Modeling Future Climate Change Impacts on North American Bumblebee Distributions

Catherine Sirois-Delisle

Thesis submitted to the
Faculty of Graduate and Postdoctoral Studies
in partial fulfillment of the requirements for the degree of

Master of Environmental Sustainability

uOttawa

University of Ottawa
Ottawa, Ontario, Canada
December 2017

ABSTRACT

Climate change is an important contributor to the modification of many bumblebee species' range boundaries. It was linked to widespread decline at the southern edge of their distribution and to their inability to colonize new areas at the northern edge. Additionally, bumblebee decline is aggravated by other anthropogenic threats like land use change, agricultural practices and pathogen spillover. Predicted consequences are numerous, and could lead to severe economic and ecological impacts on human populations. A species-specific assessment of potential climate change impacts on North American bumblebees, based on the most recent global change scenarios as used in the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC), was done for the first time. Using a massive dataset of georeferenced bumblebee observations and general circulation models, a series of species distribution models explore the impact of different climate change scenarios on climatically suitable areas of 30 bumblebee species. Northward range shifts occur in most bumblebee species' projected climatic niches, revealing potential hotspots – places projected to be climatically suitable to multiple species – under future climate scenarios. Areas where species are likely to be lost in the absence of intervention are substantial, particularly in eastern parts of the continent. Models showed significant contractions of current ranges even under the very optimistic scenario in which all species disperse at 10 km/year. Results indicate that managed relocation as well as habitat management should be considered as a conservation strategy for some species. This research serves as a foundation for broader discussion and research in a nascent research area. It may assist in establishing localities where first conservation efforts could be directed for vulnerable bumblebee species.

RÉSUMÉ

Les changements climatiques contribuent de manière importante à la modification des limites de répartition des bourdons. Ils sont liés au déclin généralisé à la limite sud de leur distribution et à leur incapacité de coloniser de nouveaux endroits à la limite nord. En outre, le déclin des bourdons est aggravé par diverses menaces anthropiques comme la transformation de l’habitat, les pratiques agricoles et les pathogènes importés par les bourdons domestiques. Les conséquences attendues sont nombreuses et peuvent entraîner de graves répercussions économiques et écologiques sur les populations humaines. Une étude à grande échelle spécifique à l’espèce qui évalue les impacts potentiels des changements climatiques sur les bourdons en Amérique du Nord, basée sur les scénarios des changements climatiques les plus récents tels qu’utilisés dans le cinquième Rapport d’évaluation du Groupe d’experts intergouvernemental sur l’évolution du climat (GIEC), a été réalisée pour la première fois. En utilisant un ensemble de données massif d'observations géoréférencées de bourdons et des modèles de circulation générale, une série de modèles de distribution explorent l'impact de différents scénarios de changements climatiques sur des zones climatiques tolérées par 30 espèces de bourdons. Un mouvement vers le nord de la niche climatique de la majorité des espèces est observé, ce qui révèle des endroits potentiellement importants pour multiples espèces de bourdons dans le futur. Les zones où les espèces sont susceptibles d’être perdues en absence d’intervention sont importantes, particulièrement dans la partie est du continent. Les modèles démontrent une réduction significative des zones de répartition actuelles même pour le scénario optimiste dans lequel le taux de dispersion était de 10 km/année. Les résultats indiquent que la migration assistée, accompagnée de

la gestion de l'habitat, devrait être considérée comme stratégie de conservation pour certaines espèces. Cette recherche servira de base à une discussion et à une investigation plus vastes dans un domaine de recherche naissant. Elle peut aider à établir des localités où les premiers efforts de conservation pourraient être dirigés pour les espèces de bourdons vulnérables.

ACKNOWLEDGEMENTS

I would like to thank my thesis supervisor, Dr. Jeremy Kerr, of the Biology department at the University of Ottawa. He was truly exceptional at listening to my ideas while steering me in the right direction, and continuously provided me with thoughts and ideas that were invaluable to the development of this thesis. His professional advice and support during this past year provided me with instrumental experiences as I continue my studies. I am *extremely* grateful and feel privileged to have had the opportunity to work with Dr. Kerr.

I would also like to thank the examiners of this thesis, Heather Kharouba and Jessica Forrest, for their helpful comments on the proposal of this research. I am thankful to the University of Ottawa and Dr. Kerr for funding this project. Thank you to past and present lab members for their help and who made the lab a pleasant place to work.

Finally, I would like to express my gratitude towards my family and best friends Claire Sirois, Jean Claude Delisle, Philippe Bergeron, Valérie Sirois-Delisle and Caroline Lemay-Martel, for their endless support and encouragement, but most of all, for their persistent confidence in my ability to accomplish this degree.

Thank you.

Catherine Sirois-Delisle

Table of Contents

List of Figures

Main Text

Figure 6: Overlays across future projections of all species and RCP scenarios likely to (a) gain suitable range for multiple species by 2070, and (b) lose multiple species by 2070.

Figure 7: Predictive accuracy of maxent models using the Area Under the Receiver Operator Characteristic Curve (AUC) (Hanley & McNeil 1982), and the True Skill Statistic (TSS) (Allouche et al. 2006). AUC > 0.75 and TSS > 0.4 indicate meaningful models that can be used for analysis.

Appendix

Figure A1: Species richness maps of North America for 30 bumblebee species under the RCP scenarios (a) RCP2.6, (b) RCP4.5, (c) RCP6.0, and (d) RCP8.5 in year 2050, assuming unlimited dispersal ability.

Figure A2: Species richness maps of North America for 30 bumblebee species under the RCP scenarios (a) RCP2.6, (b) RCP4.5, (c) RCP6.0, and (d) RCP8.5 in year 2070, assuming unlimited dispersal ability.

Figure A3: Species richness maps of North America for 30 bumblebee species under the RCP scenarios (a) RCP2.6, (b) RCP4.5, (c) RCP6.0, and (d) RCP8.5 in year 2050, assuming a high dispersal rate (10 km/year).

Figure A4: Species richness maps of North America for 30 bumblebee species under the RCP scenarios (a) RCP2.6, (b) RCP4.5, (c) RCP6.0, and (d) RCP8.5 in year 2070, assuming a high dispersal rate (10 km/year).

Figure A5: Species richness maps of North America for 30 bumblebee species under the RCP scenarios (a) RCP2.6, (b) RCP4.5, (c) RCP6.0, and (d) RCP8.5 in year 2050, assuming a dispersal rate of 0 km/year.

Figure A6: Species richness maps of North America for 30 bumblebee species under the RCP scenarios (a) RCP2.6, (b) RCP4.5, (c) RCP6.0, and (d) RCP8.5 in year 2070, assuming a dispersal rate of 0 km/year.

Introduction

Global climate change affects large-scale species distributions and range boundaries (Thomas 2010; Schweiger et al. 2012; IPCC 2014). Most biological communities are now exposed to new combinations of climatic conditions since pre-industrial years (Schweiger et al. 2010; IPCC 2014). High proportions of species-level extinctions are estimated in the future due to such changes (Thomas et al. 2006; Ceballos et al. 2017). Alternatively, depending on physiological traits and external drivers of change, species may tolerate novel climatic conditions through adaptations, shift their distribution to track tolerated climatic conditions (Chen et al. 2011), or exhibit phenological shifts (Polgar et al. 2013; Kharouba et al. 2014).

Certain pollinator groups are shifting latitudinally or along elevation gradients as a response to the gradually changing climate (Parmesan et al. 1999; Chen et al. 2011). Range-shifts allow species to remain in climatically suitable areas, reducing exposure to conditions that they cannot tolerate (Parmesan et al. 1999; Chen et al. 2011). Some species appear unable to track environmentally suitable habitats due to low dispersal abilities (Davis & Shaw 2001; Hulme 2005), increasing risks of local extinction under climate change (Loarie et al. 2009; Leroux et al. 2013). Pollinators affected by this phenomenon include butterfly (Bedford et al. 2012; Devictor et al. 2012) and bumblebee species across Europe and North America.

Numerous bumblebee species failed to track climate change at the leading latitudinal limit on a continental scale, which may reflect their inability to colonize new areas in response to global warming (Kerr et al. 2015). Local extinctions at the southern range limit may be linked to increased probabilities of extreme temperature events. Bumblebees are sensitive to these extremes (Ploquin et al. 2013; Herrera et al. 2014), particularly events of heat waves and drought, which can cause local extinctions and modify bumblebee communities (Rasmont & Iserbyt 2012). They may already be exposed to conditions outside their climatic niche (Rasmont et al. 2015).

Bumblebees are vulnerable to several threats that can interact, aggravating the ongoing reductions in range and abundance (IPBES 2016). These include anthropogenic factors like habitat loss and fragmentation (Goulson et al. 2008; Williams & Osborne 2009; Hatten et al. 2013), pesticides (e.g. Goulson et al., 2015), parasites and pathogen spillover (Cameron et al. 2011; Meeus et al. 2011; Fürst et al. 2014), and climate change (Potts et al. 2010; Rasmont & Iserbyt 2012; Ploquin et al. 2013; Herrera et al. 2014).

Main managed responses discussed in the literature to accelerate bumblebees' poleward shifts under climate change include landscape management (Hatfield et al. 2012; Goulson et al. 2015) and managed relocation (Kerr et al. 2015; Rasmont et al. 2015). Traditional conservation focused on the former, preventing habitat destruction and/or restoring habitats to maximize population sizes (Hatfield et al. 2012). Considering bumblebees' general inability to expand their geographical ranges poleward and into cool areas that have warmed, landscape management efforts are likely insufficient (Thomas et al. 2004; Parmesan 2006; McLachlan et al. 2007).

Species geographical range limits can be distinct from the limits of their tolerances to environmental conditions and consequent capacity to persist in particular localities (Hutchinson 1957). The ability to predict range limits, and how these relate to niche limits across continuous environments over time, is basic to understand species-specific range shifts in response to climate change (Lee-Yaw et al. 2016; Searcy & Shaffer 2016). Niche limits often constrain range limits, which causes fitness and suitability to decline beyond range limits (Hargreaves et al. 2014; Lee-Yaw et al. 2016). When limits do not coincide, dispersal is key for range-shifts to occur, and is an important factor in determining the position of range vs. niche limits (Hargreaves et al. 2014).

