2005; Newbold et al. 2015). Climate change is expected to surpass land-use change as a dominant driver of biodiversity declines in the coming decades (Newbold 2018), and can threaten species by exposing them to conditions and temperatures beyond their tolerances (Sunday et al. 2014; Soroye et al. 2020). Understanding the mechanisms through which land-use change and climate change influence species is critical, as is understanding the efficacy of potential conservation solutions (Watson et al. 2014; Visconti et al. 2019; Maxwell et al. 2020).

Protected areas (PAs) are one of the main tools for conserving biodiversity (Watson et al. 2014; Maxwell et al. 2020), and have the potential to safeguard species from the negative impacts of global change pressures like climate change and land-use change (Maxwell et al. 2020). As a tool to protect species, ecosystems, and ecological processes and functions, PAs are a key part of international strategies for conserving biodiversity (e.g., Convention on Biological Diversity; https://www.cbd.int/protected/pacbd/). PAs can reduce land-use change or habitat loss and harbor greater local biodiversity compared to surrounding areas (Joppa & Pfaff 2011; Gray et al. 2016; Geldmann et al. 2019). They can also act as important stepping stones for range-shifting species (Kharouba & Kerr 2010; Hiley et al. 2013; Robillard et al. 2015; Berteaux et al. 2018), and can protect novel or disappearing climates (Wiens et al. 2011). By alleviating pressures from land-use change, PAs may also protect critical microrefugia in the landscape and lessen the potential for negative interactions between climate change and land-use change (e.g., Chapter 3).

Developing effective conservation solutions is especially important for wild pollinators like bumblebees (*Bombus*), given the potential ecological consequences of losses in this taxon (Biesmeijer et al. 2006; IPBES 2016). As a group of species notably under threat and declining from factors including climate change and land-use change (Williams & Osborne 2009; Potts et al. 2010; Szabo et al. 2012; Goulson et al. 2015; Kerr et al. 2015; Wood et al. 2019), better understanding whether PAs can play a role in mitigating declines is important. Current global coverage of PAs indicates that climatically stable areas and future hotspots of range expansion for bumblebees may not be adequately protected, at least for North and South American species (Sirois-Delisle & Kerr 2018; Krechemer & Marchioro 2020). Yet, bumblebees and other pollinators may not benefit greatly from protected areas. In the UK, bumblebee richness and abundance was observed to be similar or even greater in urban sites or farmland compared to nature reserves (Baldock et al. 2015). Human-dominated areas can be hotspots for nectar and floral resource diversity, benefiting many pollinator species (Tew et al. 2021). Understanding whether PAs consistently aid bumblebees in weathering climate change and land-use change is important for determining whether PAs can be an effective conservation strategy for these species.

Here, I test whether the presence and extent of PAs in a landscape helps mitigate against climate change and land-use change-related biodiversity loss in bumblebees. I use a large dataset of occurrences for 74 species across North America and Europe, several measures of biodiversity change between a historic (1900-1974) and recent period (2000-2018), concurrent data on climate and land-use change, and information on the global PA network (UNEP-WCMC 2016) (Figure 4.1). I expect that when species and assemblages are in or near PAs, they will be more resilient in the face of climate change and land-use change pressures, as PAs may maintain areas containing the microrefugia and resources required for species. I expect that these effects will be especially pronounced in areas where land-use pressures have been historically high, as PAs may be more important in these more challenging environments. Size and management (e.g., IUCN category) are typically considered important characteristics determining the efficacy of PAs, and I also test whether they appear important for bumblebee persistence. Finally, I investigate whether observed continental differences in the associations between biodiversity change and extent of PAs in a landscape may be the result of regional differences in where PAs are located across North America and Europe.

Methods

Biodiversity data

Using the occurrence dataset and methods from the previous chapters, I measured extirpation, local colonization, change in probability of site occupancy, percentage change in observed assemblage richness (Figure S4.2), and change in detection-corrected assemblage richness (Figure S4.3) between the historic (1900-1974) and recent (2000-2018) periods, within 100 km X 100 km equal area quadrats across North America and Europe.

The occurrence dataset used contained 333,423 spatiotemporally unique occurrence observations of 74 North America and European bumblebees (*Bombus*). This dataset was created using North American data from the Bumblebees of North America dataset (Williams et al. 2014) and Williams et al. (2019), and European data from the Global Biodiversity Information Facility (GBIF.org 2020) and Williams et al. (2019). More details on the composition of the dataset, species selection, and methods for calculating biodiversity change can be found in Methods of Chapter 3.

Climatic positioning and land-use data

As in previous chapters, I calculated the individual thermal positions for each of the 74 species across their ranges using global climate data obtained from the University of East Anglia's Climatic Research Unit (Harris et al. 2020). I calculated the historic (1900-1974) thermal position for each species, and its change between the recent period (2000-2018). I also calculated the community-averaged thermal position (Figure S4.4), which represents the mean proximity of the assemblage as a whole to historic temperature tolerances. Climate data were obtained at a resolution of 0.5 X 0.5 degrees, and, after the calculation of the climatic position index, data were projected and resampled to the Cylindrical Equal Area projection at 100 km X 100 km resolution to match the biodiversity data.

I estimated historic and changing landscape-scale land-use using the HYDE 3.2.1 dataset (Goldewijk et al. 2016, 2017) as described in the previous chapter. Starting from global estimates of area (km^2) used for pasture, grazing, and urban land-use at a 5-arcminute resolution (about 8.3 km x 8.3 km at the equator), I calculated the proportion of land area dedicated to human-dominated land-use for the 100 km by 100 km equal-area grids matching the biodiversity data in the historic (1900-1974) and recent (2000-2018) periods (Figure S4.5). I used the historic proportion of human-dominated land-use and change between periods for analyses.

Protected Areas data

I downloaded information on PAs from the World Database on Protected Areas (WDPA; protectedplanet.net; downloaded April 2019; UNEP-WCMC 2016), and removed non-terrestrial PAs, PAs outside of North America and western Europe, and PAs with a "proposed" or unknown designation status. Following UNEP-WCMC suggestion, I also excluded UNESCO Man and Biosphere Reserves (MAB) sites, as these often include buffer zones that are not PAs and core areas which are already designated as PAs at a national level. Size can be an important determinant of PA effectiveness, so to test whether it was important for buffering against climate change or land-use change, I divided PAs into large (< 400 km^2) and small (>= 400 km^2) groups; (Figure S4.1). IUCN category is also expected to play a role in the effectiveness of PAs, so I also divided PAs into high strictness (IUCN categories Ia, Ib, and II), low strictness (IUCN categories III, IV, V, and VI), and unknown strictness (IUCN category not reported, not assigned, or not applicable; Figure S4.1). These size and management thresholds are somewhat arbitrary, but have previously shown to be relevant for biodiversity in terrestrial PAs (Gray et al. 2016)

Using ArcGIS Pro (ESRI 2021), I converted the PA polygon layers into equal-area rasters at a 1 km x 1 km resolution. I then aggregated the rasters to match the 100 km by 100 km resolution of the biodiversity data, and calculated the percentage of terrestrial landscape within each cell that was protected area (Figure 4.1). I repeated this for large and small PAs, high and low strictness PAs, and all combinations of these. Proportion of PA in the landscape was *log(1+x)* transformed in models to improve normality. Results of main models, which did not consider year of establishment, were qualitatively similar to results of models which used only the extent of PAs established in or before the historic period.

Statistical analysis

PAs and biodiversity change – extirpation, colonization, change in probability of occupancy

I examined whether PAs mitigate the effects of climate change or land-use change by testing whether extent of PA per quadrat influenced the relationship of biodiversity change to thermal position and land-use change. For extirpation and colonization, I ran a series of binomial generalized linear mixed models (GLMM) that included thermal position variables (historic, change since baseline, interaction between these) and human-dominated land-use variables (baseline, change since baseline, interaction between these). These variables are shown to be related to biodiversity change in bumblebees (e.g. Soroye et al. 2020, Chapter 3). Climate change and land-use change interactions can also be important (Chapter 3), but I do not include them here to reduce the number of predictor variables and potential interactions in the models. To test for a potential effect of PAs influencing the effect of climate change and land-use on bumblebees, I included extent of PA as a direct effect, and as an interaction with changing thermal position and land-use change variables (e.g., Tables 4.1 and S4.1). The models included species as a random effect, as well as sampling intensity (the number of unique spatiotemporal occurrence observations within a site in a period). Continent was included as a categorical variable to account for potential differences in rates of change between North America and Europe, and after assessing the distribution of extent of PA across North America and Europe (Figure S4.1), I included continent interactions with all extent of PA fixed effects, to account for potential continental differences.

I repeated this modelling procedure for the change in probability of occupancy variable using a linear mixed model. The fixed and random effects of this model were identical to the extirpation and colonization models, except that I did not include sampling effort, as it was already used to estimate probability of occupancy (Table S4.1). For all models, I calculated the Deviance Information Criterion (DIC), and conditional and marginal R^2 (Nakagawa & Schielzeth 2013). I ran all models to convergence and visually assessed model assumptions.

To account for phylogeny in the analyses, I repeated the species-level models (extirpation, colonization, and change in probability of occupancy) using a phylogenetic generalized linear mixed model framework. I used a comprehensive mitochondrial and nuclear bumblebee phylogeny (Cameron et al. 2007) and followed established frameworks (de Villemereuil & Nakagawa 2014), programing the models using the *MCMCglmm* (Hadfield 2010) and *ape* (Paradis & Schliep 2018) packages in R. All models used uninformative univariate priors for random effects corresponding to an inverse-Gamma with shape and scale parameters equal to 0.01. Models were run with a minimum of 105,000 iterations, with a thinning factor of 20 and discarding the first 5000, resulting in a minimum of 5000 samples from the joint posterior distribution. I visually assessed model parameters for convergence, and if all parameters did not appear to converge then they were rerun for more iterations and with a longer burn-in. Using code adapted from de Villemereuil & Nakagawa (2014), I estimated marginal and conditional

R^2, and phylogenetic signal (Pagel's λ). As is common with Bayesian models, I compared models using DIC. *B. magnus* and *B. kirbiellus* were not present in the phylogeny and were excluded from these analyses. The structure of fixed model effects tested was identical to the descriptions provided above, and I found that model parameter values using the PGLMMs were very consistent with non-phylogenetic models. I present results from the PGLMMs in the main text because while DIC was very similar (0-2% lower DIC), the PGLMMs explained greater variation in the responses (7-33% higher marginal R^2).

PAs and biodiversity change – species richness

I built an analysis of covariance (ANCOVA) model to test whether the amount of PA in a landscape was related to change in detection-corrected species richness (Tables 4.1 and S4.1). The model structure here was identical to the change in occupancy models but used community-averaged measures of thermal positioning and did not include a random effect of species. I used a similar ANCOVA structure to model observed (i.e., non-detection corrected) species richness. This used the same process as the detection-corrected model but included a covariate in the model which accounted for sampling intensity (Table S4.2). As an additional measure to control for variable sampling, I restricted this analysis to sites that had 30 or more unique spatiotemporal observations in each period. To minimize potential overfitting due to the smaller sample size of these models (n= 310 here vs n= 1258 with the change in detection-corrected richness models), I did not test for the importance of PA characteristics with this biodiversity variable. I tested the effect of extreme outliers in these models, and found consistent results after excluding any outliers.

I checked for spatial autocorrelation in the residuals of both assemblage richness models by visually inspecting a correlogram of Moran's I. I found evidence of spatial autocorrelation and proceeded by constructing a simultaneous autoregressive (SAR) spatial error model to correct for residual autocorrelation, as suggested by Kissling & Carl (2008) and Dormann et al. (2007). This reduced much of the variability in Moran's I (Figures 4.6-4.7). Model results with the SAR error models were qualitatively similar to the ANCOVA results that are reported here (Table S4.2). I calculated the Nagelkerke Pseudo-R^2 as a measure of the variance explained and used Akaike's Information Criterion (AIC) and the Bayesian information Criterion (BIC) to evaluate the fit of models. Results from the models appeared robust to the presence of outliers, and aside from violations of spatial autocorrelation in the residuals, appeared to satisfy all other assumptions.

Importance of PA in highly human-dominated areas

If PAs provide a benefit to species by mitigating pressures from human land use, then I expect the impact of PAs to be greatest (and most detectable) in places that have long histories of high land-use. To test for this, I repeated the PA-biodiversity change models for extirpation, colonization, change in probability of occupancy, detection-corrected species richness, and observed richness with a subset of the sites where extent of human-dominated land-use was over 50% in the historic and recent period (Tables 4.2 and Sv3). I otherwise followed the same modelling procedures as described above. Assemblage richness models (both detection-corrected and non-detection-corrected) both showed evidence of spatial autocorrelation, so I ran SAR spatial error models and found qualitatively similar results (Figure S4.8-4.9; Table S4.4).

Testing importance of PA characteristics

I tested whether PA characteristics like size and IUCN category were important by repeating PA-biodiversity change models and replacing the proportion of total PA in a site variable with i) proportion of large PA and proportion of small PA variables, ii) proportion of high strictness PA and proportion of low strictness PA variables, and iii) proportion of high strictness-large PA, proportion of high strictness-small PA, proportion of low strictness-large PA, and proportion of low strictness-small PA variables (Tables S4.5-4.7). By separating the PA variable into components based on characteristics of the PA, I can test whether these characteristics are important for improving the model fit or variance explained in the biodiversity variable response (Table 4.3). I compared these more complex models (and the main models using total extent of PA) to a reference model which did not include any fixed effects of PA (Table S4.8). Aside from the addition of the new PA variables and interactions, the structure of fixed and random effects remained the same. I compared DIC (or AIC and BIC for ANCOVA models) and explained variance between models to determine whether accounting for characteristics of PAs was informative.

Testing for environmental covariates to extent of PA

I found important continental variability in the interactions between extent of PA and biodiversity responses to changing thermal position and land-use, and investigated whether these could be driven by differences in where PAs are distributed across continents. Using a series of ANCOVA models, I modelled the relationship between extent of PA and a) historic community-averaged thermal position, b) change in community-averaged thermal position, c) historic extent of human-dominated land-use, and d) change in extent of human-dominated land-use, to assess whether relationships between these variables were significant and differed between continents (Table S4.9; Figure 4.4).

Landcover could be another potentially important driver of continental differences in observed trends, if PAs in North America or Europe tend to be placed in some landcover types more than others. For bumblebees, a largely generalist taxa, forested landcover types generally support lower abundances and numbers of species than open landcover (Williams et al. 2014) (although some species do favor forested landcover e.g., Liczner & Colla 2020). Similar to the thermal position and land-use variables above, I used ANCOVA models to model the relationship between extent of PA and a) forested landcover, and b) open landcover, to assess whether these were significantly related and varied between continents (Table S4.10; Figure 4.5). I used the USGS Global Land Cover Characterization (GLCC) landcover database (DOI: 10.5066/F7GB230D), which is based on classification of remotely sensed Advanced Very High Resolution Radiometer (AVHRR) Normalized Difference Vegetation Index (NDVI) composite images. This dataset is internally consistent across both continents, produced at a resolution of ~1 km, and is derived from images taken in 1992-1993, which falls between the historic (1900-1974) and recent (2000-2018) periods. I grouped landcover types into forested and open (Table S4.11), and aggregated and resampled data to calculate the % terrestrial cover of each landcover type within the 100 km by 100 km sites (Figure S4.10).

Geospatial and statistical software

All analyses were performed in R version 3.6.1 (R Core Team 2017), primarily with the *raster* (Hijmans et al. 2016) and *tidyverse* (Wickham 2017) packages, and others specifically mentioned. Continuous variables in all statistical models were re-scaled and centered. Mapping and visualization of data was done in ArcGIS Pro (ESRI 2021), using a Winkel Tripel projection.

Results

Extent of PA (percent of terrestrial area per 100 km by 100 km site; Figure 1) was significantly related to increased probability of site occupancy and decreased extirpation, indicating that extirpation was lower, and probability of occupancy was more likely to have increased, in regions with more PA (Figure 2). These effects were similar across continents, although nearly significantly different for extirpation (Table 1). They were independent of changes in thermal position, land-use, and sampling. Neither colonization nor detection-corrected richness appeared significantly associated to extent of PA.

I expected that any beneficial effect of PAs would be highest in very degraded landscapes where bumblebees were the most challenged by anthropogenic pressures, and, consistent with this prediction, the effect of PAs was larger in these areas (Figure 3). The positive relationship between extent of PA and change in probability of occupancy, and the negative relationship between extent of PA and extirpation, were both much stronger in areas where over 50% of terrestrial area has been dedicated to human land-uses since the historic period (Table 2).

Extent of PA also appeared to significantly influence the relationship between changing thermal position and land-use on biodiversity, although not always as predicted. The response of change in probability of occupancy, extirpation, colonization, and change in detection-corrected richness to increasing thermal position was generally less adverse (i.e., less negative for change in probability of occupancy, colonization, and richness change, and less positive for extirpation) when in landscapes with a greater extent of PA (Table 1). Yet, these trends only held in North America. A significant continent interaction indicated that the response of change in probability of occupancy, extirpation, and colonization was more adverse in European landscapes with greater amounts of PA. The reverse was observed with trends in land-use: higher extent of PA was related to a less negative response in change in probability of occupancy and colonization in Europe, and a more negative response in North America (Table 1). This could be due to continental differences in the distribution of PAs or due to pronounced differences in land use histories.

The location and conditions where PAs are placed appear to differ substantially between North America and Europe, potentially contributing to differences observed between extent of PA and biodiversity responses. In North America, landscapes with high extent of PA are warming more rapidly than other areas, but bumblebee assemblages have historically been near the center of their realized tolerance limits and experienced relatively low levels of human-dominated land-use. In contrast, landscapes with higher extent of PA in Europe were also warming more rapidly than other areas but were places where bumblebee assemblages were closer to their thermal limits than in other areas historically, and experienced slightly higher rates of human dominated land-use. While there is no significant association between changing land-use and extent of PA in either continent (Figure 4D), many areas with relatively high PA extent have also experienced increases in agricultural and urban land use extents, especially in North America. These continental differences in the distribution of PAs, and particularly in regional land use histories, could drive the interactions between extent of PA and biodiversity responses to thermal position or land-use observed here at the landscape scale.

The type of habitats in landscapes with a high extent of PA also appeared to vary significantly between continents, potentially contributing to observed differences in biodiversity responses as well. In North America, areas with a high extent of PAs are typically more forested and less open, while in Europe the reverse is true. While bumblebees generally prefer open habitats to forest (Williams et al. 2014), these places are typically more exposed to local climatic extremes (De Frenne et al. 2019; Zellweger et al. 2020), potentially contributing to the observed interactions with thermal position in high PA extent areas in Europe, which has also warmed more on average than North America (Figure S4).

I find only limited evidence to suggest that PA size and management category consistently influenced the ability of PAs to protect bumblebee species. While including additional fixed effects in biodiversity response models which accounted for the size (Table S5), IUCN category (Table S6), or both size and category (Table S7) of PAs improved the performance of models, they did not help to explain much additional variance (Table 3). Investigating the overall best fitting model, which included extent of PA broken down by size (Large >= 400 km^2, Small < 400 km^2) and IUCN category, reveals variable effects of PA between types (e.g., large and strict, small and less strict, etc.), but with no clear evidence of a single type of PA having a consistent effect across continents (Table S7).

Discussion

This cross-continental study shows that increasing the extent of PA in a landscape appears directly related to reduced extirpation risk and increasing probability of site occupancy for bumblebees, especially in highly human-dominated areas. Specifically, the greater the amount of terrestrial area in a landscape that is designated as "protected", regardless of size, IUCN category, or continent, the more likely that extirpation risk is lower and change in probability of occupancy increasing (Figure 4.2).

This beneficial direct effect of increasing extent of PAs is amplified in highly human-dominated landscapes (Figure 4.3), suggesting that increasing the extent of PAs even in areas with long histories of human land-use can provide conservation gains. Anecdotally, much evidence has pointed to the benefit of small PAs for invertebrates in fragmented and highly human-dominated landscapes. In Canada, for example, the last known sighting of the rusty-patched bumblebee (*Bombus affinis*) in 2009 was from Pinery Provincial Park (Colla & Packer 2008; Environment and Climate Change Canada 2016), a small PA within a region dominated by some of the most intensive agricultural landscapes in the country (Kerr & Cihlar 2003). This park also is also one of the last places where the Karner Blue butterfly (*Plebejus samuelis*) was sighted before its extirpation from the country (COSEWIC 2019). The landscape-scale analysis supports the conclusion that PAs within intensive, human dominated landscapes can help protect species that were historically present in those areas and facilitate colonization by others whose geographical ranges may be shifting.

While species-level trends relate positively to extent on PA in a region, there is not a similar relationship with assemblage richness (Table 4.1). Given how climate and land-use change influence species (Chapter 4.2 and 4.3), I expected species richness to increase with extent of PA. However, previous studies have found that bee species richness is generally similar or higher in human-dominated environments compared to PAs (e.g., Baldock et al. 2015; Tew et al. 2021), and others have found that PA extent and biodiversity patterns are often independent (Deguise & Kerr 2006). One possible explanation for the observed mismatch here could be that trends in colonization, while noisy, still act to mask regional losses of species. Power to detect an effect within the species richness analyses are lower than for the extirpation, colonization, or probability of occupancy change measures (1248 measures of detection-corrected species richness change, compared to 14,665 site-species measures of population change), making it harder to distinguish biological signal from background noise, especially when location effects are strong (see below). But considering that increasing extent of PA does not drive higher species richness, combining complementary conservation tools in addition to PAs may be an important consideration when managing bumblebee communities. Managing land-use in ways to benefit communities of wild pollinators can offset the effects of warming and benefit biodiversity for bees (Chapter 3, Papanikolaou et al. 2017; Millard et al. 2021; Prestele et al. 2021), and could be an effective complementary strategy alongside increasing the extent of PAs in a landscape.

While increasing extent of PA was related to more positive biodiversity outcomes, there was no consistent indication of PAs mitigating the specific historic effects of climate change and land-use across continents. The significant interactions between extent of PA and biodiversity responses to changing thermal position and land-use change varied in their strength and direction in North America compared to Europe (Table 4.1). This could be driven by different management regimes of PAs between continents, or by differences in where PAs are distributed across them. Landscapes with a high extent of PA in North America and Europe have diverging histories of historic thermal position, land-use, and landcover (Figures 4.4 and 4.5), which would explain some of the interactions in the main models. For example, landscapes with a high extent of PA are places where bumblebee assemblages were historically far from their realized upper tolerance limits in North America, whereas in Europe assemblages in these regions were closer to their realized thermal tolerance limits than other places (Figure 4.4A). Given the effect of warming temperatures are worse when bumblebees are already near their warm realized tolerance limits (Soroye et al. 2020), this location effect could explain why extent of PA in the landscape appeared to mitigate the negative effects of increasing thermal position in North America, but amplify them in Europe.

Interestingly, I found only weak evidence that PA characteristics such as size or IUCN category are relevant for bumblebees. There was only a minor increase in explanatory power of biodiversity responses by accounting for these characteristics, suggesting that models were not more biologically informative when considering these characteristics. While size and IUCN category are often related to efficacy of PAs for biodiversity (Coetzee et al. 2014; Gray et al. 2016), these factors may be less relevant for bumblebees, which have relatively small foraging requirements (typically observed foraging less than 3 km from nest, although *B. pascuorum* has been observed foraging up to 10 km away, see Greenleaf et al. 2007), and are often relatively tolerant of changes in land-use and human dominated landscapes (e.g., Chapter 3, also see Murray et al. 2012; Baldock et al. 2015; Hemberger et al. 2021; Millard et al. 2021). However, given that further subdividing PAs tends to increase PA location bias (e.g., Joppa & Pfaff 2009; Figure S4.1), these more complex models (Tables S4.5-4.7) are more likely describing regional trends as opposed to detecting real influences of these types of PAs. Finer, local-scale effects of PA may exist that are not detectable at the landscape scale. Future studies could test for these more powerfully using matching study designs that compare biodiversity trends inside PAs to similar unprotected areas, although this would require sacrificing geographic scale and taxonomic scope.

Conclusion

Increasing the amount of PA is strongly related to lower extirpation risk for bumblebees across North America and Europe. This benefit appears over the last few decades, is regardless of PA size or management category, and appears strongest in intensively human-dominated landscapes. This highlights the important role of PAs and area-based conservation, especially in highly human-dominated landscapes. While the analyses here are unable to definitively identify a mechanism causing this benefit, more focused studies using comparative approaches and higher-resolution data may be able to uncover one. As nations prepare to set post-2020 conservation targets, highly human-dominated areas represent areas of potentially high value for protection.

Figures 1-5

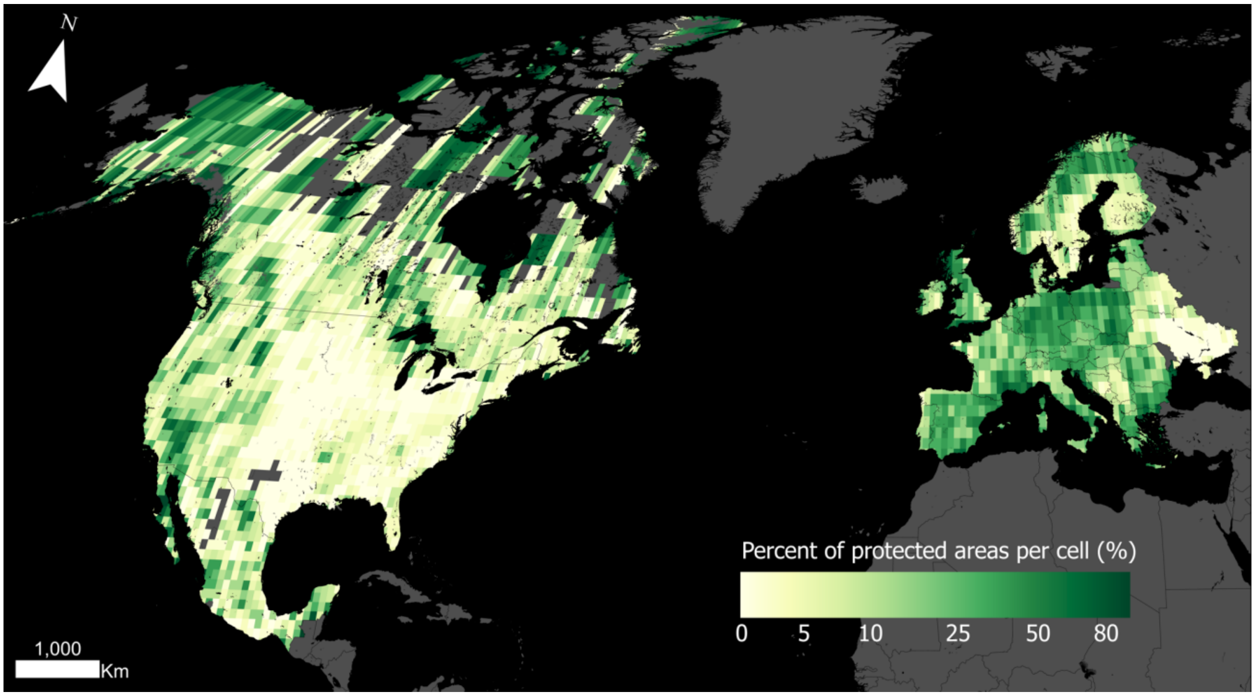


Figure 4.1. Extent of PAs (% of terrestrial area) per cell across North America and Europe.

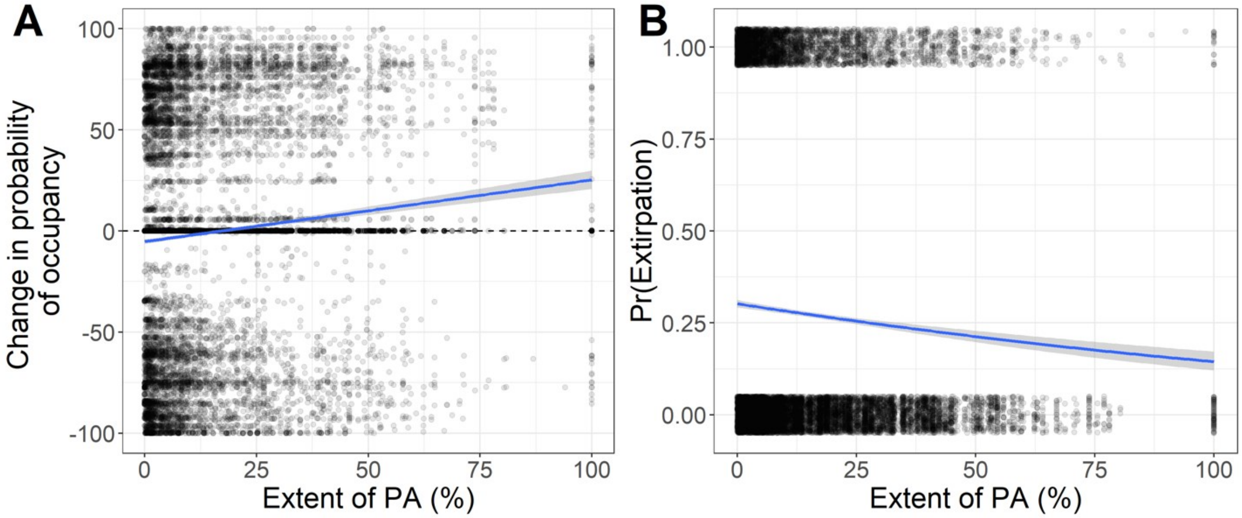


Figure 4.2. Change in probability of site occupancy (A) and probability of extirpation (B) between historic (1900-1975) and recent (2000-2018) periods in relation to extent of PA per site (% terrestrial area) based on quadrats extending across regions of Europe and North America. Linear trendline (A) and simple logistic trendline (B) with 95% CIs displayed with point data, no significant continent interaction. Binary point data is vertically shifted by random amounts around 0 and 1 for clearer visualization.

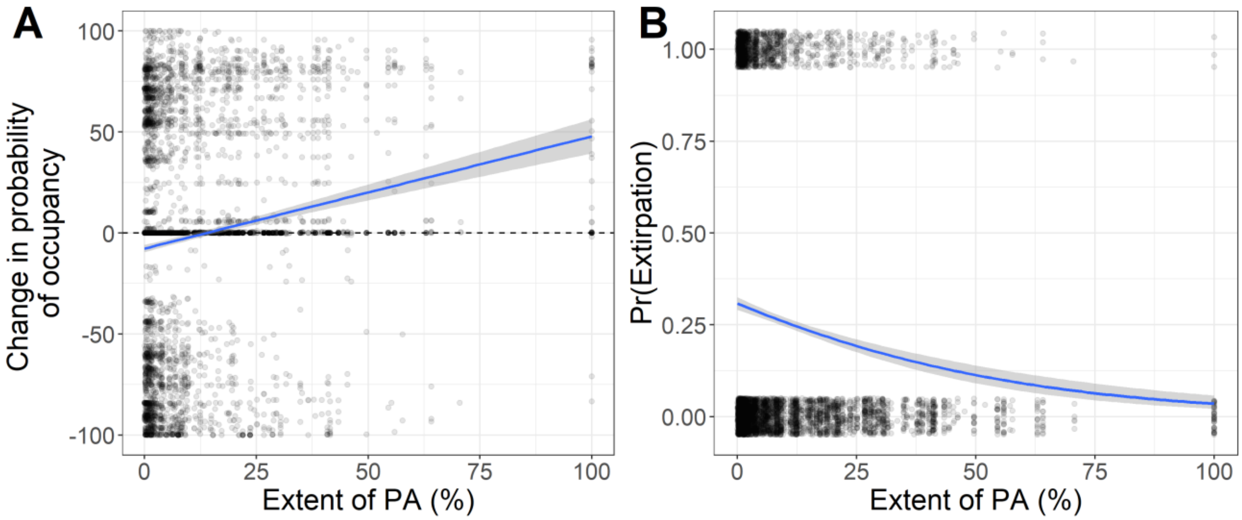


Figure 4.3. Change in probability of site occupancy (A) and probability of extirpation (B) between the historic (1900-1975) and recent (2000-2018) periods in relation to extent of PA per site (% terrestrial area) across areas of human-dominated land use. Human-dominated land-use quadrats have had over >50% of the terrestrial area dedicated to human dominated land uses (including grazing, cropland, and urban land use) in both the historic and recent period (n= 486). Some forms of this land-use can occur inside PAs, meaning extent of PA per quadrat can also exceed 50%. Linear trendline (A) and simple logistic trendline (B) with 95% CIs displayed with point data, no significant continent interaction. Binary point data is vertically shifted by random amounts around 0 and 1 for clearer visualization.