Range limit changes do not necessarily reflect changes in niche limits; low dispersal under climate change can create mismatches between species' range limits and climatically suitable areas (Holt et al. 2005; Hargreaves & Eckert 2014; Hargreaves et al. 2014). Broad-scale environmental changes generate a directional change to either expand or contract species' distributions over time (Hargreaves et al. 2014). At the leading range edge, dispersal can limit range expansion (Svenning et al. 2008), while at the trailing edge, it is the rate of mortality that governs changes from source to sink populations (Jump et al. 2009). If the trailing edge retracts while the leading edge is stable, the ratio of extinction to colonization increases, causing the overall realised range to shrink (Parmesan et al. 1999). Net extinction rates decrease if range limits track niche limits where the climate is increasingly suitable (Thomas 2011). Many species' survival therefore depends on their capacity to track climate change (Menéndez et al. 2006; Hoegh-Guldberg et al. 2008; Devictor et al. 2012).

High dispersal capacity is linked to the ability to track suitable conditions (Devictor et al. 2012). Bumblebees' dispersal ability corresponds to the distance that mated queens can travel to establish a new colony (Goulson 2010). Different bumblebee species have distinct dispersal abilities (Darvill 2007) but species-specific dispersal abilities remain ambiguous or unknown. Dispersal was estimated to peak at 1 km (Bowers 1985), but long distance dispersal events, of unknown frequency and scale, are possible (Goulson 2010). Recent estimates suggest dispersal abilities of 3 km for *B. pascuorum* queens, 5 km for *B. lapidarius* (Lepais et al. 2010), and 4 km for *B. moderatus* (Owen et al. 2012). The invasive species *Bombus terrestris* dispersed 10 km per year after being introduced in parts of Tasmania (Stout & Goulson 2000). *B. impatiens* also expanded its range in eastern Canada but the dispersal rate is unknown (Sheffield et al. 2003). Natural expansions since the last ice age, the decline of other species previously occupying the niche and introductions outside the natural range may contribute to bumblebees' observed range expansions (Ratti & Colla 2010; Owen et al. 2012).

Pollinator decline, including numerous bumblebee species, is expected to impair crop production, compromising ecosystem stability and human welfare (IPBES 2016). Bumblebees are important pollinators of native plant species, particularly in temperate and high-elevation regions, and are associated with vegetation abundance and diversity (Michener 2000; Klein et al. 2007). Furthermore, bumblebees play a crucial role in the pollination of multibillion-dollar crops (Potts et al. 2010; Cameron et al. 2011) due to their tolerance of a wide range of environmental conditions relative to other bees, and their buzz pollination abilities (Tuell & Isaacs 2010).

Considering the importance of bumblebees' ecological services, it is of paramount importance to explore bumblebee species' responses to the rapidly changing climate (Potts et al. 2010; Cameron et al. 2011). Therefore, I asked: how are bumblebee species' climatically suitable range projected to change under different future climate scenarios and dispersal abilities? Additionally, are there potential hotspots for the conservation of North American bumblebee species under different climate change scenarios? I generated a series of species distribution models (SDMs) using a massive dataset of georeferenced bumblebee observations (Kerr et al. 2015) and general circulation models (Hijmans et al. 2005). Distribution models can provide insight into species' performance in new areas based on the projected movement of their climatic niche limits (Lee-Yaw et al. 2016). Species richness maps were produced for different climate change scenarios and dispersal outcomes. Study results support previous findings regarding potentially drastic range losses at the trailing edge of several species as well as their inability to expand under climate change. Results highlight the need for prioritizing discussions on managed relocation, and establishing landscape management in areas where range losses are most likely, to halt potentially drastic range contractions.

Design and Methodology

Study Area and Bumblebee Data

The study area is the North American continent (~24 230 000 km^2). Primary bumblebee data included 324,502 observations (See Appendix A for list of data contributors). Georeferenced observations of years 1960 to 1990 inclusively were extracted. Records with incomplete information for species identification, locality or year, or inaccurate georeferenced points, and duplicate records, were removed. Points less than 2500m from shoreline were moved to the closest point on the coast. Georeferencing data from GeoNames (http://geonames.org; Creative Commons Attribution 3.0 License) were used for GBIF points lacking geographical coordinates. A total of 19,753 records for 31 bumblebee species were extracted (Figure 1). Clusters of observations can cause the model to be overfit, which leads to predicted ranges conforming too narrowly to areas where the species has been observed, an effect that can deceptively increase model performance statistics (Veloz 2009; Hijmans 2012; Boria et al. 2014). To address this issue, presence points were spatially rarefied based on climate heterogeneity to decrease the possibility for sampling bias and autocorrelation (Brown 2014). Two heterogeneity classes with minimum distance set to 10 km, and maximum to 15 km were used (classification type set to “Natural breaks”) (Penado et al. 2016). The rarefied dataset holds 10,628 records for 31 North American bumblebee species (See Appendix B for the list of species), sampled from 1960 to 1990, inclusively.

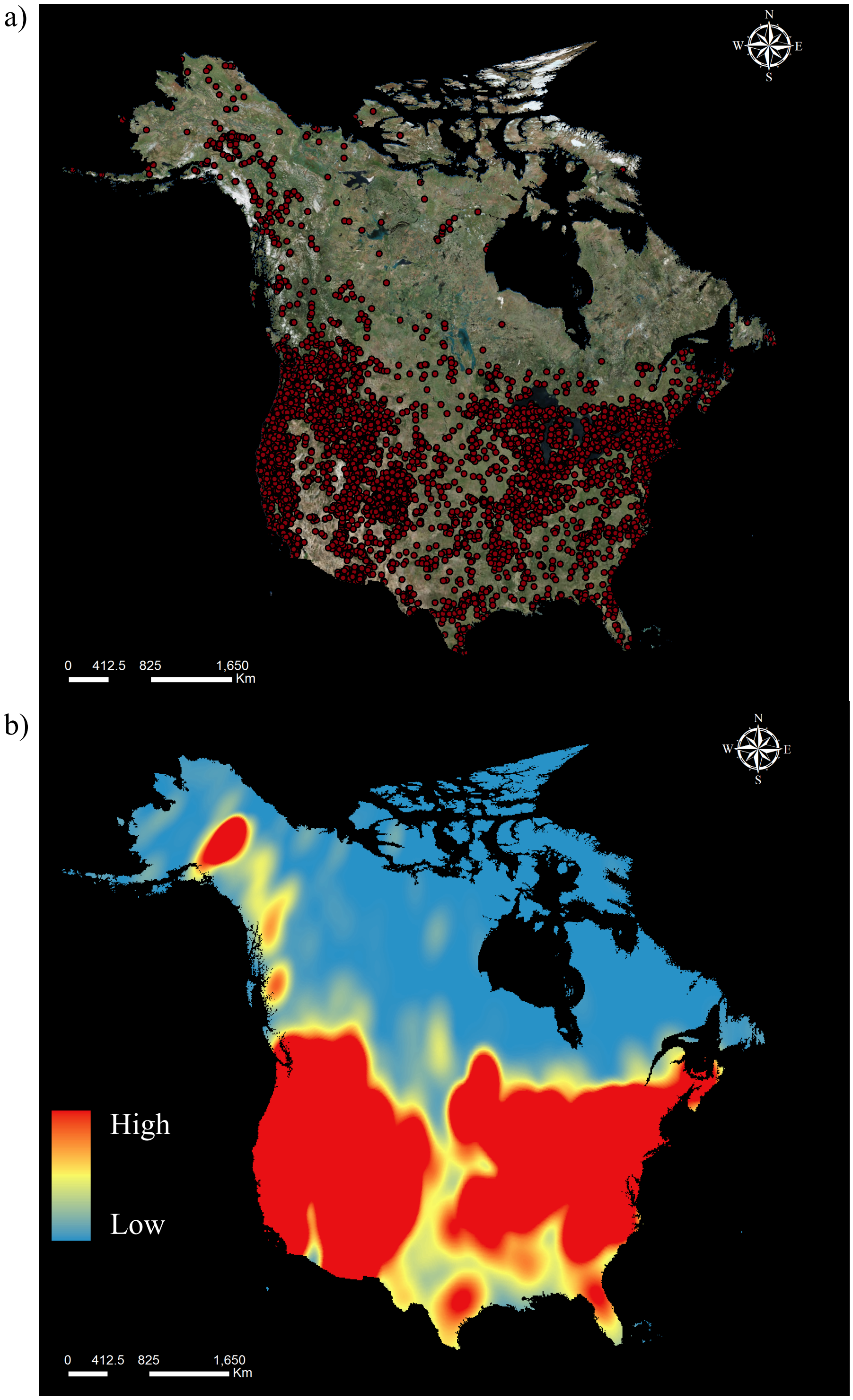

Figure 1: Dataset of georeferenced records for 31 bumblebee species sampled in North America between 1960 and 1990, represented by (a) observation points and (b) a heatmap of relative sampling densities.

Climate Data

Current climate data at 5 arc-minutes resolution were downloaded at http://www.worldclim.org (Hijmans et al. 2005). 19 bioclimatic variables were considered for this analysis. These data originate mainly from Environment Canada and NOAA's National Climatic Data Center (NCDC). All climate data were generated using ANUSPLIN modeling software except for temperature and precipitation seasonality, which correspond to the standard deviation of monthly values, expressed as a percentage of the mean for those estimates (Hijmans et al. 2005).

Four bioclimatic variables were selected for distribution modeling of bumblebees: annual mean temperature (Bioclim1), temperature seasonality (Bioclim4), annual precipitation (Bioclim12), and precipitation seasonality (Bioclim15). These environmental characteristics are ecologically significant for bumblebees (Rasmont et al. 2015) that measure different aspects of climate that minimizes multicollinearity, a recommended approach for variable selection (Merow et al. 2013). These variables have been applied to SDMs of bumblebee species in the past (Casey et al. 2015; Rasmont et al. 2015; Penado et al. 2016). Annual mean temperature and annual precipitation are among the most representative of climate data since they are not derived from other variables (Brown 2014).

General Circulation Models (GCMs) at 5 arc-minutes resolution were used as future climate data (Hijmans et al. 2005). GCMs predict climatic conditions based on underlying physical processes and changing atmospheric CO_2 concentrations. Four GCMs by major institutes recognized by the IPCC report were used, for future years 2050 (average of 2041 to 2060) and 2070 (average of 2061 to 2080). Selected GCMs are the GISS-E2-R model from the NASA Goddard Institute for Space Sciences, the HadGEM2-AO model from the Meteorological Office Hadley Centre, the MIROC5 model from the University of Tokyo Center for Climate System Research, and the CCSM4 model from the National Center for Atmospheric Research.