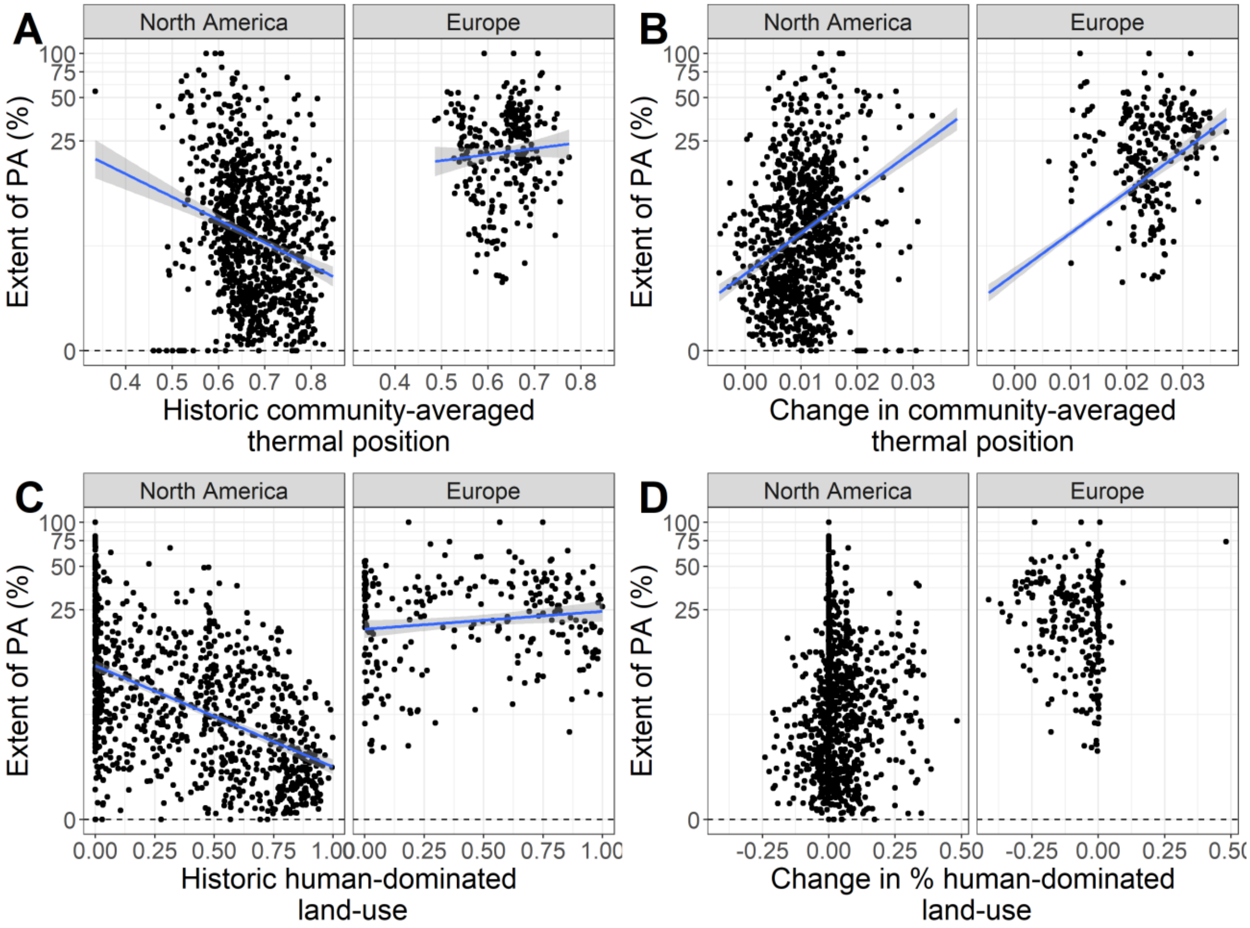


Figure 4.4. Relationship between extent of PA per site (% terrestrial area) and site-level historic community-averaged thermal position (A), change in community-averaged thermal position (B), historic human-dominated land-use (C), and change in human-dominated land-use (D). High human-dominated land-use are areas where >50% of terrestrial area was human dominated in both historic and current period, where dominated land-use indicates the % of terrestrial area dedicated to human land-uses including grazing, cropland, and urban use. Some forms of this land-use can occur inside PAs, meaning extent of PA per quadrat can also exceed 50%. Linear trendlines are shown for significant trends across North America (n= 991) and Europe (n= 267).

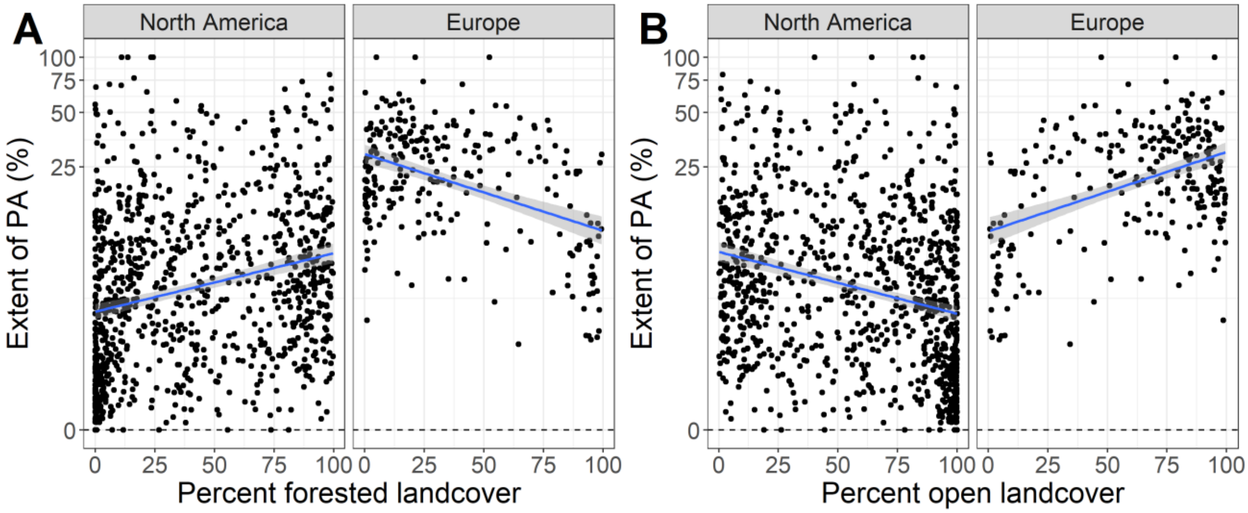


Figure 4.5. Relationship between extent of PA per site (% terrestrial area) and extent of forested (A) and open (B) landcover (% terrestrial area). Forested and open landcover determined using the USGS Global Land Cover Characterization data product (see Table S4.11 for a breakdown of landcover groupings). Landcover estimated derived from 1992-1993, between the historic and recent period. Pearson's correlation coefficient is displayed for trends across North America (n= 991) and Europe (n= 267).

Tables 4.1-4.3

Table 4.1. Estimated model coefficients showing the relationship between extent of protected area (% terrestrial area) per quadrat and bumblebee extirpation, colonization, change in probability of occupancy, and percent change in detection-corrected species richness models. Posterior means and 95% Bayesian credible intervals are shown for phylogenetic generalized linear mixed models (PGLMM). For analysis of covariance models (ANCOVA), t-values are included as a measure of significance. Generally, coefficients with t-values < -1.96 or > 1.96 are considered statistically significant, these and coefficients where the 95% CI does not overlap zero are in bold text in the table. Results shown here are for a subset of the included variables, see Table S4.1 for a table of all model coefficient estimates.

	Change in probability of occupancy (PGLMM)		Extirpation (PGLMM)		Colonization (PGLMM)		Change in detection-corrected richness (ANCOVA)	
	Posterior mean	95% CI	Posterior mean	95% CI	Posterior mean	95% CI	Estimate (SE)	t-value
Direct PA variables								
Total extent PA	**1.99**	**0.49 - 3.36**	**-12.21**	**-19.68 - -4.72**	1.25	-6.37 - 8.9	-0.01 (0.02)	-0.4
Total extent PA: Europe interaction	-0.82	-4.45 - 2.79	23.8	-0.32 - 47.28	-9.73	-28.5 - 8.28	-0.1 (0.06)	-1.85
PA interactions with TPI								
Extent PA: change in TPI	**4.08**	**2.35 - 5.77**	**-15.83**	**-24.77 - -7.23**	**26.26**	**16.65 - 35.64**	**0.07 (0.02)**	**3.99**
Extent PA: change in TPI: Europe interaction	**-5.03**	**-8.32 - -1.75**	**37.54**	**17.1 - 58.53**	**-52.18**	**-70.2 - -33.95**	-0.04 (0.04)	-1.15
PA interactions with LU								
Extent PA: change in LU	**-1.83**	**-3.66 - -0.02**	1.52	-7.89 - 11.27	**-15.55**	**-25.64 - -5.43**	**-0.04 (0.02)**	**-2.44**
Extent PA: change in LU: Europe interaction	**5.49**	**2.2 - 8.72**	-3.88	-21.98 - 14.95	**37.5**	**19.53 - 55.21**	0.06 (0.03)	1.75

Table 4.2. Estimated model coefficients showing the relationship between extent of protected area (% terrestrial area) per quadrat and bumblebee extirpation, colonization, change in probability of occupancy, and percent change in detection-corrected species richness models, for highly human-dominated areas. Posterior means and 95% Bayesian credible intervals are shown for phylogenetic generalized linear mixed models (PGLMM). For analysis of covariance models (ANCOVA), t-values are included as a measure of significance. Generally, coefficients with t-values < -1.96 or > 1.96 are considered statistically significant, these and coefficients where the 95% CI does not overlap zero are in bold text in the table. Results shown here are for a subset of the included variables, see Table S4.3 for a table of all model coefficient estimates.

	Occupancy (PGLMM)		Extirpation (PGLMM)		Colonization (PGLMM)		Detection-corrected richness (ANCOVA)	
	Posterior mean	95% CI	Posterior mean	95% CI	Posterior mean	95% CI	Estimate (SE)	t-value
Direct PA variables								
Total extent PA	**7.3**	**2.94 - 11.23**	**-46.47**	**-72.75 - -20.15**	9	-15.84 - 33.44	0.07 (0.05)	1.42
Total extent PA: Europe interaction	2.2	-6.1 - 9.35	3.25	-51.96 - 58.29	2.87	-40.19 - 50.03	0.02 (0.11)	0.23
PA interactions with TPI								
Extent PA: change in TPI	**7.4**	**2.36 - 11.89**	**-40.58**	**-71.54 - -9.1**	**43.72**	**13.82 - 73.19**	0.09 (0.05)	1.78
Extent PA: change in TPI: Europe interaction	**-10.8**	**-18.92 - -2.76**	**73.57**	**17.63 - 130.36**	**-112.68**	**-163.15 - -60.77**	-0.12 (0.1)	-1.29
PA interactions with LU								
Extent PA: change in LU	**-4.36**	**-7.29 - -1.14**	16.1	-2.68 - 34.76	-12.07	-30.53 - 6.25	**-0.08 (0.03)**	**-2.7**
Extent PA: change in LU: Europe interaction	**7.16**	**0.94 - 13.37**	-20.84	-63.76 - 21.35	5.84	-30.32 - 42.52	0.09 (0.07)	1.16

Table 4.3. Comparing number of fixed effects, variance explained, and model fit for PA-biodiversity models where total extent of PA (% terrestrial area) was divided based on PA size (Large >= 400 km^2; Small < 400 km^2), IUCN category (Strict= IUCN categories I-II; Low strictness= IUCN categories III-VI), and both. Note that for change in probability of occupancy models and detection corrected species richness models, the sampling covariate is not included as sampling is already used to estimate probability of occupancy. Deviance Information Criterion (DIC) is used as a measure of model fit for the PGLMM models, both Akaike's Information Criterion (AIC) and the Bayesian Information Criterion (BIC) are shown for ANCOVA models, negative values indicate the focal model fit is better (lower) compared to the reference model. Variance explained is expressed in terms of marginal R^2 (for PGLMM) and adjusted R^2 (for ANCOVA models). See Tables S4.1 and S4.5-4.8 for full list of fixed effects.

		Change in probability of occupancy (PGLMM; n= 14,443)		Extirpation (PGLMM; n=14,443)		Colonization (PGLMM; n=14,443)		Change in detection-corrected richness (ANCOVA; n=1258)		
Model name	Number of fixed effects	Variance explained	ΔDIC	Variance explained	ΔDIC	Variance explained	ΔDIC	Variance explained	ΔAIC	ΔBIC
No PA (reference model)	9	0.18	0	0.323	0	0.188	0	0.154	0	0
Total PA model	15	0.186	-38.3	0.327	-16.59	0.209	-25.27	0.17	-19	11
PA by IUCN category	21	0.188	-81.6	0.328	-28.48	0.246	-35.06	0.169	-10	51
PA by size	21	0.193	-74	0.334	-31.84	0.239	-33.01	0.181	-30	31
PA by IUCN category and size	33	0.198	-153.6	0.344	-46.93	0.27	-47.36	0.189	-30	92

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Supplemental Materials

Supplemental Figures S4.1-4.10

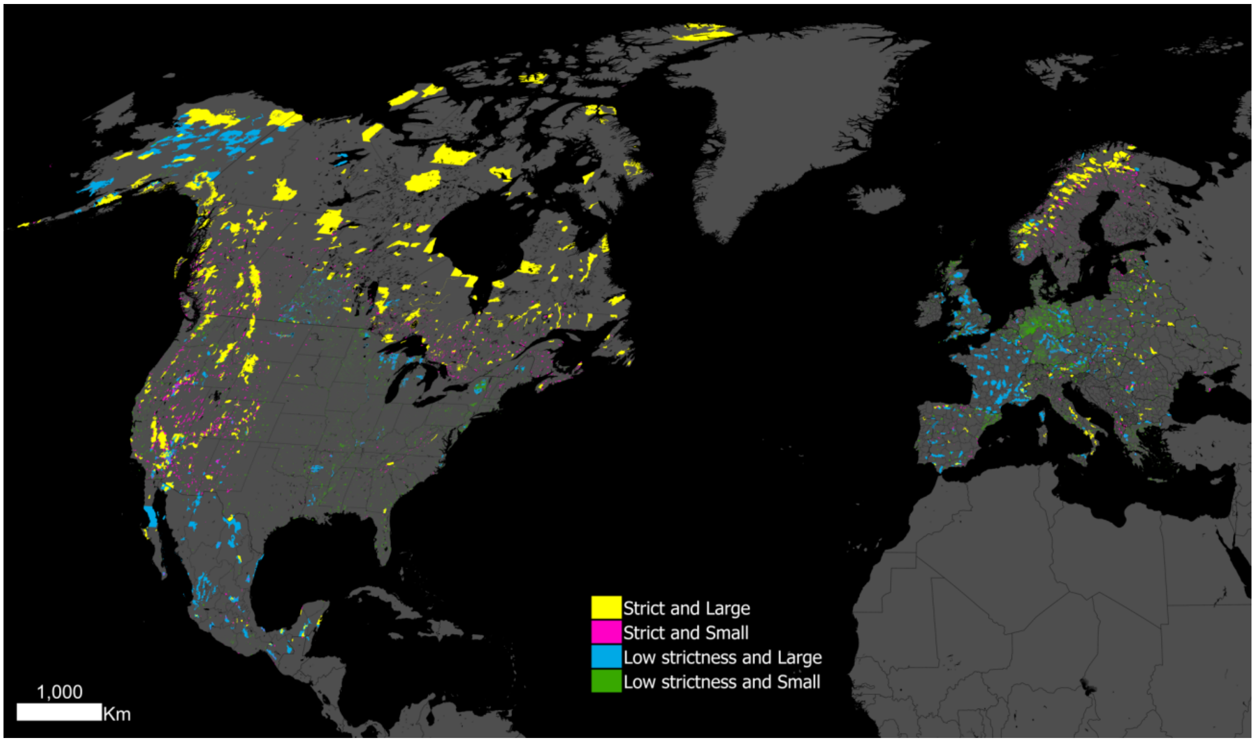


Figure S4.1. Protected areas (PAs) across North America and Europe identified by size (Large >= 400 km^2; Small < 400 km^2) and management strictness (Strict= IUCN category I-II; Low strictness= IUCN category III-VI).

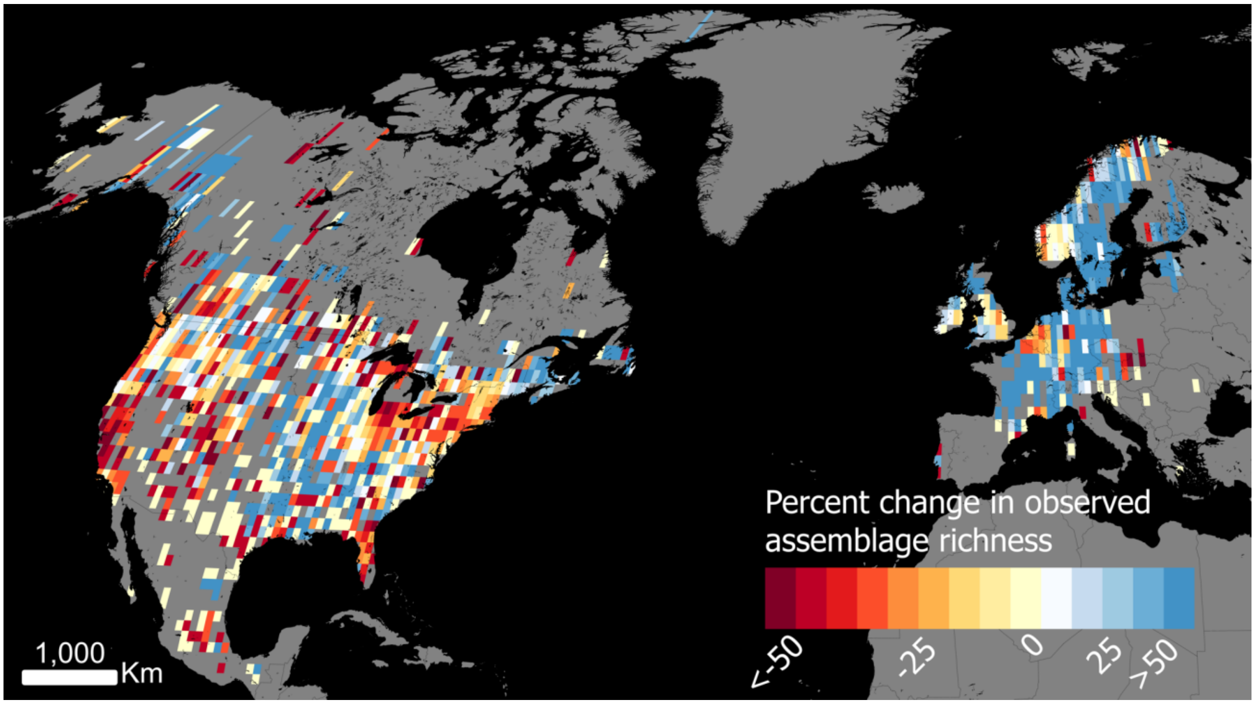


Figure S4.2. Percent change in observed assemblage richness between historic (1900-1974) and recent period (2000-2018). Grid cells shown are equal-area 100 km by 100 km. No detection or sampling correction applied.