The four Representative Concentration Pathways (RCPs), developed in the IPCC Fifth Assessment Report (IPCC 2014) were used as future potential climate change outcomes (IPCC 2014). RCPs represent different trajectories of atmospheric greenhouse gas (GHG) concentration. Economic activity, climate policy, technological developments and sociological factors like population size and lifestyle are elements that affect each scenario. GHG concentration peaks between 2010 and 2020 for RCP2.6, in 2040 for RCP4.5, in 2080 for RCP6.0, or rise continuously to 2100 for RCP8.5. According to the most recent IPCC report (2014), temperature rise for most optimistic scenario (RCP2.6) is *likely* to be between 0.3 – 1.7°C by 2100, compared to pre-industrial temperatures (1850 – 1900). This scenario includes the adoption of stringent climate policy and mitigation measures. RCP4.5 projects a rise of 1.1 – 2.6°C (*likely* below 2.0°C), also achieved through the adoption of new climate policies. A rise of 1.4 – 3.1°C for RCP6.0 or of 2.6 – 4.8°C for the most pessimistic scenario (RCP8.5) are projected if no climate mitigation measures are adopted (IPCC 2014). Across all scenarios, it is *very likely* that hot temperature extremes will be longer lasting and more frequent, while cold extremes will be less prevalent throughout most terrestrial habitats. Precipitation patterns are projected to change drastically across all scenarios. For RCP8.5, temperatures are likely to increase toward high latitudes, the equatorial pacific, and mid-latitude wet regions, and decrease under mid-latitude and subtropical dry regions (IPCC 2014). The most recent climate scenarios as published in IPCC (2014) were used for the first time to explain large-scale distribution of bees.

Modeling Current and Future Suitable Ranges

Current and future species-specific distributions were projected using four climatic variables (annual mean temperature, temperature seasonality, annual precipitation, and precipitation seasonality) in maxent models. Maxent was downloaded at http://www.cs.princeton.edu/~schapire/maxent (Phillips et al. 2006). Maxent compares conditions at presence and background points – localities where the modeled species has not been sampled – and estimates the best probability distribution using the concept of maximum entropy (Phillips et al. 2006). It is an appropriate approach for niche modeling with presence-only data (Hällfors et al. 2016; Searcy & Shaffer 2016) and has been used to model bumblebee distribution in previous work (Kadoya et al. 2009; Koch & Strange 2009; Cameron et al. 2011; Herrera et al. 2014; Pradervand et al. 2014; Casey et al. 2015; Penado et al. 2016).

A conservative approach was applied throughout the modeling process, due to uncertainty in future climate change and data limitations. Species-specific bias files (minimum convex polygons) were used to decrease the probability of including suitable but uncolonised localities in the model which can lead to commission errors (Anderson & Raza 2010; Barbet-Massin et al. 2012). Models were replicated using 10-fold cross-validation to assess model fit and uncertainties in spatial predictions (Merow et al. 2013). Limitations of this validation method include the potential spatial correlation between folds, which can overestimate model performance and underestimate the standard error of predictions (Anderson & Raza 2010). The default regularization multiplier was used, such as most published maxent models on bumblebee species (Kadoya et al. 2009; Koch & Strange 2009; Casey et al. 2015). This value accommodates a group of species within a wide range of environmental conditions (Elith et al. 2006). Clamping was used, setting values outside the training data within projections to the maximum training range. This is useful for conservatively projecting into the future since bumblebees' survival in future novel climatic conditions is unknown. The logistic output format was chosen to obtain a relative probability of occurrence and compare models for several species.

Dispersal was integrated into models. Since information about dispersal abilities of bumblebee queens in the spring is sparse, three different dispersal rates were investigated. Low dispersal was assumed to be negligible, where only retractions from currently suitable ranges are possible, as inferred for the majority of surveyed species at their northern range limit (Kerr et al. 2015). High dispersal was set to 10 km per year, which corresponds to the largest recorded dispersal rate to the best of my knowledge (Stout & Goulson 2000; Goulson 2010). Unlimited dispersal maps were also produced to reveal changes in the position of species' climatic niche, regardless of dispersal ability (Rasmont et al. 2015).

Mapping Suitable Range Changes

Species-specific maps containing logistic probabilities of occurrence were averaged across GCMs, for each RCP scenario. Binary presence-absence maps were created using the probability of occurrence threshold that maximized the True Skill Statistic (TSS). Maps were summed across all species for four RCPs, three dispersal scenarios, and two time periods to generate a total of 24 species richness maps. Changes in species' suitable range across North America were plotted using R statistical software.

Differences between current suitable range and future scenarios revealed areas that may gain or lose multiple species, further examined using land-use data. Richness changes were assessed within current agricultural areas specifically. Land use data as of year 2016 were downloaded from the History Database of the Global Environment (HYDE) at http://themasites.pbl.nl/tridion/en/themasites/hyde (Goldewijk et al. 2011). The HYDE dataset combines satellite data and statistics of world population, cropland and pasture in 5 arc-minutes resolution maps.

Predictive Accuracy

Using multiple measures of model evaluation is recommended, especially with presence-only data (Hernandez et al. 2006). Common methods include the Area Under the Receiver Operator Characteristic Curve (AUC) (Hanley & McNeil 1982), and the True Skill Statistic (TSS) (Allouche et al. 2006). The threshold independent AUC is calculated by maxent. If AUC < 0.75, model predictions are not meaningful and cannot be interpreted (Elith et al. 2006). AUC > 0.75 was considered acceptable, 0.8-0.9, good, and 0.9-1, very good, in terms of how well the model can explain present distribution (Swets 1988). TSS is threshold dependent, as it is based on binary presence-absence maps. The threshold that yields the highest TSS was selected to produce binary maps (Allouche et al. 2006). The formula to calculate TSS is:

$$(\text{TSS} = \text{sensitivity} + \text{specificity} - 1),$$

where sensitivity corresponds to the true positive rate and specificity is the true negative function (Pearson 2008), considering that maxent models the absences. TSS greater or equal to 0.4 was considered better than random (Landis & Koch 1997). TSS was shown to be a reliable measure of predictive ability (Allouche et al. 2006) since it does not depend on the size of the validation dataset like other statistics (Lobo et al. 2010).

Results

Evaluating Bumblebee Range Changes

The scale of climatically suitable range changes differed between species, time periods, and dispersal assumptions (See Appendix C for all species richness maps). Climate scenarios linked to greater GHG emissions usually generated more severe range losses than scenarios linked to climate mitigation policies and decreased emissions. The discrepancy of range changes between different RCPs was more significant in 2070; mean standard deviation in suitable range changes doubled from 2050 to 2070 under all three dispersal scenarios.

Comparisons of current and projected suitable range (TSS > 0.4 and AUC > 0.75) revealed statistically significant (alpha = 0.5) expansions for about half of modeled species by 2050 when dispersal and colonization capacities were assumed to be unlimited (Figure 2). Between 0 – 13% of species expanded in suitable range when dispersal was closer to realistic abilities (10 km per year) by 2050, and 0 – 30% by 2070. In the latter scenario, as many as seven species expanded only under the one climate scenario (RCP2.6) (Figure 3). Only *Bombus pensylvanicus* expands in all RCPs in both 2050 and 2070 under this dispersal assumption. Expansions were not possible under the assumption of no dispersal (Figure 4).

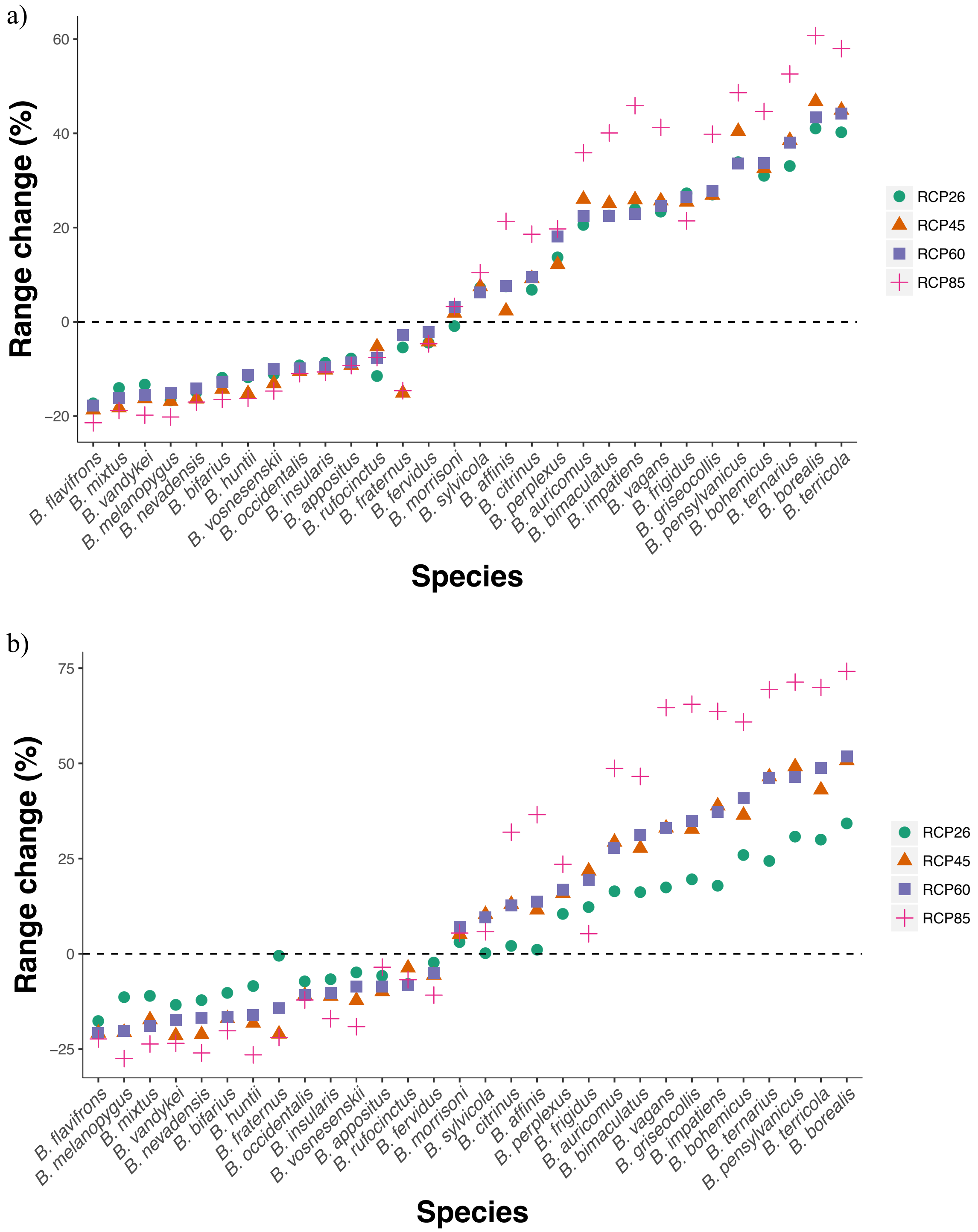

Figure 2: Range changes based on maxent models for 30 North American bumblebee species between baseline (1960-1990) and future projections of years (a) 2050 and (b) 2070, assuming unlimited dispersal ability. Results were ordered by range change (%) under the RCP6.0 scenario.

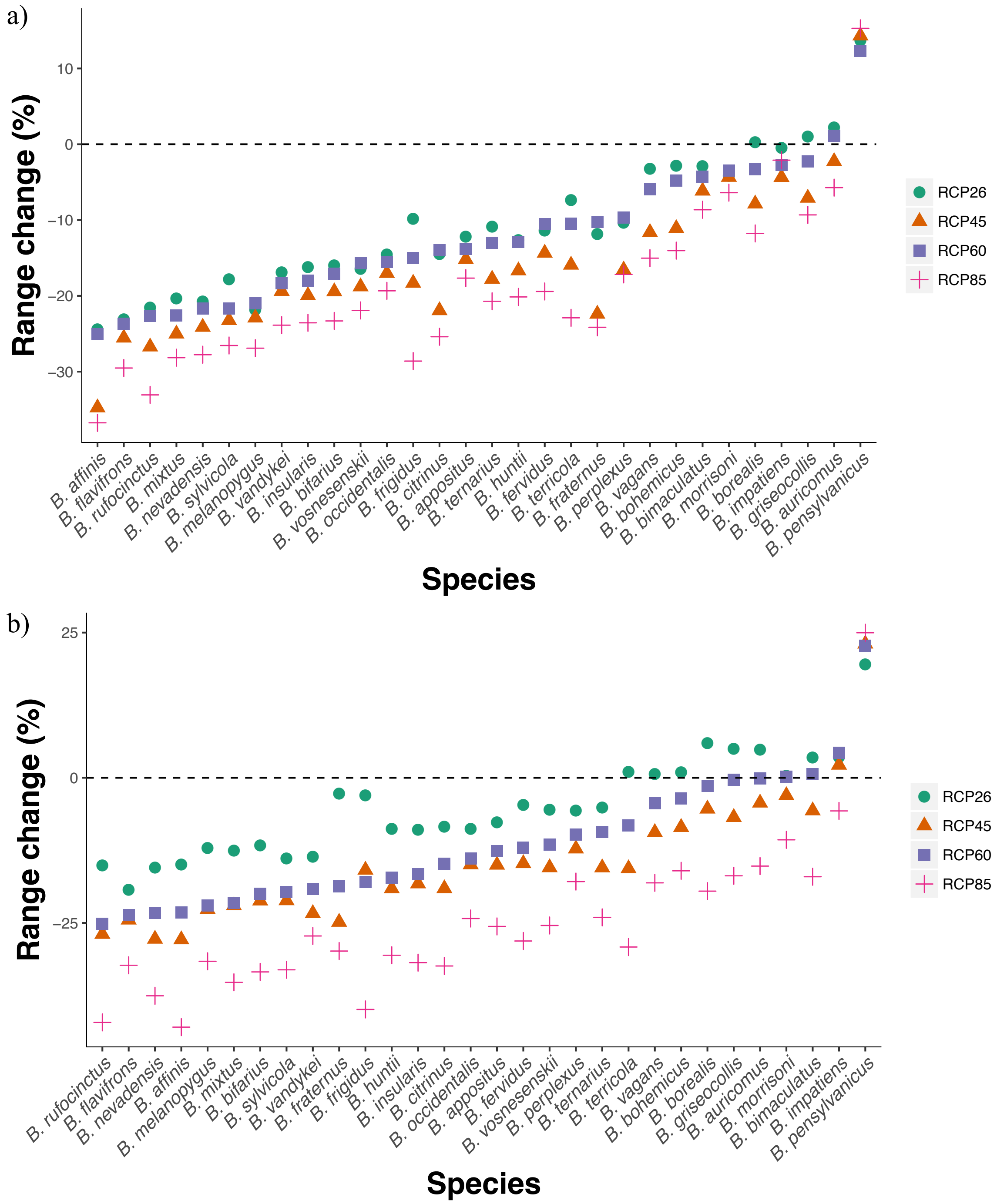

Figure 3: Range changes based on maxent models for 30 North American bumblebee species between baseline (1960-1990) and future projections of years (a) 2050 and (b) 2070, assuming a high dispersal rate (10 km/year). Results were ordered by range change (%) under the RCP6.0 scenario.

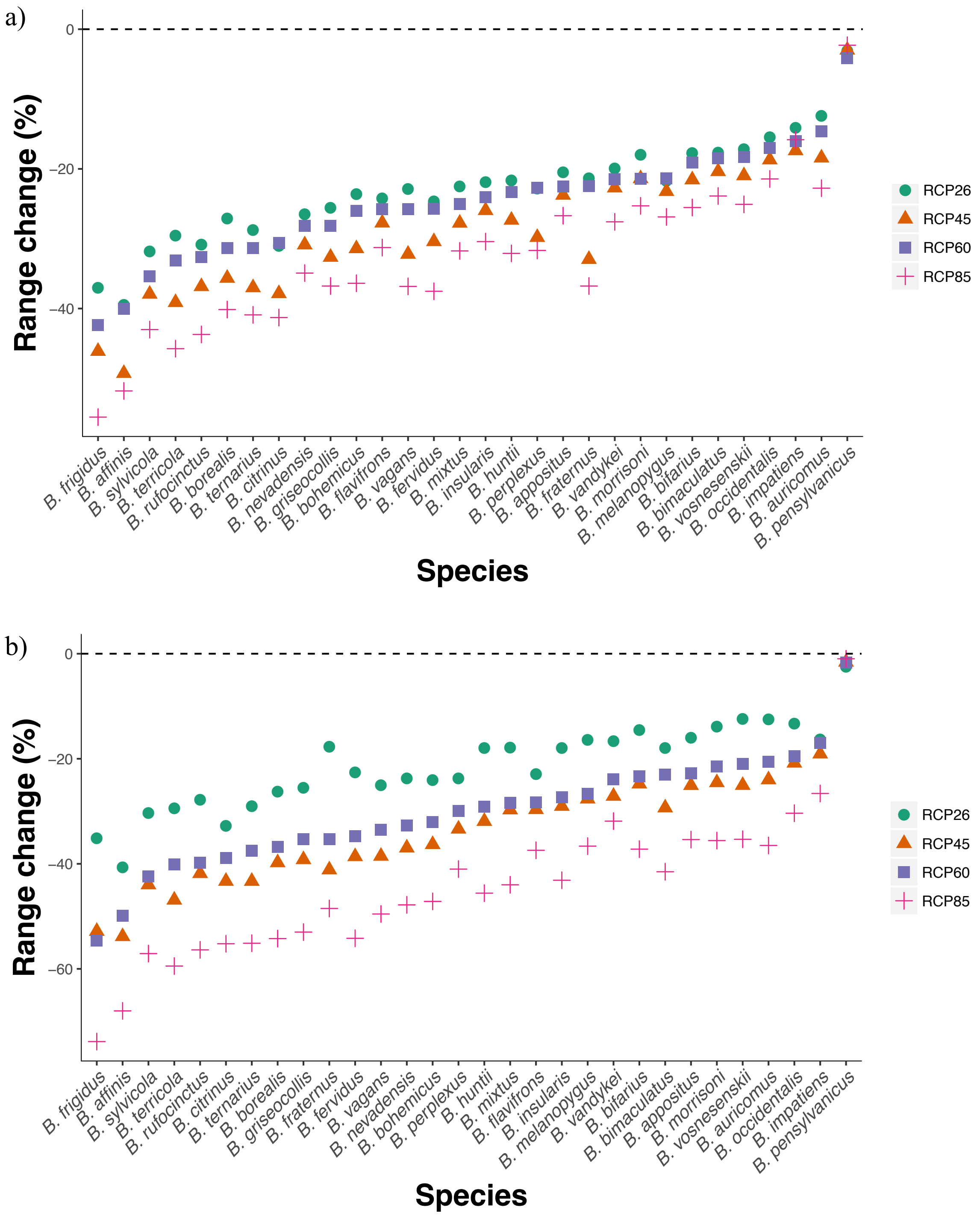

Figure 4: Range changes based on maxent models for 30 North American bumblebee species between baseline (1960-1990) and future projections of years (a) 2050 and (b) 2070, assuming a dispersal rate of 0 km/year. Results were ordered by range change (%) under the RCP6.0 scenario.

Even assuming unlimited dispersal nearly half of bumblebee species were projected to face significant range losses by 2050 (Figure 2). Assuming high dispersal abilities, this proportion increased drastically to 87 – 97% of modeled species by 2050, and to 70 – 97% by 2070, depending on the RCP outcome (Figure 3). Under the assumption of no dispersal, only *Bombus pensylvanicus* maintained relatively stable distributions in all RCP scenarios, for both time periods (Figure 4). Up to 56% of current climatically suitable range was lost by 2050 for *Bombus frigidus*, rising to 74% by 2070.

Species richness changes in agricultural areas were left-skewed, such that most areas lost species and few gained species (Figure 5). Areas estimated to lose multiple species are particularly concentrated within current agricultural areas. The most optimistic scenario (RCP2.6) is distinct from the other three scenarios (RCP4.5, RCP6.0, RCP8.5) in which species richness loss was consistently superior. Dispersal assumptions did not change the general shape of the curve, although slower dispersal resulted in stronger skewed curves since range-shifts were not compensating for species losses.