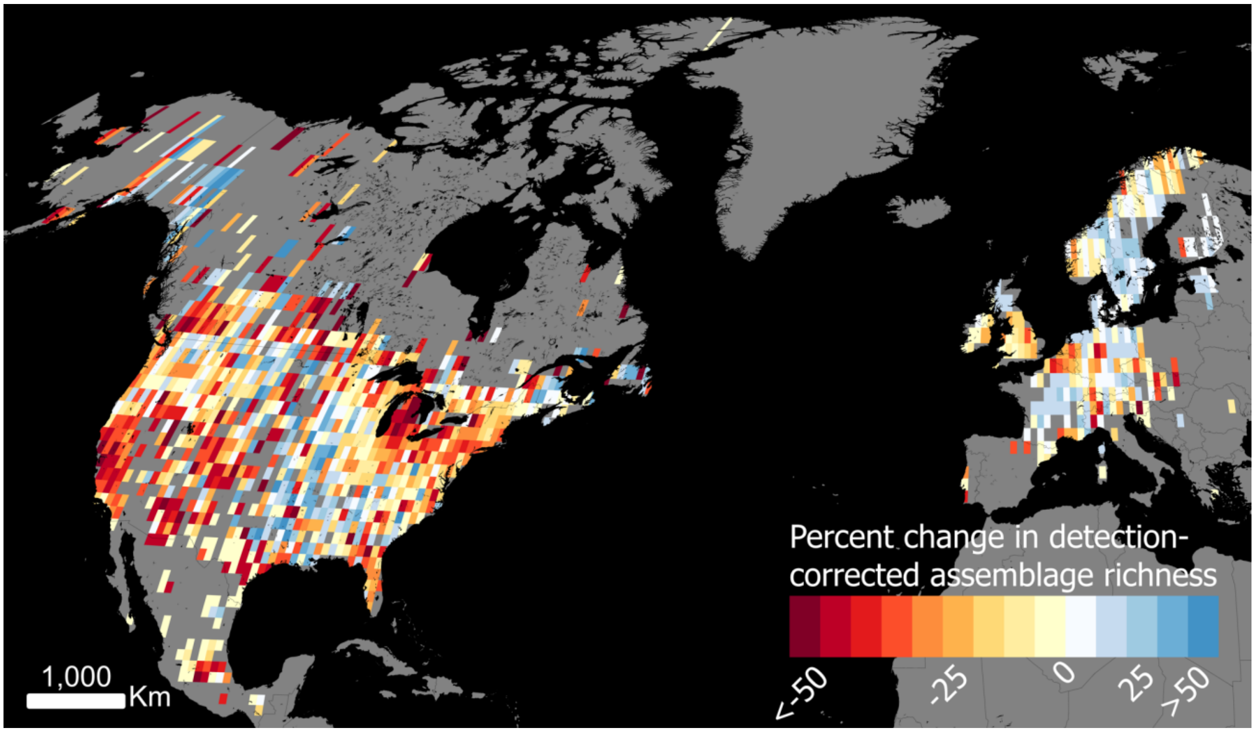


Figure S4.3. Percent change in detection-corrected assemblage richness between historic (1900-1974) and recent period (2000-2018). Grid cells shown are equal-area 100 km by 100 km.

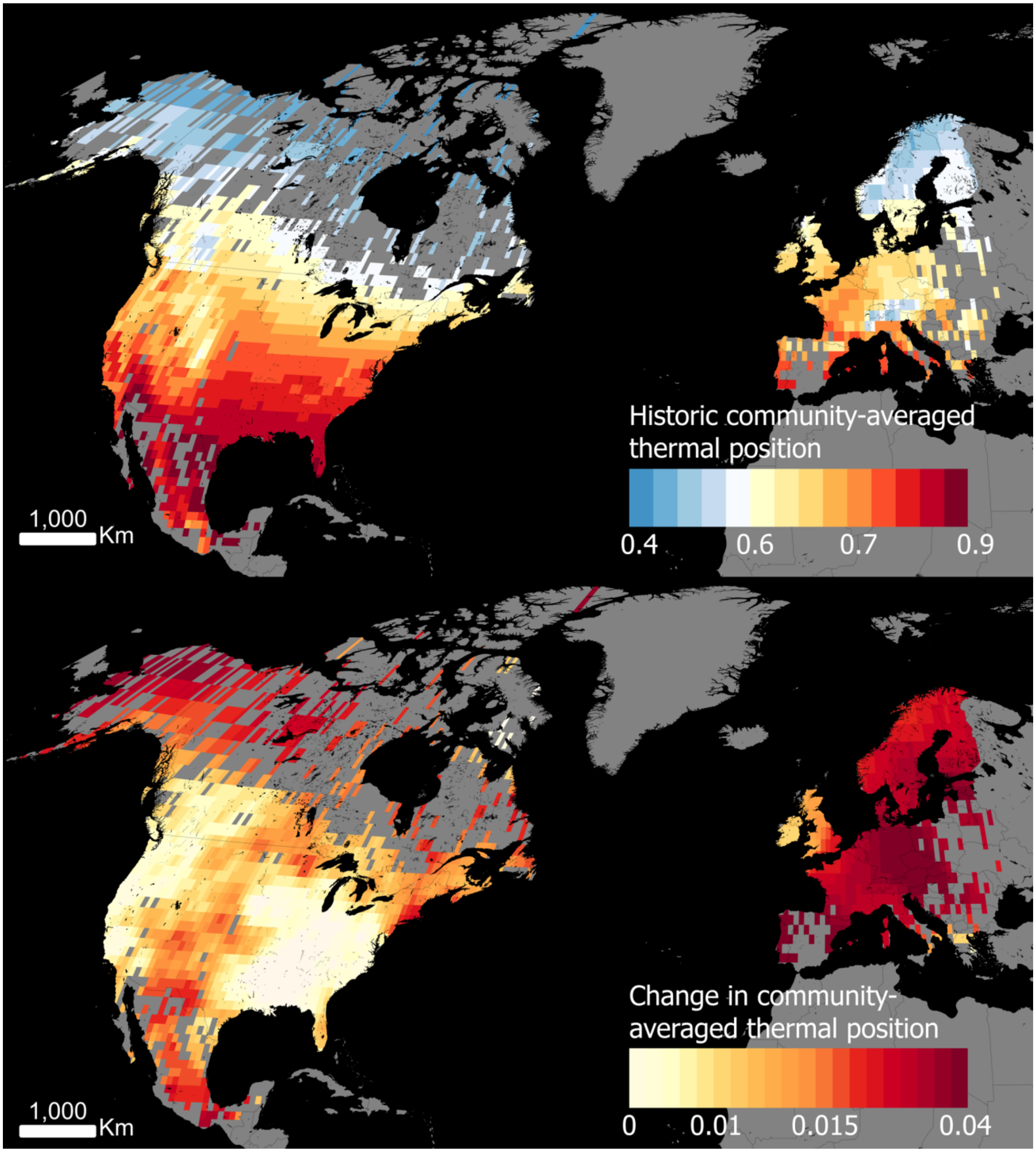


Figure S4.4. Historic community-averaged thermal position across North America and Europe (A) and change in thermal position between historic period (1900-1974) to recent period (2000-2018) (B). Historic thermal position has a potential range of 0 to 1. Zero indicates that species in the assemblage are on average at their historic cold tolerance limit for the entirety of the year in the period. One indicates that species in the assemblage are on average at their historic hot tolerance limit for the entirety of the year in the period. Recent thermal position can exceed 1 or go below zero if local climate change means species are exceeding their historic tolerance limits.

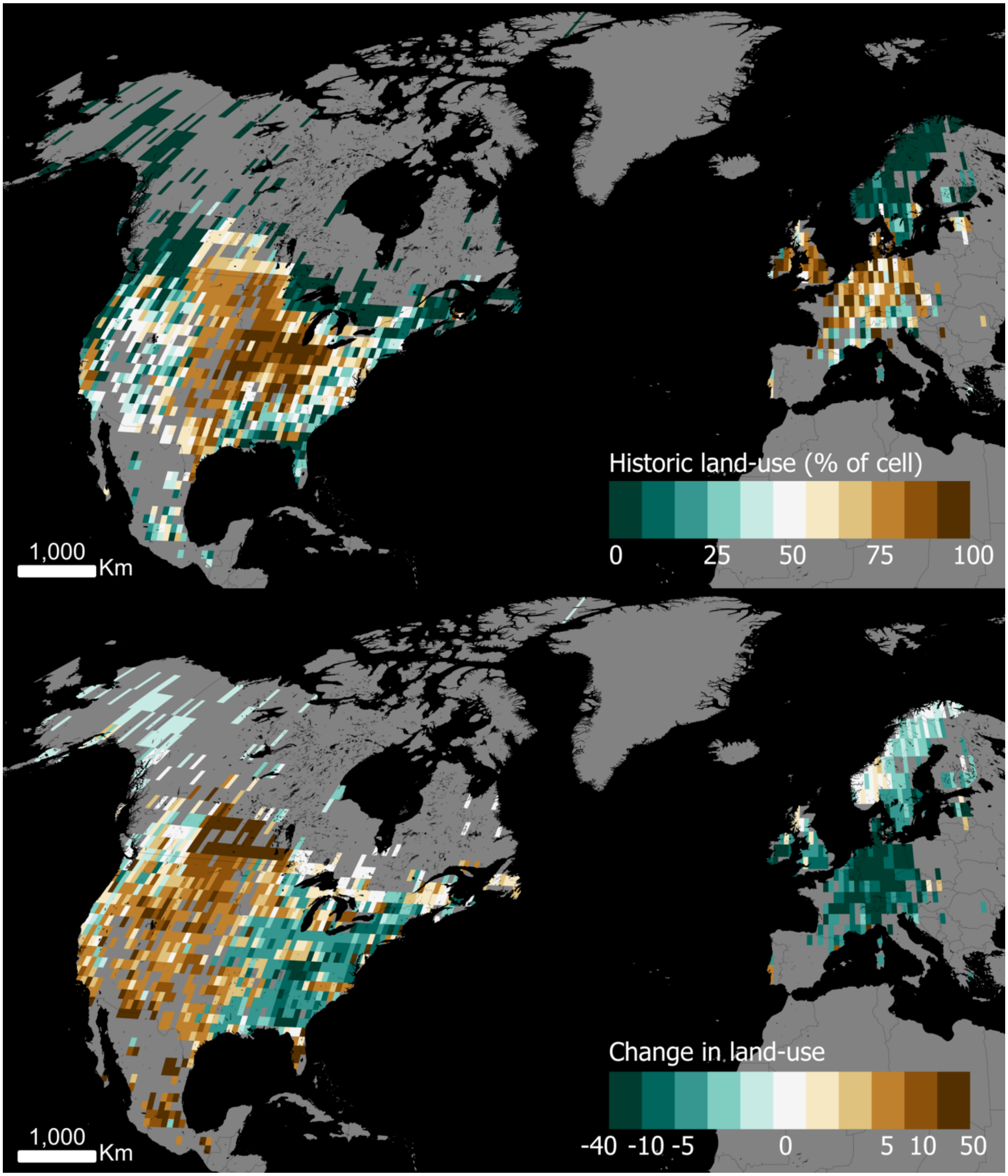


Figure S4.5. Historic human-dominated land-use across the study area (A; % of terrestrial area per cell), and change in land-use between historic period (1900-1974) to recent period (2000-2018) (B). Human-dominated land-use is estimated from the HYDE 3.2.1 dataset (Goldewijk et al. 2016), and is the summed proportion of land area in a cell used by pasture, grazing, or urban land-use.

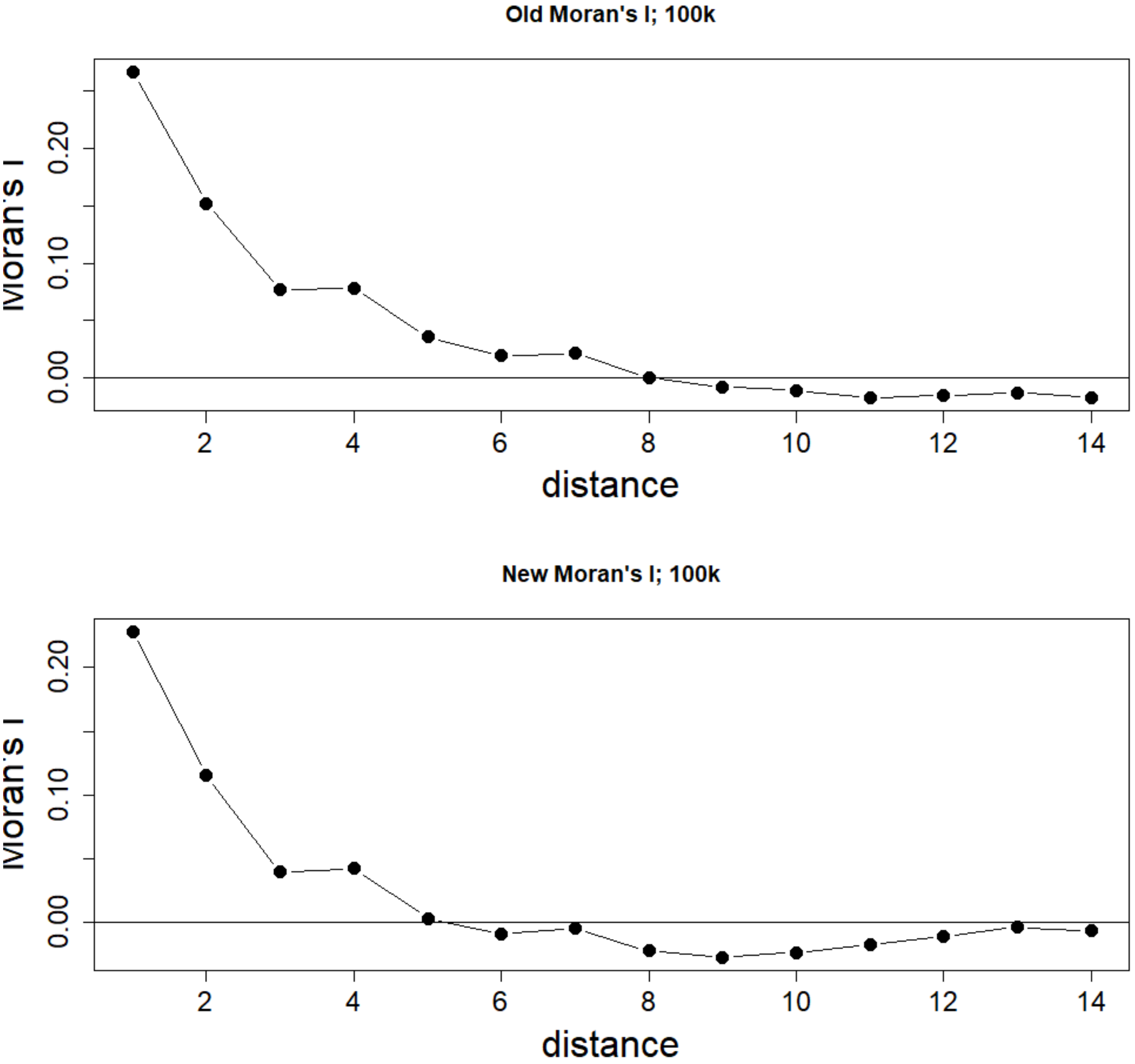


Figure S4.6. Correlogram of Moran’s I for detection-corrected species richness-extent of total PA model. Moran’s I calculated from ANCOVA model (top) and simultaneous autoregressive (SAR) error model (bottom). SAR model was a significantly better fit (according to log likelihood). Model coefficients were qualitatively similar between both models.