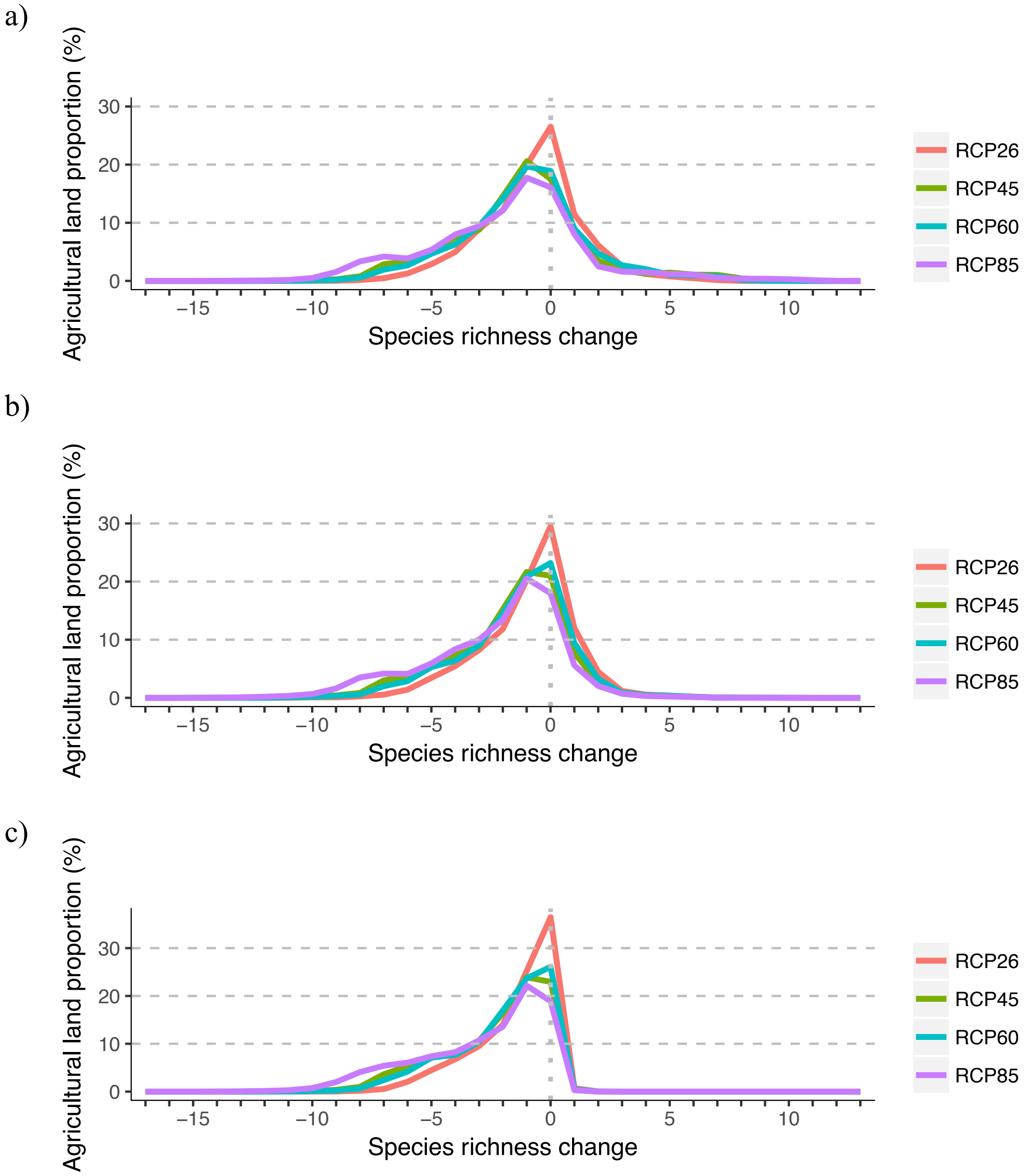

Figure 5: Histograms of species richness change in agricultural areas of North America based on three dispersal assumptions; (a) unlimited dispersal, (b) high dispersal and (c) no dispersal for all 30 modeled bumblebee species. The Y axis represents the percentage of all North American agricultural areas based on the HYDE (2016) land use dataset. The X axis corresponds to species richness changes (unit: number of species).

Regions where multiple bumblebee species' climatic niche was projected to expand in 2070 were concentrated. Hotspots across all RCP scenarios were mapped and overlapped to identify areas suitable for new species in the future regardless of climate trajectory (Figure 6a). By 2070, these ranged from 11 419 km^2 (9 species) to 2 447 283 km^2 (3 species). Less than 25% of these areas are currently developed or disturbed for agricultural purposes, according to the HYDE land use dataset. Areas where species losses overlap were also concentrated in certain regions (Figure 6b). By 2070, these ranged from 75 km^2 (11 species) to 2 173 231 km^2 (3 species). These areas are characterized by high intensity land uses in the form of crop and grazing lands.

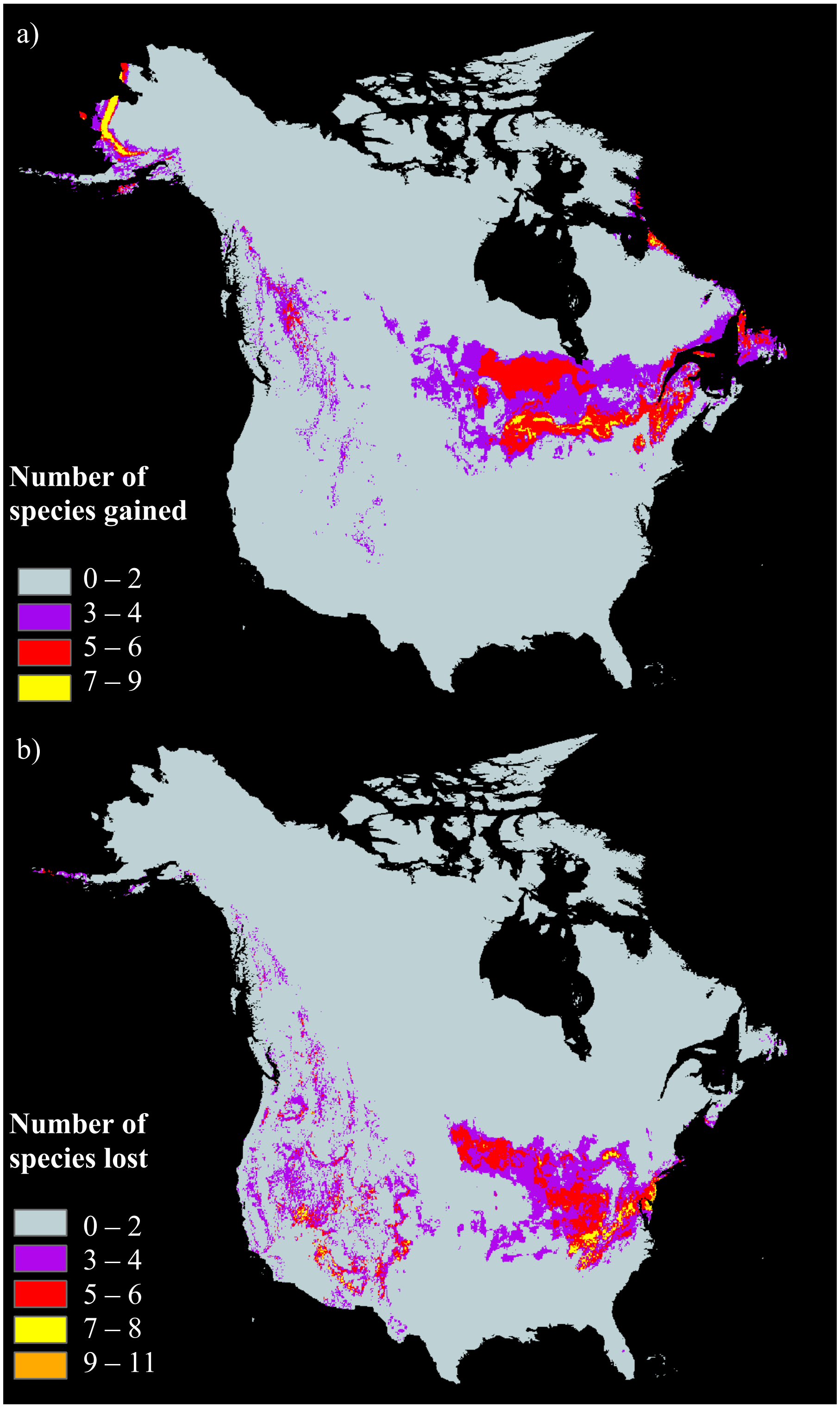

Figure 6: Overlays across future projections of all species and RCP scenarios likely to (a) gain suitable range for multiple species by 2070, and (b) lose multiple species by 2070.

Predictive Accuracy

Predictive accuracy of maxent models was generally high (Figure 7), indicating useful models (Elith et al. 2006). Models produced acceptable AUC values (AUC > 0.75) and TSS values (TSS > 0.4) for all species except *Bombus centralis*, which was consequently removed from the analysis. Mean AUC for all species was 0.85, and mean TSS, 0.62. For all modeled species, TSS was maximized when using the "maximum of sensitivity plus specificity logistic threshold" to produce binary maps. This threshold corresponds to the point that has a tangent with a slope of 1 on the ROC curve (Cantor et al. 1999).

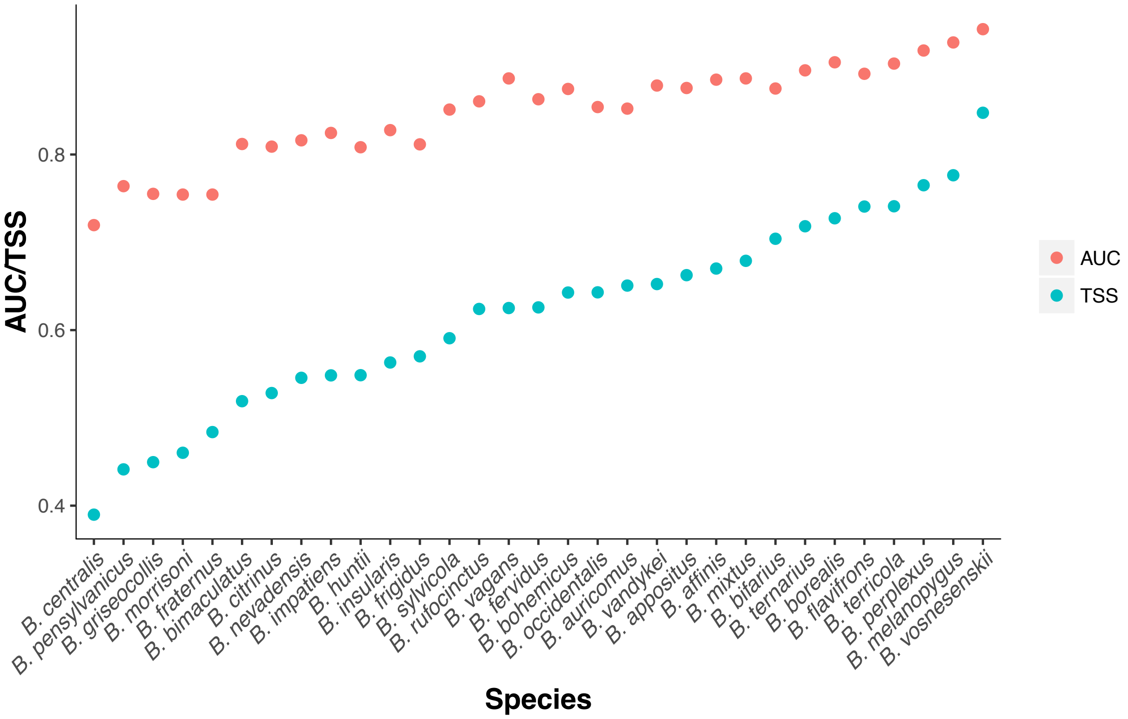

Figure 7: Predictive accuracy of maxent models using the Area Under the Receiver Operator Characteristic Curve (AUC) (Hanley & McNeil 1982), and the True Skill Statistic (TSS) (Allouche et al. 2006). AUC > 0.75 and TSS > 0.4 indicate meaningful models that can be used for analysis.