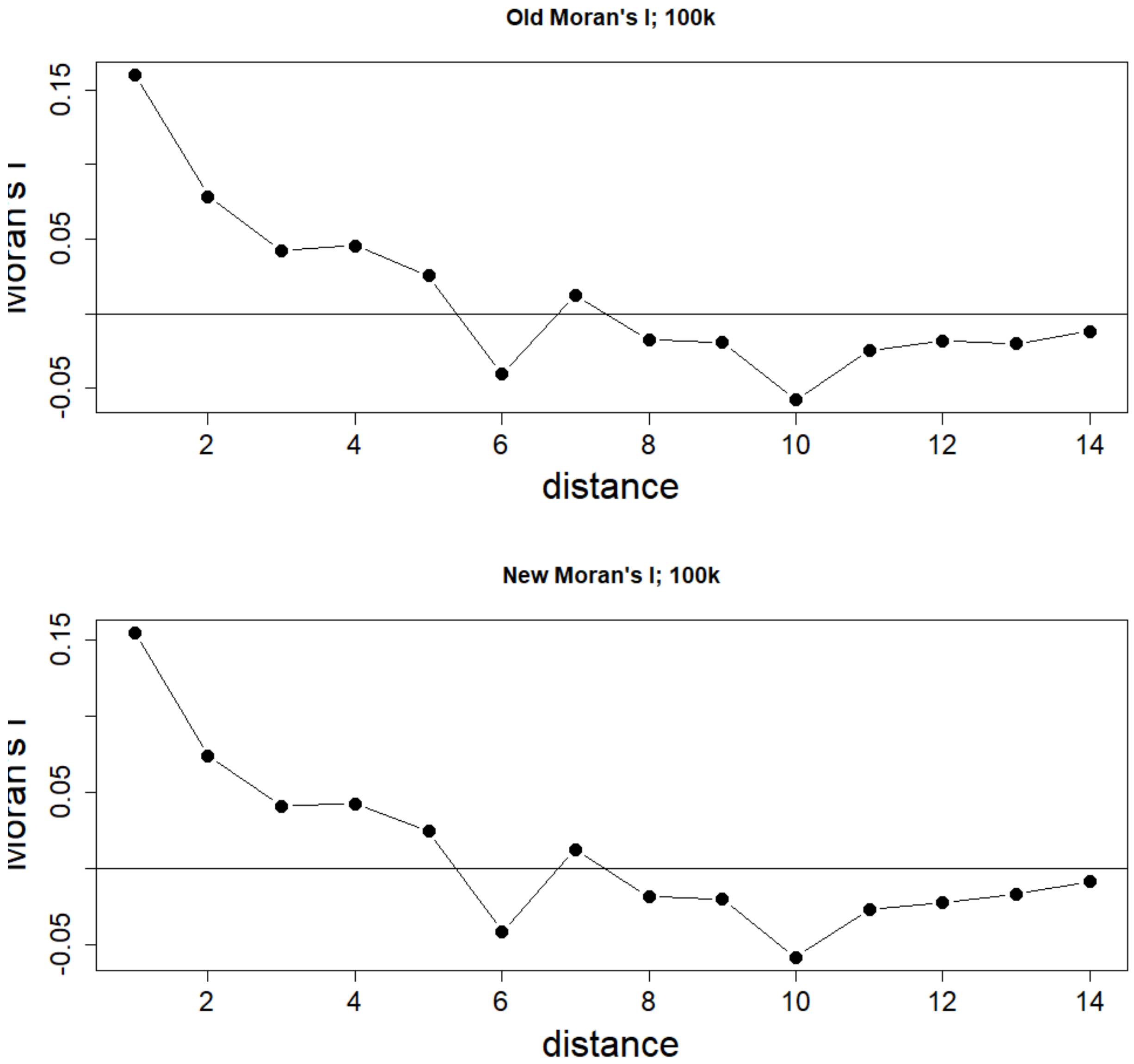
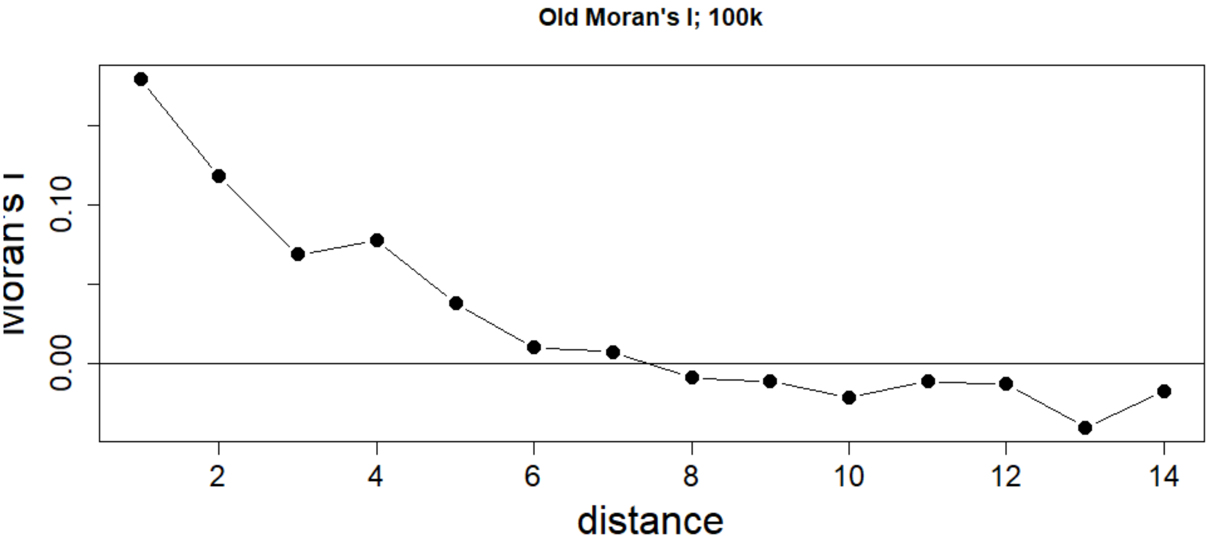


Figure S4.7. Correlogram of Moran's I for observed (non detection-corrected) species richness-extent of total PA model. Moran's I calculated from ANCOVA model (top) and simultaneous autoregressive (SAR) error model (bottom). SAR model was not a significantly better fit (according to log likelihood). Model coefficients were qualitatively similar between both models.



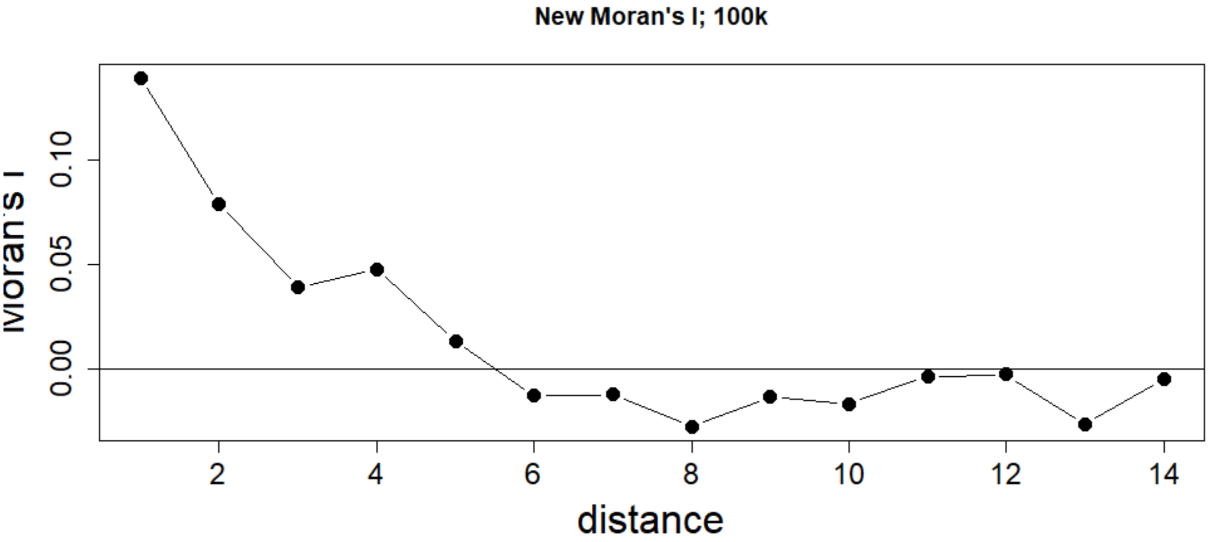


Figure S4.8. Correlogram of Moran's I for detection-corrected species richness-extent of total PA model in high land-use areas. Moran's I calculated from ANCOVA model (top) and simultaneous autoregressive (SAR) error model (bottom). SAR model was a significantly better fit (according to log likelihood). Model coefficients were qualitatively similar between both models.

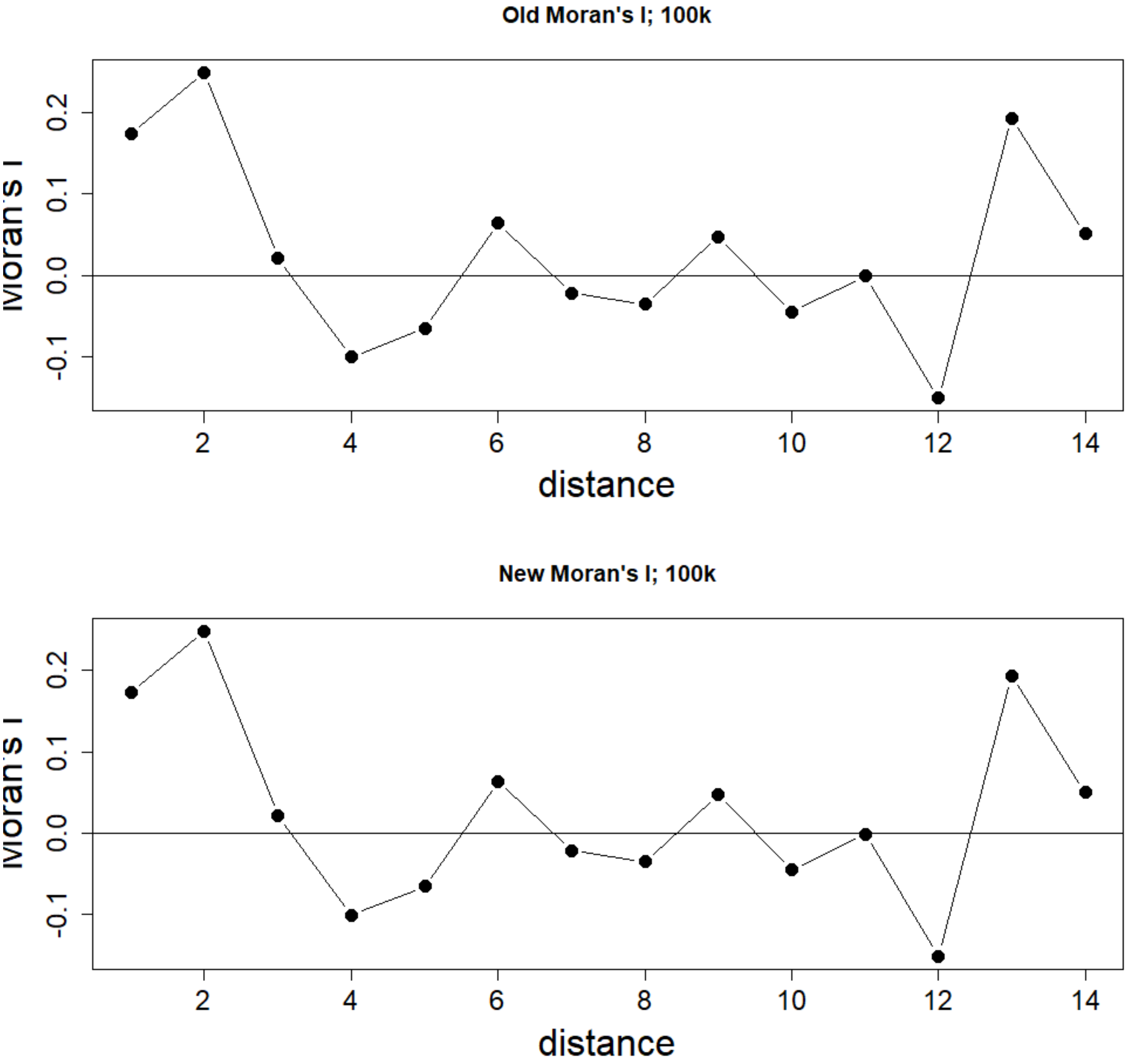


Figure S4.9. Correlogram of Moran's I for observed (non-detection-corrected) species richness-extent of total PA model in high land-use areas. Moran's I calculated ANCOVA model (top) and simultaneous autoregressive (SAR) error model (bottom). SAR model was not a significantly better fit (according to log likelihood). Model coefficients were qualitatively similar between both models.

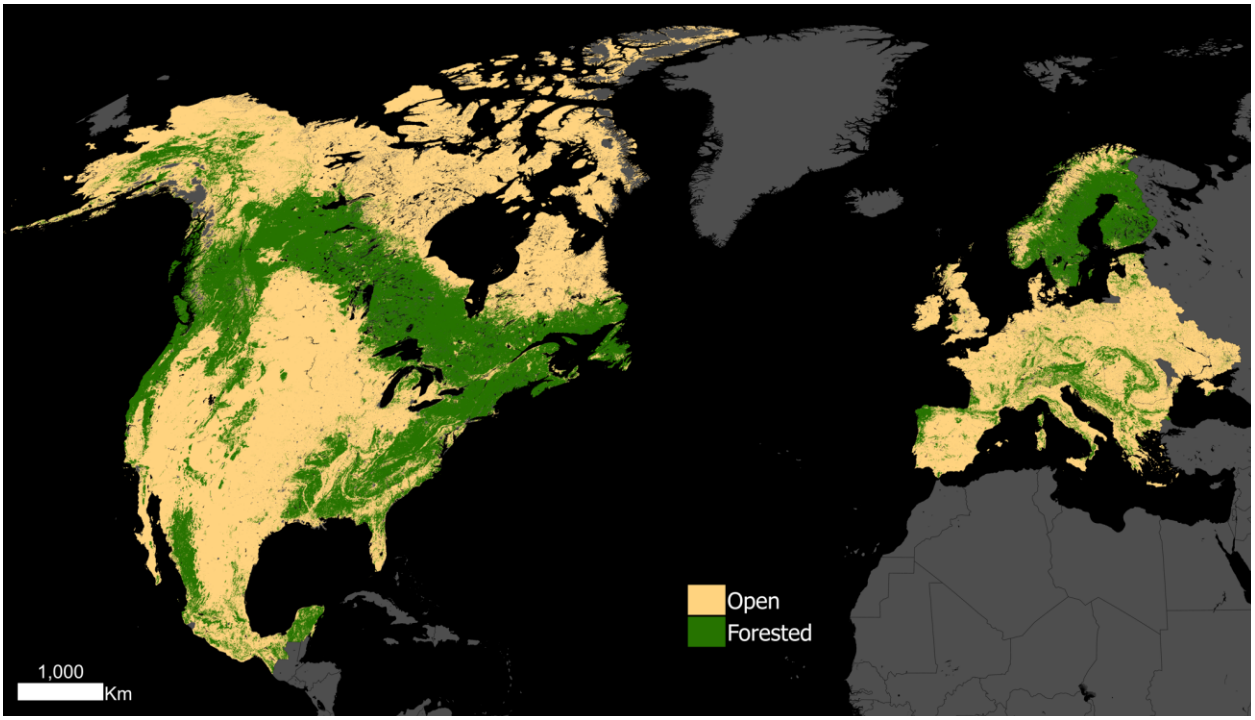


Figure S4.10. Open and forested landcover across North America and Europe, at 1 km X 1 km equal area resolution, derived from USGS GLCC land use land cover classes (See Table S4.11 for groupings). Landcover estimated derived from 1992-1993, between the historic and recent periods.

Supplemental Tables S4.1-4.11

Table S4.1. All estimated model coefficients showing the relationship between total percent of protected area in a landscape and bumblebee extirpation, colonization, change in probability of occupancy, and percent change in detection-corrected species richness models. Posterior means and 95% Bayesian credible intervals are shown for phylogenetic generalized linear mixed models (PGLMM). For analysis of covariance models (ANCOVA), t-values are included as a measure of significance. Generally, coefficients with t-values < -1.96 or > 1.96 are considered statistically significant, these and coefficients where the 95% CI does not overlap zero are in bold text in the table. Variance explained is expressed in terms of marginal R^2 (for PGLMM) and adjusted R^2 (for ANCOVA models).

	Occupancy (PGLMM)		Extirpation (PGLMM)		Colonization (PGLMM)		Detection-corrected richness (ANCOVA)	
	Posterior mean	95% CI	Posterior mean	95% CI	Posterior mean	95% CI	Estimate (SE)	t-value
Intercept	-37.62	-102.05 - 24.14	82.37	-196.07 - 346.5	-160.33	-331.26 - 8.68	**-0.05 (0.01)**	**-3.12**
<u>Base thermal position (TPI) variables</u>								
TPI baseline (1st polynomial)	**-364.76**	**-481.95 - -242.02**	**1632.81**	**942.39 - 2341.64**	**-1015.7**	**-1642.02 - -401.56**	**-1.21 (0.46)**	**-2.65**
TPI baseline (2nd polynomial)	**-423.52**	**-547.81 - -316.35**	**4383.9**	**3352.34 - 5354.89**	**851.43**	**263.95 - 1441.38**	-0.04 (0.5)	-0.09
TPI delta	0.12	-2.3 - 2.63	**39.02**	**24.18 - 54.03**	**49.09**	**34.72 - 64.3**	0 (0.02)	0.2
TPI baseline: TPI delta	**-10.86**	**-14.99 - -6.72**	**74.49**	**48.02 - 100**	10.57	-10.66 - 30.98	-0.03 (0.01)	-1.69
<u>Base land-use (LU) variables</u>								
Historic % human LU	0.19	-1.37 - 1.79	5.72	-2.76 - 14.19	**18.69**	**10.02 - 28**	0 (0.01)	0.32
Change in % human LU	**-2.72**	**-5.32 - -0.18**	3.74	-10.04 - 17.56	**-34.96**	**-50.5 - -19.99**	-0.03 (0.02)	-1.67
Historic LU: Change in LU	1.42	-0.32 - 3.35	5.29	-4.64 - 15.99	**18.18**	**8.29 - 28.08**	0.01 (0.02)	0.61
<u>Direct PA variables</u>								
Total extent PA	**1.99**	**0.49 - 3.36**	**-12.21**	**-19.68 - -4.72**	1.25	-6.37 - 8.9	-0.01 (0.02)	-0.4
Total extent PA: continent	-0.82	-4.45 - 2.79	23.8	-0.32 - 47.28	-9.73	-28.5 - 8.28	-0.1 (0.06)	-1.85

PA interactions with TPI								
Extent PA: change in TPI	**4.08**	**2.35 - 5.77**	**-15.83**	**-24.77 - -7.23**	**26.26**	**16.65 - 35.64**	**0.07 (0.02)**	**3.99**
Extent PA: change in TPI: continent	**-5.03**	**-8.32 - -1.75**	**37.54**	**17.1 - 58.53**	**-52.18**	**-70.2 - -33.95**	-0.04 (0.04)	-1.15
PA interactions with LU								
Extent PA: change in LU	**-1.83**	**-3.66 - -0.02**	1.52	-7.89 - 11.27	**-15.55**	**-25.64 - -5.43**	**-0.04 (0.02)**	**-2.44**
Extent PA: change in LU: continent	**5.49**	**2.2 - 8.72**	-3.88	-21.98 - 14.95	**37.5**	**19.53 - 55.21**	0.06 (0.03)	1.75
Covariates								
Continent (Europe)	**44.04**	**37.85 - 49.54**	**-269.07**	**-326.77 - -207.83**	**168.7**	**132.59 - 206.65**	**0.4 (0.06)**	**7.05**
Sampling	-	-	**-9.96**	**-14.16 - -5.75**	**-32.67**	**-38.77 - -26.5**	-	-
			82.37	-196.07 - 346.5				
Random effect	Variance (95% CI)		Variance (95% CI)		Variance (95% CI)			
Species	250.3	168.5 - 346.4	4501	2279 - 6932	1776	879.4 - 2808		
Model summary								
Effective sampling	5000 - 6042		275.4 - 27500		214.3 - 14035.1		1258	
Variance explained	0.19		0.33		0.21		0.17	

Table S4.2. Estimated model coefficients for the detection-corrected and observed (non-detection-corrected) species richness models. t-values, for analysis of covariance (ANCOVA) models, and z-values, for simultaneous autoregressive error model (SAR error), are included as measures of significance. Generally, coefficients with t-values or z-values < -1.96 or > 1.96 are considered statistically significant, and these are in bold text in the table. Variance explained is expressed in terms of adjusted R^2 (ANCOVA) and Nagelkerke pseudo-R^2 (SAR error).