Discussion

Modeling Future Suitable Ranges

All future climate scenarios led to aggravated declines and richness changes in currently suitable range of surveyed bumblebee species across much of North America. Projections constrained by high dispersal abilities suggest that most modeled species' actual dispersal rates are insufficient to track their climatic niche by 2050, indicating potentially massive future range losses. Results agree with expectations based on observed widespread range contractions (Cameron et al. 2011; Kerr et al. 2015). Range changes differed strongly depending on the severity of the RCP scenarios in 2070, relative to 2050 projections. For the first time, North American bumblebees' future climatic niche projections led to the investigation of new broad-scale conservation strategies.

Future climatic niche projections showed poleward range shifts would be possible, indicating potential new habitable areas for most species. However, species' traits determine their ability to reach these areas in the absence of environmental or anthropogenic barriers (Chen et al. 2011; Leroux et al. 2013). Despite assuming the unlimited ability to disperse and colonize new areas, some species' climatic niche still contracted. While *B. flavifrons*, *B. mixtus*, *B. vandykei*, *B. melanopygus* and *B. nevadensis* are currently relatively common throughout their range (Williams et al. 2014), projections revealed they were among the most climatic-limited species by future climates. This indicates that some common bumblebee species are more vulnerable to climate change than other rare or endangered species. Similarly, thousands of vertebrate and mammal species that are not currently at risk of global extinction could face high population extinction rates in the future (Ceballos et al. 2017), a prospect that models suggest could extend to bumblebee species (Rasmont et al. 2015).

Regions likely to become climatically suitable to multiple species in future projections are concentrated at the northern part of current distributions. Identifying hotspot overlaps across climate scenarios minimized impacts of future climate uncertainty on their position. Hotspots are mostly in Ontario, Quebec, northern parts of Michigan, and scattered in adjacent US states and Canadian provinces. Less prevalent in western parts of the continent, they were found in limited parts of British Columbia. Ecoregion types associated with hotspots are mainly mixed wood plains, mixed wood shield and softwood shield (WWF 2016). These areas are not typically dominated by developed or agricultural land (Sleeter et al. 2014), corresponding to results of land use analyses. Uniform topography in eastern regions generates weak climate gradients, therefore large latitudinal changes are necessary to reach variations in climatic conditions (Leadley et al. 2010; Leroux et al. 2013). Comparatively, smaller distances need to be traveled to track similar climatic changes within mountainous areas (Chen et al. 2011).

Dispersal-constrained models show that projected shifts were insufficient for the majority of species to track their climatic niche by 2050, which suggests that climate change could be a greater threat than previously thought. *B. affinis*, currently listed as endangered under Schedule 1 of the Species At Risk Act, was projected to face the most drastic range loss. Range losses for this species were extremely high despite a conservative approach, including the selection of a dispersal rate which likely exceeds all 30 species' actual capacities to colonize new areas (Goulson 2010). The goal of this approach was to constrain model behavior because of the uncertainties associated with predictions of biotic responses decades in the future. Together with study results, this suggests that realistic dispersal abilities hinder the possibility for bumblebees to track future climate change. Species with high dispersal and colonization capacities can still accumulate substantial climate debt over time (Bedford et al. 2012; Devictor et al. 2012). High dispersal was only sufficient for *B. pensylvanicus* to expand its range under all climate change scenarios. While this species has declined in northern parts of its range (Williams et al. 2014), its broad climatic tolerances together with model results suggest that climate change is unlikely to be this species' main threat in the future.

Projections revealed that places likely to become climatically unsuitable for multiple species were large and concentrated at the edge of current distributions. Bumblebees are particularly vulnerable to local extinctions in these places (Carvalheiro et al. 2013). Areas projected to be unsuitable in the future are more severe and concentrated in eastern parts of the continent. Losses primarily occur in Tennessee, Kentucky, Virginia, Maryland, Delaware, as well as small parts of surrounding states and southern Canada. These areas are essentially dominated by ecoregion types Ozark, Ouachita-Appalachian Forests, southestern USA plains, central USA plains, and mixed wood plains (WWF 2016). These ecoregions are generally dominated by agricultural lands, developed land, or by mosaics of forest, pasture, cropland, developed land, and/or wetlands (Sleeter et al. 2014). These spatial patterns were expected since climate velocity is greater in eastern parts of North America (Loarie et al. 2009). Unsuitable conditions require large and rapid latitudinal shifts for species to track suitable areas and expand their range (Leadley et al. 2010; Leroux et al. 2013).

Future projections within agricultural areas of North America revealed widespread species richness decline. Substantial changes in pollination networks are expected in these areas (IPBES 2016) including significant pollination service declines (e.g. Schweiger et al. 2012). Negative impacts on food yields (Young et al. 2016) and on human welfare may occur (Garibaldi et al. 2011). Similarly, wild bee species' suitable habitat in Brazil was estimated to decline under both pessimistic and optimistic climate change scenarios (Giannini et al. 2012). Landscape connectivity, dispersal, and effects on plants could drastically alter future expected impacts (IPBES 2016). Impacts of pollinator decline on crops needs further investigation (Garibaldi et al. 2011).

Mitigation Measures

Models that predict biotic responses to climate change are valuable for improving management of landscapes through which species must move to expand their geographical ranges successfully (Littlefield et al. 2017). While relatively few such efforts have yet been made for bees, these models show promise in terms of improving understanding of bumblebee species' responses to environmental change (Herrera et al. 2014). Even when assuming high dispersal rates, range shifts are likely to lag behind climate change. Findings support the need for effective mitigation strategies that aim to increase the likelihood of i) successful colonizations at novel climatically suitable areas and of ii) survival in areas predicted to become unsuitable in the absence of intervention (Hoegh-Guldberg et al. 2008; Rasmont et al. 2015).

To the extent that changing climatic conditions increase the likelihood that species could establish and maintain novel populations in some areas, new opportunities for conservation arise (Wiens et al. 2011). Managed relocation (MR) could potentially assist bumblebees in colonizing climatically suitable areas that are outside their current range (Richardson et al. 2009). MR is intended to facilitate the dispersal of species with insufficient intrinsic dispersal capacity into novel areas to which they would disperse given enough time. MR involves the introduction of organisms to target sites to increase their probability of survival while reducing the prospects of species extinctions and the erosion of ecological services (e.g., Hoegh-Guldberg et al., 2008; Kreyling et al., 2011; Richardson et al., 2009; Thomas, 2011). Bumblebees' high risk of decline under climate change, the simplicity of translocation, and potentially low costs of relocating single fertilized queens in the spring, support the choice of MR among other conservation strategies (Hoegh-Guldberg et al. 2008). However, MR is controversial (Thomas 2011; Vilà & Hulme 2011; Webber et al. 2011; Muller & Eriksson 2013).

Concerns regarding MR primarily stem from past ecological and socioeconomic consequences that followed disastrous introduction of invasive species (Hoegh-Guldberg et al. 2008). While many species' introductions have proven benign, others have caused severe damage through competition, predation, or pathogen spread among native species (Hunter 2007; Harris et al. 2013). Such severe impacts have been widely observed following introduction of species to islands, different continents, or across biogeographical boundaries (Hoegh-Guldberg et al. 2008). Intra-continental invasions are relatively rare in the US, with inter-continental invasions being significantly more prevalent and harmful (Mueller & Hellmann 2008). MR refers to the movement of organisms to locations adjacent to currently occupied areas and precludes introductions of species across biogeographical boundaries (Hoegh-Guldberg et al. 2008; Harris et al. 2013). Risks of harm to species already present in the target area highlight uncertainties regarding risks to biodiversity and ecosystem integrity (Ricciardi & Simberloff 2009). However, there are significant uncertainties and potentially irreversible impacts from climate-driven extinctions if no successful conservation actions are undertaken (Sax et al. 2009; Colla 2016). Research shows that probabilities of preventing extinctions through MR exceed likely risks that it causes (Muller & Eriksson 2013), but these effects need to be evaluated on a case-by-case basis. Carefully planned selection of site and candidate species are critical to keep MR at low-risk (Hunter 2007; Thomas 2011). Candidate localities for relocating organisms must first be constrained to those expected to be suitable under future climatic conditions, as shown in a successful six year MR trial of two UK butterfly species (Willis et al. 2009).

Management in areas where species losses are likely to be most concentrated in the absence of intervention, could effectively slow future range contractions (Hatfield et al. 2012). These areas are mainly used for agricultural activities, which should be taken into consideration to develop effective management planning. Reducing other threats and providing micro-refugia where species are limited by climate should be a priority in these areas (Rasmont et al. 2015). Access to microclimatic heterogeneity could improve probabilities of survival at the edge of species' distributions (Lawson et al. 2014) where they are most vulnerable to other threats (e.g. Williams et al. 2007). The trailing edge is important to species' survival and evolution under climate change as it plays a role in maintaining genetic diversity (Hampe & Petit 2005). Providing a variety of pollen and nectar sources especially from native plants, limiting or discontinuing pesticide use, recreating grassland and wooded areas and/or providing nesting boxes in highly modified landscapes (like urban or agricultural area), limiting or timing habitat disturbances (mowing, tilling, burning) to mitigate impacts on nesting and foraging, and monitoring, are activities shown to decrease anthropogenic pressures on bumblebees (See full review: Colla et al. 2016).

Limitations

SDMs make a number of simplifying assumptions (e.g. Araújo & Guisan, 2006; Pearson & Dawson, 2003). Models assume that selected environmental conditions are the main contributors to the position of species' ranges, but other biotic and abiotic interactions have an effect on their distributions (e.g. Hanspach et al., 2014). SDMs can also underestimate species' niches because they assume that all suitable habitat is colonised, even though biotic or anthropogenic barriers prevent equilibrium with environmental conditions (Pearson & Dawson 2003). Impacts of these assumptions are alleviated at the continental scale because climate is a main contributing factor to species distributions at this scale (Schweiger et al. 2012). Further, factors like pesticides and land use change do not interfere with bumblebees' inability to range-shift and overall range contractions on a broad scale (Kerr et al. 2015). SDMs can produce useful results as they avoid overly complex factors like species interactions or other specific context dependant factors (Rasmont et al. 2015).