	Change in detection-corrected richness (ANCOVA)		Change in detection-corrected richness (SAR error)		Change in observed richness (ANCOVA)		Change in observed richness (SAR error)	
	Estimate (SE)	t-value	Estimate (SE)	z-value	Estimate (SE)	t-value	Estimate (SE)	z-value
Intercept	**-0.05 (0.01)**	**-3.12**	-0.04 (0.04)	-1.11	**-0.13 (0.03)**	**-4.78**	**-0.14 (0.03)**	**-4.43**
Base thermal position (TPI) variables								
TPI baseline (1st polynomial)	**-1.21 (0.46)**	**-2.65**	-0.12 (0.66)	-0.18	**-1.21 (0.39)**	**-3.11**	**-1.07 (0.4)**	**-2.68**
TPI baseline (2nd polynomial)	-0.04 (0.5)	-0.09	-0.91 (0.55)	-1.66	-0.18 (0.39)	-0.47	-0.32 (0.38)	-0.83
TPI delta	0 (0.02)	0.2	0.01 (0.03)	0.47	-0.03 (0.04)	-0.82	-0.05 (0.04)	-1.15
TPI baseline: TPI delta	-0.03 (0.01)	-1.69	-0.03 (0.02)	-1.49	-0.02 (0.04)	-0.41	-0.02 (0.04)	-0.45
Base land-use (LU) variables								
Historic % human LU	0 (0.01)	0.32	0 (0.02)	-0.17	0 (0.03)	0.1	-0.01 (0.03)	-0.29
Change in % human LU	-0.03 (0.02)	-1.67	-0.03 (0.02)	-1.32	0.03 (0.03)	0.79	0.03 (0.03)	0.89
Historic LU: Change in LU	0.01 (0.02)	0.61	0.01 (0.02)	0.28	0.01 (0.04)	0.22	0.01 (0.04)	0.2
Direct PA variables								
Total extent PA	-0.01 (0.02)	-0.4	0.01 (0.02)	0.38	0.04 (0.04)	1.15	0.03 (0.04)	0.93
Total extent PA: continent	-0.1 (0.06)	-1.85	-0.07 (0.06)	-1.08	-0.09 (0.08)	-1.04	-0.08 (0.08)	-0.97
PA interactions with TPI								
Extent PA: change in TPI	**0.07 (0.02)**	**3.99**	**0.06 (0.02)**	**2.97**	-0.02 (0.05)	-0.39	-0.03 (0.05)	-0.7
Extent PA: change in TPI: continent	-0.04 (0.04)	-1.15	-0.07 (0.04)	-1.55	0.04 (0.08)	0.54	0.07 (0.08)	0.88
PA interactions with LU								
Extent PA: change in LU	**-0.04 (0.02)**	**-2.44**	**-0.04 (0.02)**	**-2.21**	0.02 (0.03)	0.48	0.02 (0.03)	0.58

Extent PA: change in LU: continent	0.06 (0.03)	1.75	0.05 (0.03)	1.47	-0.06 (0.07)	-0.93	-0.06 (0.07)	-0.96
Covariates								
Continent (Europe)	**0.4 (0.06)**	**7.05**	**0.37 (0.1)**	**3.7**	**0.21 (0.09)**	**2.39**	**0.24 (0.09)**	**2.54**
Model summary								
AIC	1028		989.1		135		136.1	
Variance explained	0.17		0.21		0.13		0.17	
n	1258		1258		310		310	

Table S4.3. All estimated model coefficients showing the relationship between total percent of protected area in a landscape and bumblebee extirpation, colonization, change in probability of occupancy, and percent change in detection-corrected species richness models in human dominated areas (>50% of terrestrial area occupied by human land uses in both time periods). Posterior means and 95% Bayesian credible intervals are shown for phylogenetic generalized linear mixed models (PGLMM). For analysis of covariance (ANCOVA) models, t-values are included as a measure of significance. Generally, coefficients with t-values < -1.96 or > 1.96 are considered statistically significant, these and coefficients where the 95% CI does not overlap zero are in bold text in the table. Variance explained is expressed in terms of marginal R^2 (for PGLMM) and adjusted R^2 (for ANCOVA models).

	Change in probability of occupancy (PGLMM)		Extirpation (PGLMM)		Colonization (PGLMM)		Change in detection-corrected richness (ANCOVA)	
	Posterior mean	95% CI	Posterior mean	95% CI	Posterior mean	95% CI	Estimate (SE)	t-value
Intercept	-36.75	-109.85 - 40.96	39.55	-369.37 - 417.08	**-162.55**	**-305.87 - -17.56**	-0.03 (0.07)	-0.39
<u>Base thermal position (TPI) variables</u>								
TPI baseline (1st polynomial)	**-167.4**	**-286.74 - -43.68**	**1779.7**	**979.39 - 2578.3**	-292.4	-1006.71 - 366.78	-0.62 (0.42)	-1.47
TPI baseline (2nd polynomial)	**-320.8**	**-430.33 - -216.12**	**3275.6**	**2386.96 - 4133.8**	**747.51**	**129.71 - 1398.04**	0.4 (0.42)	0.94
TPI delta	**6.46**	**1.46 - 11.64**	2.37	-30.21 - 35.02	**42.72**	**11.2 - 72.14**	0.02 (0.05)	0.45
TPI baseline: TPI delta	-3.81	-13.01 - 4.92	7.16	-50.22 - 65.18	**-55.47**	**-108.56 - -6.64**	0 (0.03)	-0.07
<u>Base land-use (LU) variables</u>								
Historic % human LU	1.45	-3.37 - 6.31	**34.9**	**4.6 - 66.48**	16.26	-11.99 - 46.61	0.07 (0.06)	1.14
Change in % human LU	0.61	-5.88 - 6.56	-8.3	-49.07 - 29.62	6.83	-32.2 - 43.08	-0.03 (0.05)	-0.74
Historic LU: Change in LU	-1.57	-5.79 - 2.16	**29.9**	**2.88 - 57.88**	0.18	-24.25 - 23.94	-0.02 (0.05)	-0.52
<u>Direct PA variables</u>								
Total extent PA	**7.3**	**2.94 - 11.23**	**-46.47**	**-72.75 - -20.15**	9	-15.84 - 33.44	0.07 (0.05)	1.42
Total extent PA: continent	2.2	-6.1 - 9.35	3.25	-51.96 - 58.29	2.87	-40.19 - 50.03	0.02 (0.11)	0.23
<u>PA interactions with TPI</u>								
Extent PA: change in TPI	**7.4**	**2.36 - 11.89**	**-40.58**	**-71.54 - -9.1**	**43.72**	**13.82 - 73.19**	0.09 (0.05)	1.78

Extent PA: change in TPI: continent	**-10.8**	**-18.92 - -2.76**	**73.57**	**17.63 - 130.36**	**-112.68**	**-163.15 - -60.77**	-0.12 (0.1)	-1.29
PA interactions with LU								
Extent PA: change in LU	**-4.36**	**-7.29 - -1.14**	16.1	-2.68 - 34.76	-12.07	-30.53 - 6.25	**-0.08 (0.03)**	**-2.7**
Extent PA: change in LU: continent	**7.16**	**0.94 - 13.37**	-20.84	-63.76 - 21.35	5.84	-30.32 - 42.52	0.09 (0.07)	1.16
Covariates								
Continent (Europe)	**27.28**	**13.19 - 42.27**	**-196.03**	**-296.13 - -99.48**	**185.39**	**111.05 - 256.8**	0.02 (0.15)	0.13
Sampling	-	-	**-11.69**	**-18.98 - -4.11**	**-42.17**	**-52.23 - -31.75**	-	-
Random effect	Variance (95% CI)		Variance (95% CI)		Variance (95% CI)			
Species	359.6	222.9 - 513.1	9308	4257 - 15239	1008	287.5 - 1973		
Model summary								
Effective sampling	4498 - 5213		720.2 - 20000		652.8 - 14346.2		486	
Variance explained	0.16		0.32		0.18		0.07	

Table S4.4. Estimated model coefficients for the detection-corrected species richness models in human-dominated areas. t-values, for analysis of covariance (ANCOVA) models, and z-values, for simultaneous autoregressive error model (SAR error), are included as measures of significance. Generally, coefficients with t-values or z-values < -1.96 or > 1.96 are considered statistically significant, and these are in bold text in the table. Variance explained is expressed in terms of adjusted R^2 (ANCOVA) and Nagelkerke pseudo-R^2 (SAR error). Observed richness models are not included as they only had 116 observations.

	Change in detection-corrected richness (ANCOVA)		Change in detection-corrected richness (SAR error)	
	Estimate (SE)	t-value	Estimate (SE)	z-value
Intercept	-0.03 (0.07)	-0.39	0.02 (0.08)	0.26
Base thermal position (TPI) variables				
TPI baseline (1st polynomial)	-0.62 (0.42)	-1.47	-0.68 (0.54)	-1.26
TPI baseline (2nd polynomial)	0.4 (0.42)	0.94	0.15 (0.44)	0.35
TPI delta	0.02 (0.05)	0.45	0 (0.06)	0.04
TPI baseline: TPI delta	0 (0.03)	-0.07	0.01 (0.04)	0.21
Base land-use (LU) variables				
Historic % human LU	0.07 (0.06)	1.14	0.02 (0.06)	0.31
Change in % human LU	-0.03 (0.05)	-0.74	-0.04 (0.05)	-0.89
Historic LU: Change in LU	-0.02 (0.05)	-0.52	-0.04 (0.05)	-0.9
Direct PA variables				
Total extent PA	0.07 (0.05)	1.42	0.09 (0.05)	1.75
Total extent PA: continent	0.02 (0.11)	0.23	0.07 (0.11)	0.61
PA interactions with TPI				
Extent PA: change in TPI	0.09 (0.05)	1.78	0.1 (0.05)	1.8
Extent PA: change in TPI: continent	-0.12 (0.1)	-1.29	-0.12 (0.09)	-1.3
PA interactions with LU				
Extent PA: change in LU	**-0.08 (0.03)**	**-2.7**	**-0.09 (0.03)**	**-2.95**
Extent PA: change in LU: continent	0.09 (0.07)	1.16	0.13 (0.07)	1.75
Covariates				
Continent (Europe)	0.02 (0.15)	0.13	0.01 (0.16)	0.04
Model summary				
AIC	434		426.25	
Variance explained	0.07		0.12	
n	486		486	

Table S4.5. All estimated model coefficients showing the relationship between percent of protected area in a landscape and bumblebee extirpation, colonization, change in probability of occupancy, and percent change in detection-corrected species richness models, where protected areas have been split by size (Large >= 400 km^2; Small < 400 km^2). Posterior means and 95% Bayesian credible intervals are shown for phylogenetic generalized linear mixed models (PGLMM). For analysis of covariance models (ANCOVA), t-values are included as a measure of significance. Generally, coefficients with t-values < -1.96 or > 1.96 are considered statistically significant, these and coefficients where the 95% CI does not overlap zero are in bold text in the table. Variance explained is expressed in terms of marginal R2 (for PGLMM) and adjusted R2 (for ANCOVA models).

	Change in probability of occupancy (PGLMM)		Extirpation (PGLMM)		Colonization (PGLMM)		Change in detection-corrected richness (ANCOVA)	
	Posterior mean	95% CI	Posterior mean	95% CI	Posterior mean	95% CI	Estimate (SE)	t-value
Intercept	-36.88	-101.29 - 24.23	82.67	-203.85 - 358.2	**-162.68**	**-325.9 - -2.26**	**-0.05 (0.02)**	**-2.87**
<u>Base thermal position (TPI) variables</u>								
TPI baseline (1st polynomial)	**-412.04**	**-545.75 - -292**	2085.72	1309.35 - 2834.91	**-1344.99**	**-2058.53 - -690.32**	**-1.5 (0.48)**	**-3.12**
TPI baseline (2nd polynomial)	**-400.73**	**-515.55 - -284.18**	4402.53	3487.68 - 5272.8	**975.43**	**388.21 - 1618.45**	-0.05 (0.52)	-0.09
TPI delta	1.38	-1.15 - 3.9	35.71	20.36 - 50.84	**50.18**	**35.45 - 66.15**	0.01 (0.02)	0.43
TPI baseline: TPI delta	**-12.58**	**-16.47 - -8.17**	81.99	56.48 - 110.06	-2.37	-23.65 - 19.39	-0.03 (0.02)	-1.88
<u>Base land-use (LU) variables</u>								
Historic % human LU	-0.74	-2.29 - 0.86	**9.48**	**0.66 - 18.61**	**13.74**	**4.95 - 22.68**	0 (0.01)	0.11
Change in % human LU	-2.44	-5.01 - 0.21	1.22	-13.65 - 16.17	**-34.82**	**-51.05 - -19.38**	-0.03 (0.02)	-1.48
Historic LU: Change in LU	0.04	-1.79 - 1.92	9.76	-0.87 - 21.44	**11.48**	**1.34 - 21.61**	0 (0.02)	-0.08
<u>Direct PA variables</u>								
Extent Large PA	1.54	-0.07 - 2.94	-2.81	-10.78 - 5.14	**12.75**	**4.62 - 21.52**	-0.01 (0.01)	-0.43
Extent Large PA: Europe	**-7.98**	**-11.73 - -4.13**	**48.63**	**20.89 - 76.74**	**-87.16**	**-109.73 - -64.67**	**-0.13 (0.06)**	**-2.13**
Extent Small PA	0.72	-1.22 - 2.59	**-12.47**	**-22.85 - -2.55**	**-14.63**	**-25.07 - -4.36**	-0.01 (0.02)	-0.78
Extent Small PA: Europe	**7.54**	**3.58 - 11.2**	-10.05	-36.14 - 14.74	**96.12**	**73.06 - 120.44**	0.06 (0.05)	1.15
<u>PA interactions with TPI</u>								

Extent Large PA: change in TPI	**2.78**	**1.06 - 4.56**	**-12.03**	**-21.67 - -2.75**	**19.71**	**10.26 - 30.1**	**0.06 (0.02)**	**3.43**
Extent Large PA: change in TPI: Europe	**-3.28**	**-6.85 - -0.07**	**23.14**	**0.53 - 46.04**	**-21.64**	**-40.18 - -4.33**	-0.06 (0.05)	-1.28
Extent Small PA: change in TPI	**5.79**	**3.44 - 8.12**	**-19.74**	**-33.22 - -7.31**	**30.93**	**17.89 - 44.01**	0.04 (0.02)	1.63
Extent Small PA: change in TPI: Europe	**-7.76**	**-11.54 - -4.06**	**36.28**	**12.71 - 59.18**	**-63.94**	**-85.52 - -42.54**	-0.04 (0.04)	-0.96
PA interactions with LU								
Extent Large PA: change in LU	-1.47	-3.49 - 0.46	1.95	-8.66 - 12.65	-3.68	-15.04 - 7.53	-0.01 (0.02)	-0.31
Extent Large PA: change in LU: Europe	-2.33	-5.59 - 0.84	**22.27**	**1.01 - 43.3**	**-18.95**	**-35.91 - -1.72**	-0.06 (0.03)	-1.8
Extent Small PA: change in LU	-1.26	-3.55 - 1.06	-1.07	-13.08 - 12.05	**-19.69**	**-33.08 - -6.28**	**-0.05 (0.02)**	**-2.32**
Extent Small PA: change in LU: Europe	**7.26**	**3.83 - 10.63**	-16.04	-36.38 - 4.5	**59.84**	**39.03 - 80.01**	**0.1 (0.03)**	**3.26**
Covariates								
Continent (Europe)	**41.25**	**35.53 - 47.56**	**-275.68**	**-330.24 - -223.8**	**157.81**	**122.27 - 193.18**	**0.37 (0.06)**	**6.16**
Sampling	-	-	**-10.07**	**-14.38 - -5.71**	**-34.89**	**-41.01 - -28.95**	-	-
Random effect								
Species	249	167.4 - 337.8	4944	2739 - 7426	1603	803.3 - 2457	-	-
Model summary								
Effective sampling	5000 - 6011		326 - 15000		406.2 - 19041.6		1258	
Variance explained	0.19		0.33		0.24		0.18	

Table S4.6. All estimated model coefficients showing the relationship between percent of protected area in a landscape and bumblebee extirpation, colonization, change in probability of occupancy, and percent change in detection-corrected species richness models, where protected areas have been split by IUCN management category (Strict= IUCN category I-II; Less strict= IUCN category III-VI). Posterior means and 95% Bayesian credible intervals are shown for phylogenetic generalized linear mixed models (PGLMM). For analysis of covariance models (ANCOVA), t-values are included as a measure of significance. Generally, coefficients with t-values < -1.96 or > 1.96 are considered statistically significant, these and coefficients where the 95% CI does not overlap zero are in bold text in the table. Variance explained is expressed in terms of marginal R^2 (for PGLMM) and adjusted R^2 (for ANCOVA models).