Conclusion

Models developed here estimate substantial range losses for North American bumblebees in the future even when predictions assume exceptionally rapid dispersal rates similar to those observed for invasive *Bombus terrestris* after its introduction to new environments. Results suggest that bumblebee species' dispersal capacities are unlikely to be sufficient to permit net range expansions, with the single species exception of *Bombus pensylvanicus*. Carefully planned managed relocation could benefit some species. Conservation actions in areas where many species could benefit from intensive habitat management and short-distance managed relocation for the most vulnerable species should not be delayed indefinitely in pursuit of scientific certainty (United Nations Conference on Environment and Development 1992).

Irreversible damage caused by local extinctions is a growing likelihood given recently observed rates of range loss among bumblebees, as well as models suggesting these losses are likely to continue or accelerate (Rasmont et al. 2015). Bumblebee species are particularly valuable in provision of pollination services (IPBES 2016), so global change-induced erosion of those services could have economic, as well as ecological, significance (Gallai et al. 2009). Discussions on whether, where, and for which species managed relocation should be considered are needed, as are expanded efforts to manage habitats to retain species in areas where climatic conditions are likely to become less suitable in the near future.

References

Allouche O, Tsoar A, Kadmon R. 2006. Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology **43**:1223–1232.

Anderson RP, Raza A. 2010. The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: Preliminary tests with montane rodents (genus Nephelomys) in Venezuela. Journal of Biogeography **37**:1378–1393.

Araújo MB, Guisan A. 2006. Five (or so) challenges for species distribution modelling. Journal of Biogeography **33**:1677–1688.

Barbet-Massin M, Jiguet F, Albert CH, Thuiller W. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? Methods in Ecology and Evolution:327–338.

Bedford FE, Whittaker RJ, Kerr JT. 2012. Systemic range shift lags among a pollinator species assemblage following rapid climate change. Botany **90**:1–11.

Boria RA, Olson LE, Goodman SM, Anderson RP. 2014. Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. Ecological Modelling **275**:73–77.

Bowers MA. 1985. Bumblebee colonization, extinction, and reproduction in subalpine meadows in Northeastern Utah. Ecology **66**:914–927.

Brown JL. 2014. SDMtoolbox: A python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. Methods in Ecology and Evolution **5**:694–700.

Cameron SA, Lozier JD, Strange JP, Koch JB, Cordes N, Solter LF, Griswold TL. 2011. Patterns of widespread decline in North American bumble bees. Proceedings of the National Academy of Sciences **108**:662–667.

Cantor SB, Sun CC, Tortolero-Luna G, Richards-Kortum R, Follen M. 1999. A Comparison of C/B Ratios from Studies Using Receiver Operating Characteristic Curve Analysis. J Clin Epidemiol **52**:885–892.

Carvalheiro LG et al. 2013. Species richness declines and biotic homogenisation have slowed down for NW-European pollinators and plants. Ecology Letters **16**:870–878.

Casey LM, Rebelo H, Rotheray E, Goulson D. 2015. Evidence for habitat and climatic specializations driving the long-term distribution trends of UK and Irish bumblebees. Diversity and Distributions **21**:864–875.

Ceballos G, Ehrlich PR, Dirzo R. 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proceedings of the National Academy of Sciences:1–8.

Chen I, Hill JK, Ohlemüller R, Roy DB, Thomas CD. 2011. Rapid range shifts of species of climate warming. Science **333**:1024–1026.

Colla SR. 2016. Status, Threats and Conservation Recommendations for Wild Bumble Bees (Bombus spp.) in Ontario, Canada: A Review for Policymakers and Practitioners. Natural Areas Journal **36**:412–426.

Darvill B. 2007. The conservation genetics of the bumblebees Bombus muscorum and Bombus jonellus in a model island system. PhD thesis, University of Southampton.

Davis MB, Shaw RG. 2001. Range Shifts and Adaptive Responses to Quaternary Climate

Change. Science **292**:673–680.

Devictor V et al. 2012. Differences in the climatic debts of birds and butterflies at a continental scale. Nature Climate Change **2**:121–124.

Elith J et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography **29**:129–151.

Fürst M, McMahon D, Osborne J, Paxton R, Brown M. 2014. Disease associations between honeybees and bumblebees as a threat to wild pollinators. Nature **506**:364–366.

Gallai N, Salles JM, Settele J, Vaissière BE. 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecological Economics **68**:810–821.

Garibaldi LA, Aizen MA, Klein AM, Cunningham SA, Harder LD. 2011. Global growth and stability of agricultural yield decrease with pollinator dependence. Proceedings of the National Academy of Sciences **108**:5909–5914.

Giannini TC, Acosta AL, Garófalo CA, Saraiva AM, Alves-dos-Santos I, Imperatriz-Fonseca VL. 2012. Pollination services at risk: Bee habitats will decrease owing to climate change in Brazil. Ecological Modelling **244**:127–131.

Goldewijk KK, Beusen A, Van Drecht G, De Vos M. 2011. The HYDE 3.1 spatially explicit database of human-induced global land-use change over the past 12,000 years. Global Ecology and Biogeography **20**:73–86.

Goulson D. 2010. Bumblebees Behaviour, Ecology, and ConservationSecond Edi. Oxford University Press, New York (US).

Goulson D, Lye GC, Darvill B. 2008. Decline and Conservation of Bumble bees. Annual Review of Entomology **53**:191–208.

Goulson D, Nicholls E, Botías C, Rotheray EL. 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science **347**:1255957.

Hällfors MH, Aikio S, Fronzek S, Hellmann JJ, Ryttäri T, Heikkinen RK. 2016. Assessing the need and potential of assisted migration using species distribution models. Biological Conservation **196**:60–68.

Hampe A, Petit RJ. 2005. Conserving biodiversity under climate change: the rear edge matters. Ecology Letters **8**:461–467.

Hanley AJ, McNeil JB. 1982. The Meaning and Use of the Area under a Receiver Operating Characteristic (ROC) Curve. Radiology **143**:29–36.

Hanspach J, Schweiger O, Kühn I, Plattner M, Pearman PB, Zimmermann NE, Settele J. 2014. Host plant availability potentially limits butterfly distributions under cold environmental conditions. Ecography **37**:301–308.

Hargreaves AL, Eckert CG. 2014. Evolution of dispersal and mating systems along geographic gradients: Implications for shifting ranges. Functional Ecology **28**:5–21.

Hargreaves AL, Samis KE, Eckert CG. 2014. Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. The American Naturalist **183**:157–73.

Harris S, Arnall S, Byrne M, Coates D, Hayward M, Martin T, Mitchell N, Garnett S. 2013. Whose backyard? Some precautions in choosing recipient sites for assisted colonisation of Australian plants and animals. Ecological Management and Restoration **14**:106–111.

Hatfield R, Jepsen S, Mader E, Black S, Shepherd M. 2012. Conserving Bumble Bees:

Guidelines for Creating and Managing Habitat for America's Declining Pollinators. Page The Xerces Society for Invertebrate Conservation.

Hatten TD, Looney C, Strange JP, Bosque-Pérez NA. 2013. Bumble bee fauna of Palouse Prairie: survey of native bee pollinators in a fragmented ecosystem. Journal of insect science **13**:1–19.

Hernandez PA, Graham CH, Master LL, Albert DL. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography **29**:773–785.

Herrera JM, Ploquin EF, Rodriguez-Pérez J, Obeso JR. 2014. Determining habitat suitability for bumblebees in a mountain system : a baseline approach for testing the impact of climate change on the occurrence and abundance of species. Journal of Biogeography **41**:700–712.

Hijmans RJ. 2012. Cross-validation of species distribution models : removing spatial sorting bias and calibration with a null model. Ecology **93**:679–688.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology **25**:1965–1978.

Hoegh-Guldberg O, Hughes L, McIntyre S, Lindenmayer DB, Parmesan C, Possingham HP, Thomas CD. 2008. Ecology. Assisted colonization and rapid climate change. Science **321**:345–346.

Holt RD, Keitt TH, Lewis MA, Maurer BA, Taper ML. 2005. Theoretical models of species' borders: Single species approaches. Oikos **108**:18–27.

Hulme PE. 2005. Adapting to climate change: Is there scope for ecological management in the face of a global threat? Journal of Applied Ecology **42**:784–794.

Hunter ML. 2007. Climate change and moving species: Furthering the debate on assisted colonization. Conservation Biology **21**:1356–1358.

Hutchinson GE. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology **22**:415–427.

IPBES. 2016. The assessment report on pollinators, pollination and food production of the intergovernmental science-policy platform on biodiversity and ecosystem services; Summary for policymakers. Bonn, Germany.

IPCC. 2014. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.

Jump AS, Màtyàs C, Peñuelas J. 2009. The altitude-for-latitude disparity in the range retractions of woody species. Trends in Ecology and Evolution **24**:694–701.

Kadoya T, Ishii H, Kikuchi R, Suda S, Washitani I. 2009. Using monitoring data gathered by volunteers to predict the potential distribution of the invasive alien bumblebee Bombus terrestris. Biological Conservation **142**:1011–1017.

Kerr JT et al. 2015. Climate change impacts on bumblebees converge across continents. Science **349**:177–180.

Kharouba HM, Paquette SR, Kerr JT, Vellend M. 2014. Predicting the sensitivity of butterfly phenology to temperature over the past century. Global Change Biology **20**:504–514.

Klein A-M, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T. 2007. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society of London, Series B **274**:303–313.

Koch JB, Strange JP. 2009. Constructins a species database and historic range maps for North American bumblebees (Bombus sensu stricto Latreille) to inform conservation decisions. Uludag Bee Journal **9**:97–108.

Kreyling J, Bittner T, Jaeschke A, Jentsch A, Jonas Steinbauer M, Thiel D, Beierkuhnlein C. 2011. Assisted Colonization: A Question of Focal Units and Recipient Localities. Restoration Ecology **19**:433–440.

Landis JR, Koch GG. 1997. The Measurement of Observer Agreement for Categorical Data. Biometrics **33**:159–174.

Lawson CR, Bennie J, Hodgson JA, Thomas CD, Wilson RJ. 2014. Topographic microclimates drive microhabitat associations at the range margin of a butterfly. Ecography **37**:732–740.

Leadley P, Pereira HM, Alkemade R, Fernandez-Manjarrés JF, Proença V, Scharlemann JPW, Walpole MJ. 2010. Biodiversity Scenarios: Projections of 21st century change in biodiversity and associated ecosystem services. Montreal, Canada.

Lee-Yaw JA, Kharouba HM, Bontrager M, Mahony C, Csergő AM, Noreen AME, Li Q, Schuster R, Angert AL. 2016. A synthesis of transplant experiments and ecological niche models suggests that range limits are often niche limits. Ecology Letters **19**:710–722.