	Change in probability of occupancy (PGLMM)		Extirpation (PGLMM)		Colonization (PGLMM)		Change in detection-corrected richness (ANCOVA)	
	Posterior mean	95% CI	Posterior mean	95% CI	Posterior mean	95% CI	Estimate (SE)	t-value
Intercept	-36.93	-98 - 28.42	91.67	-185.05 - 383.86	**-174.76**	**-345.5 - -1.04**	**-0.05 (0.02)**	**-3.03**
Base thermal position (TPI) variables								
TPI baseline (1st polynomial)	**-334.68**	**-462.19 - -208.16**	**1491.16**	**744.26 - 2228.27**	**-1433.25**	**-2116.89 - -723.88**	**-1.37 (0.49)**	**-2.79**
TPI baseline (2nd polynomial)	**-424.67**	**-539.82 - -313.59**	**4592.33**	**3656.68 - 5547.45**	**766.39**	**155.02 - 1360.49**	-0.27 (0.5)	-0.54
TPI delta	-0.04	-2.58 - 2.5	**40.85**	**24.94 - 56.06**	**39.36**	**24.98 - 53.69**	0 (0.02)	-0.05
TPI baseline: TPI delta	**-10.85**	**-15.28 - -6.61**	**71.49**	**44.95 - 98.23**	-11.28	-34.76 - 10.35	-0.03 (0.02)	-1.67
Base land-use (LU) variables								
Historic % human LU	0.46	-1.13 - 2.18	4.43	-4.88 - 13.16	**12.63**	**3.91 - 22.23**	-0.01 (0.01)	-0.37
Change in % human LU	-1.61	-4.19 - 0.88	1.61	-12.26 - 15.96	**-20.99**	**-35.44 - -6.15**	-0.02 (0.02)	-0.83
Historic LU: Change in LU	0.94	-0.93 - 2.88	2.64	-9.1 - 13.26	**11.49**	**1.1 - 21.69**	0.01 (0.02)	0.51
Direct PA variables								
Extent Strict PA	**3.61**	**2.07 - 5.16**	**-12.43**	**-20.72 - -4.62**	**9.33**	**1.26 - 17.53**	-0.01 (0.02)	-0.71
Extent Strict PA: Europe	**-7.55**	**-11.27 - -4.16**	20.86	-2.53 - 45.06	**-78.86**	**-99.92 - -59.39**	-0.04 (0.05)	-0.74
Extent Less strict PA	-0.54	-2.02 - 1.03	**-9.92**	**-18.12 - -1.96**	**-13.36**	**-21.85 - -4.93**	-0.01 (0.01)	-0.71
Extent Less strict PA: Europe	-1.26	-4.38 - 1.61	**39.97**	**20.51 - 60.18**	**19.82**	**4.38 - 35.47**	-0.04 (0.04)	-1.11

PA interactions with TPI								
Extent Strict PA: change in TPI	**4.17**	**2.32 - 5.84**	**-10.42**	**-19.91 - -1.24**	**34.1**	**23.71 - 44.79**	**0.08 (0.02)**	**3.83**
Extent Strict PA: change in TPI: Europe	**-5.48**	**-8.82 - -2.16**	-9.85	-30.05 - 12.61	**-32.64**	**-49.93 - -14.9**	**-0.1 (0.05)**	**-2.08**
Extent Less strict PA: change in TPI	0.89	-0.98 - 2.77	**-12.17**	**-22.49 - -2.77**	1.22	-8.3 - 11.37	0.01 (0.02)	0.34
Extent Less strict PA: change in TPI: Europe	-2.12	-4.72 - 0.71	**23.68**	**6.46 - 41.11**	**-22.01**	**-36.8 - -8.16**	0 (0.03)	0.09
PA interactions with LU								
Extent Strict PA: change in LU	-1.55	-3.6 - 0.27	-0.93	-11.27 - 9.62	-20.98	-31.98 - -9.96	-0.03 (0.02)	-1.69
Extent Strict PA: change in LU: Europe	-1.36	-4.59 - 2	-10.96	-31.58 - 9.75	-7.48	-23.82 - 10.03	0 (0.04)	-0.06
Extent Less strict PA: change in LU	0.28	-1.91 - 2.42	-6.32	-18.36 - 4.6	4.09	-7.86 - 16.17	0 (0.02)	-0.05
Extent Less strict PA: change in LU: Europe	1.54	-1.44 - 4.62	17.03	-0.65 - 34.64	13.24	-2.51 - 30.3	-0.01 (0.03)	-0.32
Covariates								
Continent (Europe)	**45.83**	**40.25 - 51.43**	**-273.72**	**-327.85 - -219.83**	**183.07**	**148.59 - 218.74**	**0.37 (0.05)**	**7.81**
Sampling	-	-	**-12.17**	**-16.57 - -7.79**	**-32.52**	**-37.79 - -26.97**	-	-
Random effect								
Species	251.4	165.2 - 340.1	5032	2781 - 7649	1799	960 - 2752	-	-
Model summary								
Effective sampling	4525 - 5284		271.7 - 19165.1		399.4 - 15089.8		1258	
Variance explained	0.19		0.33		0.25		0.17	

Table S4.7. All estimated model coefficients showing the relationship between percent of protected area in a landscape and bumblebee extirpation, colonization, change in probability of occupancy, and percent change in detection-corrected species richness models, where protected areas have been split by size (Large >= 400 km^2; Small < 400 km^2) and IUCN management category (Strict= IUCN category I-II; Less strict= IUCN category III-VI). Posterior means and 95% Bayesian credible intervals are shown for phylogenetic generalized linear mixed models (PGLMM). For analysis of covariance models (ANCOVA), t-values are included as a measure of significance. Generally, coefficients with t-values < -1.96 or > 1.96 are considered statistically significant, these and coefficients where the 95% CI does not overlap zero are in bold text in the table. Variance explained is expressed in terms of marginal R^2 (for PGLMM) and adjusted R^2 (for ANCOVA models).

	Change in probability of occupancy (PGLMM)		Extirpation (PGLMM)		Colonization (PGLMM)		Change in detection-corrected richness (ANCOVA)	
	Posterior mean	95% CI	Posterior mean	95% CI	Posterior mean	95% CI	Estimate (SE)	t-value
Intercept	-36.58	-106.44 - 23.39	93.14	-212.65 - 392.5	**-184.27**	**-354.49 - -15.69**	**-0.05 (0.02)**	**-3.06**
Base thermal position (TPI) variables								
TPI baseline (1st polynomial)	**-392.3**	**-525.26 - -251.14**	**1912.27**	**1061.76 - 2743.14**	**-1795.44**	**-2547.41 - -1017.95**	**-1.57 (0.52)**	**-3.03**
TPI baseline (2nd polynomial)	**-437.75**	**-553.29 - -319.36**	**4808.7**	**3914.52 - 5643.35**	**915.51**	**299.47 - 1552.81**	-0.25 (0.53)	-0.47
TPI delta	-0.13	-2.64 - 2.53	**38.65**	**22.38 - 54.44**	**29.84**	**15.45 - 44.11**	-0.01 (0.02)	-0.28
TPI baseline: TPI delta	**-14.13**	**-18.31 - -9.48**	**80.69**	**52.49 - 109.92**	**-31.91**	**-56.16 - -7.96**	-0.03 (0.02)	-1.94
Base land-use (LU) variables								
Historic % human LU	-0.22	-1.88 - 1.42	**10.97**	**1.46 - 20.83**	**14.64**	**5.35 - 24.12**	0 (0.01)	-0.34
Change in % human LU	-1.83	-4.34 - 0.8	-0.95	-15.98 - 14.56	**-28.19**	**-43.2 - -12.78**	-0.01 (0.02)	-0.82
Historic LU: Change in LU	0.42	-1.5 - 2.47	4.56	-7.27 - 16.83	**15.3**	**4.29 - 25.87**	0.01 (0.02)	0.35
Direct PA variables								
Extent Strict and Large PA	**2.42**	**0.89 - 3.98**	-8.35	-16.83 - 0.43	**13.54**	**4.49 - 21.58**	0 (0.02)	-0.11
Extent Strict and Large PA: continent	**-9.55**	**-13.26 - -5.63**	**37.09**	**10.65 - 64.83**	**-110.26**	**-133.25 - -87.61**	**-0.24 (0.07)**	**-3.44**

Extent Strict and Small PA	-0.16	-1.85 - 1.41	4.95	-3.85 - 14.33	-4.99	-13.99 - 4.26	-0.01 (0.02)	-0.76
Extent Strict and Small PA: continent	2.94	-0.75 - 6.83	-25.03	-54.36 - 3.81	**28.44**	**8.19 - 49.1**	**0.19 (0.06)**	**2.88**
Extent Less strict and Large PA	-1.11	-2.52 - 0.5	5.67	-2.71 - 13.88	1.77	-6.35 - 10.31	-0.01 (0.01)	-0.65
Extent Less strict and Large PA: continent	0.85	-2.84 - 4.28	0.61	-24.19 - 25.76	2.57	-16.12 - 21.46	0.03 (0.05)	0.48
Extent Less strict and Small PA	1.48	-0.69 - 3.57	**-26.6**	**-38.61 - -14.55**	-17.71	-29.8 - -6.19	-0.02 (0.02)	-0.83
Extent Less strict and Small PA: continent	**-4.5**	**-8.24 - -0.85**	**64.3**	**37.92 - 91.05**	3.04	-17 - 22.48	**-0.12 (0.05)**	**-2.24**
PA interactions with TPI								
Extent Strict/Large PA: change in TPI	**2.98**	**1.19 - 4.93**	-7	-18 - 3.09	**26.34**	**15.64 - 37.21**	**0.05 (0.02)**	**2.47**
Extent Strict/Large PA: change in TPI: continent	1.72	-2.42 - 5.91	**-45.7**	**-71.95 - -17.82**	**25.92**	**4.48 - 48.09**	0.07 (0.06)	1.05
Extent Strict/Small PA: change in TPI	2.18	-0.03 - 4.46	-1.73	-14.27 - 10.84	**22.84**	**10.13 - 35.79**	0.03 (0.02)	1.52
Extent Strict/Small PA: change in TPI: continent	**-9.08**	**-12.66 - -5.38**	**30.58**	**6.08 - 54.43**	**-71.16**	**-92.45 - -50.89**	**-0.17 (0.05)**	**-3.46**
Extent Less strict/Large PA: change in TPI	1.07	-0.73 - 2.91	**-20.52**	**-30.84 - -10.51**	-6.37	-16.24 - 3.36	0.02 (0.02)	0.95
Extent Less strict/Large PA: change in TPI: continent	1.07	-2.13 - 4.06	**32.86**	**12.97 - 53.57**	4.67	-11.17 - 21.24	-0.02 (0.04)	-0.4
Extent Less strict/Small PA: change in TPI	**3.74**	**1.06 - 6.38**	**-18.07**	**-33.4 - -2.79**	**21.05**	**6.21 - 35.67**	0 (0.02)	0.13
Extent Less strict/Small PA: change in TPI: continent	**-6.86**	**-10.44 - -3.24**	22.29	-0.46 - 45.45	**-33.84**	**-53.53 - -14.28**	0.03 (0.04)	0.76
PA interactions with LU								
Extent Strict/Large PA: change in LU	**-2.44**	**-4.5 - -0.4**	6.56	-5.05 - 18.07	-6.76	-18.83 - 4.86	-0.01 (0.02)	-0.33
Extent Strict/Large PA: change in LU: continent	3.24	-0.53 - 7.28	**-48.68**	**-73.61 - -21.29**	**21.15**	**0.44 - 41.73**	0.04 (0.04)	0.9

Extent Strict/Small PA: change in LU	-0.33	-2.29 - 1.62	-9.36	-20.86 - 1.6	**-23.62**	**-35.53 - -12.01**	**-0.04 (0.02)**	**-2.22**
Extent Strict/Small PA: change in LU: continent	-2.96	-6.05 - 0.12	**27.41**	**6.61 - 49.18**	-9.65	-26.63 - 7.55	-0.03 (0.03)	-0.8
Extent Less strict/Large PA: change in LU	0.14	-1.91 - 2.27	-5.16	-17.25 - 6.14	10.1	-1.67 - 22.24	0.01 (0.02)	0.89
Extent Less strict/Large PA: change in LU: continent	0.63	-2.27 - 3.79	**20.82**	**0.81 - 40.61**	-7.07	-23.83 - 9.32	-0.02 (0.03)	-0.73
Extent Less strict/Small PA: change in LU	-0.02	-2.48 - 2.39	0.44	-12.83 - 14.34	-3.56	-17.53 - 10.54	-0.02 (0.02)	-1.05
Extent Less strict/Small PA: change in LU: continent	0.59	-2.5 - 3.8	5.7	-13.48 - 26.21	12.63	-5.29 - 30.34	0.01 (0.03)	0.5
Covariates								
Continent (Europe)	**44.63**	**38.95 - 50.62**	**-288.26**	**-339.57 - -238.68**	**185.98**	**151.82 - 218.97**	**0.39 (0.05)**	**7.58**
Sampling	-	-	**-11.96**	**-16.42 - -7.28**	**-34**	**-39.02 - -29.07**	-	-
Random effect								
Species	247.7	165.9 - 338.1	5735	3347 - 8483	1745	941 - 2629	-	-
Model summary								
Effective sampling	4487 - 5399		746.8 - 20000		1020 - 19326		1258	
Variance explained	0.2		0.34		0.27		0.19	

Table S4.8. Estimated model coefficients of the reference model (no PA variables) for extirpation, colonization, change in probability of occupancy, and percent change in detection-corrected species richness models. Posterior means and 95% Bayesian credible intervals are shown for phylogenetic generalized linear mixed models (PGLMM). For analysis of covariance models (ANCOVA), t-values are included as a measure of significance. Generally, coefficients with t-values < -1.96 or > 1.96 are considered statistically significant, these and coefficients where the 95% CI does not overlap zero are in bold text in the table. Variance explained is expressed in terms of marginal R^2 (for PGLMM) and adjusted R^2 (for ANCOVA models).

	Change in probability of occupancy (PGLMM)		Extirpation (PGLMM)		Colonization (PGLMM)		Change in detection-corrected richness (ANCOVA)	
	Posterior mean	95% CI	Posterior mean	95% CI	Posterior mean	95% CI	Estimate (SE)	t-value
Intercept	-37.21	-101 - 25.23	94.44	-176.74 - 357.71	-163.61	-339.96 - 11.9	**-0.04 (0.01)**	**-2.63**
<u>Base thermal position (TPI) variables</u>								
TPI baseline (1st polynomial)	**-416.5**	**-536.6 - -302.8**	**1892.12**	**1180.05 - 2605.81**	**-1476.53**	**-2125.12 - - 819.77**	**-1.15 (0.44)**	**-2.6**
TPI baseline (2nd polynomial)	**-419.2**	**-529.7 - -307**	**4103.01**	**3027.46 - 5135.64**	**782.37**	**223.49 - 1359.51**	-0.02 (0.48)	-0.03
TPI delta	**-2.52**	**-4.6 - -0.35**	**51.24**	**35.56 - 67.16**	**19.89**	**8.6 - 30.93**	0 (0.02)	-0.04
TPI baseline: TPI delta	**-12.48**	**-16.45 - -8.52**	**78.71**	**52.29 - 105.9**	-8.19	-27.85 - 9.89	**-0.04 (0.01)**	**-2.65**
<u>Base land-use (LU) variables</u>								
Historic % human LU	-0.01	-1.5 - 1.47	6.5	-1.28 - 14.22	**18.64**	**10.2 - 27.27**	0.02 (0.01)	1.69
Change in % human LU	-1.03	-3.4 - 1.36	1.55	-10.71 - 13.91	**-19.12**	**-31.94 - -6.59**	-0.03 (0.02)	-1.62
Historic LU: Change in LU	1.67	-0.15 - 3.38	3.64	-6 - 13.43	**21.45**	**11.21 - 31.26**	0.02 (0.02)	1.17
<u>Covariates</u>								
Continent (Europe)	**44.5**	**39.21 - 50.22**	**-250.4**	**-312.05 - - 188.44**	**151.38**	**108.18 - 191.62**	**0.32 (0.04)**	**7.69**
Sampling	-	-	**-11.08**	**-15.29 - -6.79**	**-27.3**	**-34 - -20.12**	-	-
<u>Random effect</u>	<u>Variance (95% CI)</u>		<u>Variance (95% CI)</u>		<u>Variance (95% CI)</u>			
Species	252	167.8 - 344.7	4244	2021 - 6844	1853	753.3 - 3004	-	-
<u>Model summary</u>								

Effective sampling	5000 - 5000	80.83 - 11954.21	92.08 - 12294.28	1258
Variance explained	0.18	0.32	0.19	0.1536

Table S4.9. Model coefficients of the relationships between extent of PA and historic community-averaged thermal position, change in community-averaged thermal position, historic human-dominated land-use, and change in human-dominated land-use. t-values are included as a measure of significance. Generally, coefficients with t-values < -1.96 or > 1.96 are considered statistically significant, and are in bold text in the table. Variance explained is adjusted R^2.

	Estimate	SE	t-value
Historic community averaged thermal position			
(Intercept)	**44.1**	**4.1**	**10.8**
continent (Europe)	**-33.2**	**9.98**	**-3.32**
Historic TPI	**-51.5**	**6.01**	**-8.57**
Historic TPI: continent	**75.2**	**15.5**	**4.84**
Change in community averaged thermal position			
(Intercept)	**4.21**	**0.952**	**4.42**
continent (Europe)	**16.5**	**3.78**	**4.37**
Change in TPI	**485**	**81.5**	**5.96**
Change in TPI: continent	-270	168	-1.61
Historic extent of human-dominated land-use			
(Intercept)	**16**	**0.672**	**23.8**
continent (Europe)	**8.39**	**1.47**	**5.73**
Historic extent of LU	**-16.8**	**1.29**	**-13**
Historic extent of LU: continent	**20.3**	**2.65**	**7.68**
Change in extent of human-dominated land-use			
(Intercept)	**9.31**	**0.489**	**19**
continent (Europe)	**15.9**	**1.23**	**13**
Change in LU	-2.54	4.8	-0.529
Change in LU: continent	-5.41	9.61	-0.563

Table S4.10. Model coefficients of the relationships between extent of PA and extent of open and forested land cover types. t-values are included as a measure of significance. Generally, coefficients with t-values < -1.96 or > 1.96 are considered statistically significant, and are in bold text in the table. Variance explained is adjusted R^2.

	Estimate	SE	t-value
Percent open landcover			
(Intercept)	**12.8**	**0.862**	**14.9**
continent (Europe)	2.58	2.09	1.24
% open landcover	**-0.0616**	**0.0126**	**-4.89**
% open landcover: continent	**0.229**	**0.0299**	**7.65**
Percent forested landcover			
(Intercept)	**7.18**	**0.677**	**10.6**
continent (Europe)	**24.5**	**1.45**	**16.9**
% forested landcover	**0.0504**	**0.0127**	**3.98**
% forested landcover: continent	**-0.211**	**0.0296**	**-7.14**

Table S4.11. Open and forested land cover groupings, grouped from the USGS Global Land Cover Characterization data product (DOI: 10.5066/F7GB230D). Landcover estimated derived from 1992-1993, between the historic and recent period.

General landcover type	GLCC USGS LULC Description
Forested	Deciduous Broadleaf Forest
Forested	Deciduous Needleleaf Forest
Forested	Evergreen Broadleaf Forest
Forested	Evergreen Needleleaf Forest
Forested	Mixed Forest
Open	Urban and Built-Up Land
Open	Dryland Cropland and Pasture
Open	Irrigated Cropland and Pasture
Open	Mixed Dryland/Irrigated Cropland and Pasture
Open	Cropland/Grassland Mosaic
Open	Cropland/Woodland Mosaic
Open	Grassland
Open	Shrubland
Open	Mixed Shrubland/Grassland
Open	Savanna
Open	Herbaceous Wetland
Open	Wooded Wetland
Open	Barren or Sparsely Vegetated
Open	Herbaceous Tundra
Open	Wooded Tundra
Open	Mixed Tundra
Open	Bare Ground Tundra
NA	Water Bodies
NA	Snow or Ice

Chapter 5: Synthesis and conclusion

Declines in bumblebees have long been linked to climate change and land-use change, but the precise mechanisms are ultimately complex and often unclear (Potts et al. 2010; Goulson et al. 2015). Consequently, understanding how best to mitigate or offset their effects has remained incomplete. In this thesis, I contributed to filling both of these gaps, and in doing so, revealed some particular mechanisms through which climate change and land-use change appear to cause species' ranges to decline or expand. These findings suggest some implications for conservation of bumblebees, and for other species threatened by climate and land-use change.

Mechanisms of climate change-related decline

The development and testing of the climatic position index, which measures shifts in environmental variables relative to species' estimated tolerances, indicates new avenues to understand how climate change acts. Measuring thermal or precipitation position as opposed to mean, maximum, or minimum variables better captures the danger of extreme events produced by climate change, and this additional layer of biological relevance improves the prediction of local biodiversity change (Soroye et al. 2020). This finding supports a growing body of evidence from across bumblebees and other insects noting the importance of climate change and extremes (Kerr et al. 2015; Erenler et al. 2020; Filazzola et al. 2021; Halsch et al. 2021; Raven & Wagner 2021). Independently, this climatic position index has been demonstrated to relate to variation in abundance of terrestrial vertebrate populations

(Williams & Newbold 2021). Moving from the population level to the individual, there are several potential mechanisms through which temperatures and temperature extremes may cause bumblebee declines (e.g., direct mortality, reduction in fecundity, associated reduction in plant foraging resources, etc., see Rasmont & Iserbyt 2012; Woodard 2017; Filazzola et al. 2021, for a deeper exploration). More local-scale manipulative studies and/or laboratory-based experiments could further explore the relative importance of these specific mechanisms.

In Chapter 2, I find that while there is a consistent influence of increasing temperatures driving biodiversity change in bumblebees, changing precipitation played only a minor role (Soroye et al. 2020). Yet, variation in precipitation (especially drought) has been observed to influence bumblebees and other insect communities (e.g., Barnett & Facey 2016; Woodard 2017; Filazzola et al. 2021), especially at very local-scales. In a local-scale study looking at long-term changes in subalpine bumblebee abundance, Ogilvie et al. (2017) found that precipitation was related to changes in bumblebee abundance, but only indirectly through modification of floral resources. Thomson (2016) found similar results in coastal California. I find that local-scale effects do not scale up to affect population persistence or colonization at broader scales, likely reflecting strong variation in water availability in many North American and European landscapes. However, my work did not focus intensively on the most water-limited regions, such as the xeric environments of the southwest US or Spain, and it is possible that sub-regional effects of water limitation are sufficiently important to affect the conservation of some species in those environments. New data collection and research here would be valuable for testing such a possibility, although interestingly, independent work with global terrestrial vertebrates also finds that thermal position typically relates to biodiversity change more strongly and consistently than precipitation position (Williams & Newbold 2021).

Mixed effects of land-use

While land-use change is not as consistently important as climate change in these analyses, there is no doubt that habitat loss and land-use intensification (including pesticide use) have driven declines for many species in many different instances (Goulson et al. 2008; Winfree et al. 2009; Potts et al. 2015; Wagner 2020; Raven & Wagner 2021). In Chapter 3, I used a relatively coarse measure of land use (the percentage of terrestrial area in a 100 km by 100 km quadrat that is covered in cropland, grazing, or urban landcover), which may have been too coarse to detect very local effects of land use. Additionally, the historic period which I use here (1900-1974) may be too recent to have captured the greatest historical land-use changes at a many sites (Daskalova et al. 2020). More likely however, is that land-use change (especially landscape-level land-use change) can result in both positive and negative outcomes for bumblebees in different situations.

As pollinators that depend on floral resources, human-dominated landscapes can sometimes foster an equal or greater diversity of bumblebees than some natural landscapes (McFrederick & LeBuhn 2006; Winfree et al. 2007; Baldock et al. 2015). Properly managed croplands and grazing lands can also harbor diverse pollinator communities (Tscharntke et al. 2005; Carvell et al. 2015, 2017; Redhead et al. 2016), and human land-use in forests (e.g., seismic lines) may aid bumblebee dispersal at the northern limits of their range (Nelson et al.

2021). But while land use can be managed to benefit pollinators, it does not benefit all species equally. Human-dominated landscapes can encourage “weedy”, generalist species (McFrederick & LeBuhn 2006), and may not be compatible with many rare, native species or bees with specific requirements (Winfree et al. 2007). Consistent with this, in Chapter 3 I found that biotic homogenization among bumblebee communities is driven by the lower regional presence of rare (range-restricted) species and the increasing ubiquity of common or ruderal species. When managing landscapes for pollinators, monitoring community composition is important, as measurements of species richness change can mislead discussion of conservation priorities.

Climate change and land use interactions: a double-edged sword

There is a growing appreciation for the importance of interactions between climate change and land-use change, especially for planning long-term conservation strategies (Titeux et al. 2017; Leclère et al. 2020). In Chapter 3, I find that both positive and negative interactions appear to drive trends in historic bumblebee biodiversity. Among possible mechanisms of antagonistic interaction, conversion towards more human-dominated land use could destroy microrefugia within landscapes, or further modify local climatic conditions (Kearney et al. 2009; Williams & Newbold 2020). Deliberate approaches to management can help mitigate against effects of climate change (Papanikolaou et al. 2017), although when climate change and land-use change tend to favor the same species, this can drive homogenization of communities (Frishkoff et al. 2016; Newbold et al. 2019). Prestele et al. (2021) recently projected future bumblebee distributions using species distribution models across a series of dynamic climate and land use scenarios. They found that different future land use scenarios have the potential to either amplify or offset the effects of changing climate, especially in more optimistic climate change scenarios (e.g., RCP 2.6 vs RCP 4.5 or RPC 8.5). Yet, the capacity of land use to offset climate change effects decreased under more severe climate change scenarios, and different species benefited under different potential land-use regimes (Prestele et al. 2021). However, the land-use scenario that was best able to offset the effects of climate change (even for rarer species) in Prestele et al.'s (2021) analysis was also the least equitable from a socioeconomic perspective (Riahi et al. 2017). When considering how best to modify land-use management to suit conservation ends for the future, it will be imperative to consider the human and socioeconomic elements as well (e.g., Aichi Target 11 of the Convention on Biological Diversity).

Next steps

A major challenge in determining biodiversity responses to climate change and land-use change is that historical data collections are typically very limited for most taxa (Cardoso et al. 2011; Cardoso & Leather 2019; Eisenhauer et al. 2019). While the datasets I use here are the most comprehensive sources of historic and present bumblebee occurrence data yet published, the data remain relatively sparse for some regions and species. In my analyses, I aggregated data spatially and temporally, which is commonly required in research at these extents to reduce the effects of spatiotemporal variability in sampling (Blackburn & Gaston 2002). Tests at different spatial resolutions revealed that trends are robust to these data aggregation measures (Chapter 2, Soroye et al. 2020). Variation in sampling effort across species, regions, and through time can all influence the detection and estimation of biodiversity change, and necessitate the use of methods that account for this variation. In every chapter, I restricted analyses to species that were relatively well-sampled across both time periods, and used multiple measures of biodiversity change which accounted for variable spatiotemporal sampling in different ways (Soroye et al. 2021). The result is an analysis that is robust to sampling variability and that does not rely on a single modelling framework. Encouraging the collection (e.g., through community science) and digitization of occurrence data can help further improve the picture of bumblebee biodiversity trends (Montgomery et al. 2020).

My thesis documents biodiversity trends and relationships across North America and Europe, but it is not clear how well these may represent trends on other continents. Animal pollination literature is heavily biased towards North America and Europe, with about 50% of all the literature focusing on these regions (Millard et al. 2019). Available biodiversity data is correspondingly low outside these continents, especially for historic periods (Wagner 2020). Given this limitation, my study area is the largest extent realistically possible. While there is little reason to believe that climate change would influence species through a different mechanism outside of North America and Europe, the biomes, positionality relative to realized climatic tolerance limit, and histories of land-use are sufficiently different on other continents that I would not confidently generalize results to other continents. More data from these regions is necessary to robustly estimate trends and narrow down the potential mechanisms driving change.

Conclusions for conservation

My finding of the importance of climate change, and specifically temperature extremes, as a primary driver of bumblebee declines has several implications for conservation (Chapter 2; Soroye et al. 2020). At a local scale, microrefugia (e.g., soil, tree holes, epiphytes, and vegetation) create microclimates that can reduce the duration and severity of extreme heat events experienced by small animals (Scheffers et al. 2014). Given the observed sensitivity of bumblebees to thermal extremes, protecting these microrefugia within landscapes or prioritising their creation during restoration, will likely offer significant benefits (Suggitt et al. 2018). For pollinators like bumblebees that benefit from the addition of nectar resources in small urban pollinator gardens and greenspaces (Tew et al. 2021), encouraging the addition or maintenance of microrefugia in these places can likely provide benefits as well, with the added advantage of engaging people and communities into conservation. As the negative effects of extreme events from climate change become more apparent, considering specific adaptation strategies for extreme weather and climatic extremes will become critical for management of species and protected areas (Maxwell et al. 2019; Walls et al. 2019).

In Chapter 3, I find that the effects of increasing thermal position appear exacerbated in regions where there was a historically high amount of human-dominated land-use. This suggests that pristine, natural areas have a particular value for bumblebee conservation in the context of climate change. Prioritising even small patches (see Chapter 4) of natural habitat within landscapes may help species in the face of warming and extremes. I found that not all interactions between climate change and land-use are negative, supporting a large literature that shows the importance and benefits of managing human-dominated landscapes for pollinators (Lozier 2017). A considered approach to land management (e.g., maintaining hedgerows in agricultural fields, maintaining patches of flowers which bloom spring to fall), could potentially help to offset future effects of climate change (Prestele et al. 2021), although we will need to ensure we are protecting rare and specialist species as well as common generalists.

Increasing the amount of protected area in a landscape reduces extinction risk for species, although the mechanism behind this result is not clear (Chapter 4). Work in previous chapters suggests that protected areas protect microrefugia in landscapes and historically pristine habitats, which both contribute to better outcomes for bumblebee biodiversity. The location and placement of protected areas matters – while they may not be able to eliminate the pressures on species within their boundaries and biodiversity inside them may continue to decline (Wagner 2020), the landscapes surrounding them benefit from their presence. While in Chapter 4 I did not test the effect of Other Effective Area-Based Conservation Measures (OECMs) specifically, I suspect that these will provide some benefit to bumblebees as well, given that the benefits of protected area were unrelated to IUCN management category.

Looking forward

Climate change has driven substantial shifts in global biodiversity, and this trend is expected to continue and accelerate without decisive global action (Urban 2015; Trisos et al. 2020). While trends in land-use are more variable, the potential extent of its negative interactions with climate change is also expected to increase over time (Mantyka-Pringle et al.

2012; Newbold 2018). By incorporating mechanisms into predictive models of global change risk, we can better predict changes in novel and shifting environments (Urban et al. 2016). My thesis lays the groundwork for future work which looks forward, predicting future trends in bumblebee biodiversity and species responses based on potential scenarios of climate, land use, and protection. The climatic position index developed and tested here has significant potential for improving prediction of climate change-related risk in other taxa as well, relevant for the approximately 1 million other species potentially facing extinction across the globe (IPBES 2019). In fact, a recent global analysis found that the climatic position index was able to predict variability in population abundance across over 4,000 terrestrial vertebrates, and that thermal position strongly influenced populations responses to human land use (Williams & Newbold 2021).

The effects that unmitigated climate change and land-use change could have on species (including humanity) are widespread in their scope, insidious in their pervasiveness, and terrifying in their extent (Cardinale et al. 2012; Scheffers et al. 2016; IPBES 2019). Significant decline in the diversity of pollinators, including bumblebees, would be a particularly staggering loss given their inspiring beauty and irreplaceable role in ecosystems globally (Potts et al. 2010; IPBES 2016). While the threats are severe and the stakes of global conservation efforts are high, the situation is not hopeless. Indeed, strategies exist to address the worst challenges. This thesis identified and tested mechanisms for how climate change and land-use change contribute to species declines in some areas and range expansions in others, and adds to a large and growing literature dedicated to providing solutions to the biodiversity crisis (Soulé 1985). Reversing recent anthropogenically-induced biodiversity loss is possible with united global action and integrated, ambitious, and equitable conservation strategies (Mace et al. 2018; Leclère et al. 2020; Sala et al. 2021). And while small, individual actions will not replace the need for international organization, they can make a difference nonetheless (Kawahara et al. 2021). Producing research that informs ecological understanding and conservation decision-making is critical for reaching a bright future for conservation (Mace et al. 2018; Salafsky et al. 2019), but just as important is mobilizing research, translating it into practice (Cook et al. 2013; Kadykalo et al. 2021) and engaging the public in conservation (Díaz et al. 2015; Reid et al. 2017; Jeanson et al. 2019).

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[Dr David Parenti:] We get the grant, we study the problem, we propose solutions. If they listen, they listen. If they don't, it still makes for great research. What we publish on this is gonna get a lot of attention.

[Howard "Bunny" Colvin:] From who?

[Dr David Parenti:] From other researchers, academics.

[Howard "Bunny" Colvin:] Academics?! What, they gonn' study your study? [chuckles and shakes head] When do this shit change?

- The Wire, Season 5, episode 13: *Final Grades*.