Lepais O, Darvill B, O'Connor S, Osborne JL, Sanderson RA, Cussans J, Goffe L, Goulson D. 2010. Estimation of bumblebee queen dispersal distances using sibship reconstruction method. Molecular Ecology **19**:819–831.

Leroux SJ, Larrivée M, Boucher-Lalonde V, Hurford A, Zuloaga J, Kerr JT, Lutscher F. 2013. Mechanistic models for the spatial spread of species under climate change. Ecological Applications **23**:815–828.

Littlefield CE, McRae BH, Michalak J, Lawler JJ, Carroll C. 2017. Connecting today's climates to future analogs to facilitate species movement under climate change. Conservation Biology **0**:1–12.

Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD. 2009. The velocity of climate change. Nature **462**:1052–1055.

Lobo JM, Jiménez-Valverde A, Hortal J. 2010. The uncertain nature of absences and their importance in species distribution modelling. Ecography **33**:103–114.

McLachlan JS, Hellman JJ, Schwartz MW. 2007. A Framework for Debate of Assisted Migration in an Era of Climate Change. Conservation Biology **21**:297–302.

Meeus I, Brown MJF, De Graaf DC, Smagghe G. 2011. Effects of Invasive Parasites on Bumble Bee Declines. Conservation Biology **25**:662–671.

Menéndez R, Megías AG, Hill JK, Braschler B, Willis SG, Collingham Y, Fox R, Roy DB, Thomas CD. 2006. Species richness changes lag behind climate change. Proceedings of the Royal Society B **273**:1465–1470.

Merow C, Smith MJ, Silander JA. 2013. A practical guide to MaxEnt for modeling species' distributions: What it does, and why inputs and settings matter. Ecography **36**:1058–1069.

Michener CD. 2000. The bees of the world. The Johns Hopkins University Press, Baltimore, MD.

Mueller JM, Hellmann JJ. 2008. An assessment of invasion risk from assisted migration. Conservation Biology **22**:562–567.

Muller H, Eriksson O. 2013. A pragmatic and utilitarian view of species translocation as a tool in conservation biology. Biodiversity and Conservation **22**:1837–1841.

Owen RE, Otterstatter MC, Cartar RV, Farmer A, Colla SR, O'Toole N. 2012. Significant expansion of the distribution of the bumble bee Bombus moderatus (Hymenoptera: Apidae) in Alberta over 20 years. Canadian Journal of Zoology **90**:133–138.

Parmesan C et al. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature **399**:579–583.

Parmesan C. 2006. Ecological and Evolutionary Responses to Recent Climate Change. Annual Review of Ecology Evolution and Systematics **37**:637–669.

Pearson RG. 2008. Species' Distribution Modeling for Conservation Educators and Practitioners. Synthesis. American Museum of Natural History. Available at http://ncep.amnh.org.

Pearson RG, Dawson TP. 2003. Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful? Global Ecology and Biogeography **12**:361–371.

Penado A, Rebelo H, Goulson D. 2016. Spatial distribution modelling reveals climatically suitable areas for bumblebees in undersampled parts of the Iberian Peninsula. Insect Conservation and Diversity **9**:391–401.

Phillips SB, Aneja VP, Kang D, Arya SP. 2006. Maximum entropy modeling of species geographic distributions. International Journal of Global Environmental Issues **6**:231–252.

Ploquin EF, Herrera JM, Obeso JR. 2013. Bumblebee community homogenization after uphill shifts in montane areas of northern Spain. Oecologia **173**:1649–1660.

Polgar CA, Primack RB, Williams EH, Stichter S, Hitchcock C. 2013. Climate effects on the flight period of Lycaenid butterflies in Massachusetts. Biological Conservation **160**:25–31.

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE. 2010. Global pollinator declines: trends, impacts and drivers. Trends in Ecology & Evolution **25**:345–353.

Pradervand J-N, Pellissier L, Randin CF, Guisan A. 2014. Functional homogenization of bumblebee communities in alpine landscapes under projected climate change. Climate Change Responses **1**:1–10.

Rasmont P et al. 2015. Climatic Risk and Distribution Atlas of European Bumblebees. Page BioRisk 10. Pensoft Publishers, Sofia, Bulgaria.

Rasmont P, Iserbyt S. 2012. The Bumblebees Scarcity Syndrome: Are heat waves leading to local extinctions of bumblebees (Hymenoptera: Apidae: Bombus)? International Journal of Entomology **48**:275–280.

Ratti CM, Colla SR. 2010. Discussion of the presence of an eastern bumble bee species (Bombus impatiens Cresson) in western Canada. The Pan-Pacific Entomologist **86**:29–31.

Ricciardi A, Simberloff D. 2009. Assisted colonization is not a viable conservation strategy. Trends in Ecology & Evolution **24**:248–253.

Richardson DM et al. 2009. Multidimensional evaluation of managed relocation. Proceedings of the National Academy of Sciences of the United States of America **106**:9721–9724.

Sax DF, Smith KF, Thompson AR. 2009. Managed relocation: a nuanced evaluation is needed. Trends in Ecology & Evolution **24**:472–473.

Schweiger O et al. 2010. Multiple stressors on biotic interactions: How climate change and alien species interact to affect pollination. Biological Reviews **85**:777–795.

Schweiger O, Heikkinen RK, Harpke A, Hickler T, Klotz S, Kudrna O, Kühn I, Pöyry J, Settele J. 2012. Increasing range mismatching of interacting species under global change is related to their ecological characteristics. Global Ecology and Biogeography **21**:88–99.

Searcy CA, Shaffer HB. 2016. Do Ecological Niche Models Accurately Identify Climatic Determinants of Species Ranges? The American Naturalist **187**:423–435.

Sheffield C, Kevan P, Smith R, Rigby S, Rogers R. 2003. Bee Species of Nova Scotia, Canada, with New Records and Notes on Bionomics and Floral Relations (Hymenoptera : Apoidea). Journal of the Kansas Entomological Society **76**:357–384.

Sleeter BM, Griffith GE, Wilson TS, Sleeter RR, Soulard CE, Sayler KL, Reker RR, Bouchard MA, Sohl TL. 2014. Ecoregion and Scenario Framework. Pages 17–26in Z. Zhu and B. C. Reed, editors.Baseline and Projected Future Carbon Storage and Greenhouse-Gas Fluxes in Ecosystems of the Eastern United States: U.S. Geological Survey Professional Paper 1804. Reston, United States.

Stout JC, Goulson D. 2000. Bumble bees in Tasmania: Their distribution and potential impact on Australian flora and fauna. Bee World **81**:80–86.

Svenning J-C, Normand S, Skov F. 2008. Postglacial dispersal limitation of widwspread forest plant species in nemoral Europe. Ecography **31**:316–326.

Swets J. 1988. Measuring the accuracy of diagnostic systems. Science **240**:1285–1293.

Thomas CD et al. 2004. Extinction risk from climate change. Nature **427**:145–148.

Thomas CD. 2010. Climate, climate change and range boundaries. Diversity and Distributions **16**:488–495.

Thomas CD. 2011. Translocation of species, climate change, and the end of trying to recreate past ecological communities. Trends in Ecology and Evolution **26**:216–221.

Thomas CD, Franco AMA, Hill JK. 2006. Range retractions and extinction in the face of climate warming. Trends in Ecology and Evolution **21**:415–416.

Tuell JK, Isaacs R. 2010. Weather During Bloom Affects Pollination and Yield of Highbush Blueberry. Journal of Economic Entomology **103**:557–562.

United Nations Conference on Environment and Development. 1992. Page Rio Declaration on Environment and Development.

Veloz SD. 2009. Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. Journal of Biogeography **36**:2290–2299.

Vilà M, Hulme PE. 2011. Jurassic Park? No thanks **26**:496–497.

Webber BL, Scott JK, Didham RK. 2011. Translocation or bust! A new acclimatization agenda for the 21 st century? **26**:495–496.

Wiens JA, Seavy NE, Jongsomjit D. 2011. Protected areas in climate space: What will the future bring? Biological Conservation **144**:2119–2125.

Williams P, Thorp R, Richardson L, Colla S. 2014. Bumble Bees of North America. Princeton University Press, Princeton, NJ.

Williams PH, Araújo MB, Rasmont P. 2007. Can vulnerability among British bumblebee (Bombus) species be explained by niche position and breadth? Biological

Conservation **138**:493–505.

Williams PH, Osborne JL. 2009. Bumblebee vulnerability and conservation world-wide. Apidologie **40**:367–387.

Willis SG, Hill JK, Thomas CD, Roy DB, Fox R, Blakeley DS, Huntley B. 2009. Assisted colonization in a changing climate: a test-study using two UK butterflies. Conservation Letters **2**:45–51.

Young HS, McCauley DJ, Galetti M, Dirzo R. 2016. Patterns, Causes, and Consequences of Anthropocene Defaunation. Annual Review of Ecology, Evolution, and Systematics **47**:333–358.

World Wildlife Fund (WWF) About Global Ecoregions. (2016). Retrieved from http://wwf.panda.org/about_our_earth/ecoregions/about/

APPENDIX A

List of data contributors: Bee Biology and Systematics Lab, USDA-ARS, Utah State University; John Ascher, National University of Singapore and American Museum of Natural History, New York, USA; Doug Yanega, University of California, Riverside (NSF-DBI #0956388 and #0956340), California, USA; Illinois Natural History Survey, Illinois, USA; Packer Lab Research Collection, York University, Canada; Canadian National Collection, Agriculture and Agri-Food Canada; Canada; Peabody Museum, Yale University; Sam Droege, USGS Patuxent Wildlife Research Center, USA; Boulder Museum of Natural History, University of Colorado, Colorado, USA.

APPENDIX B

The following list enumerates bumblebee species sampled across North America between 1901 and 2010, of sufficient reliability and sampling effort for data analysis. The asterix (*) identifies species of negative or unchanging northern latitudinal limits by 1999-2010, relative to the baseline (1901-1974) according to Kerr et al. (2015).

*Bombus affinis**
*Bombus appositus**
*Bombus auricomus**
*Bombus bifarius**
*Bombus bimaculatus**
*Bombus bohemicus**
Bombus borealis
*Bombus centralis**
*Bombus citrinus**
*Bombus fervidus**
*Bombus flavifrons**
Bombus fraternus
*Bombus frigidus**
*Bombus griseocollis**
*Bombus huntii**
*Bombus impatiens**
Bombus insularis
*Bombus melanopygus**
*Bombus mixtus**
*Bombus morrisoni**
Bombus nevadensis
Bombus occidentalis
*Bombus pensylvanicus**
Bombus perplexus
Bombus rufocinctus
*Bombus sylvicola**
Bombus ternarius
*Bombus terricola**
Bombus vagans
Bombus vandykei
Bombus vosnesenskii

APPENDIX C

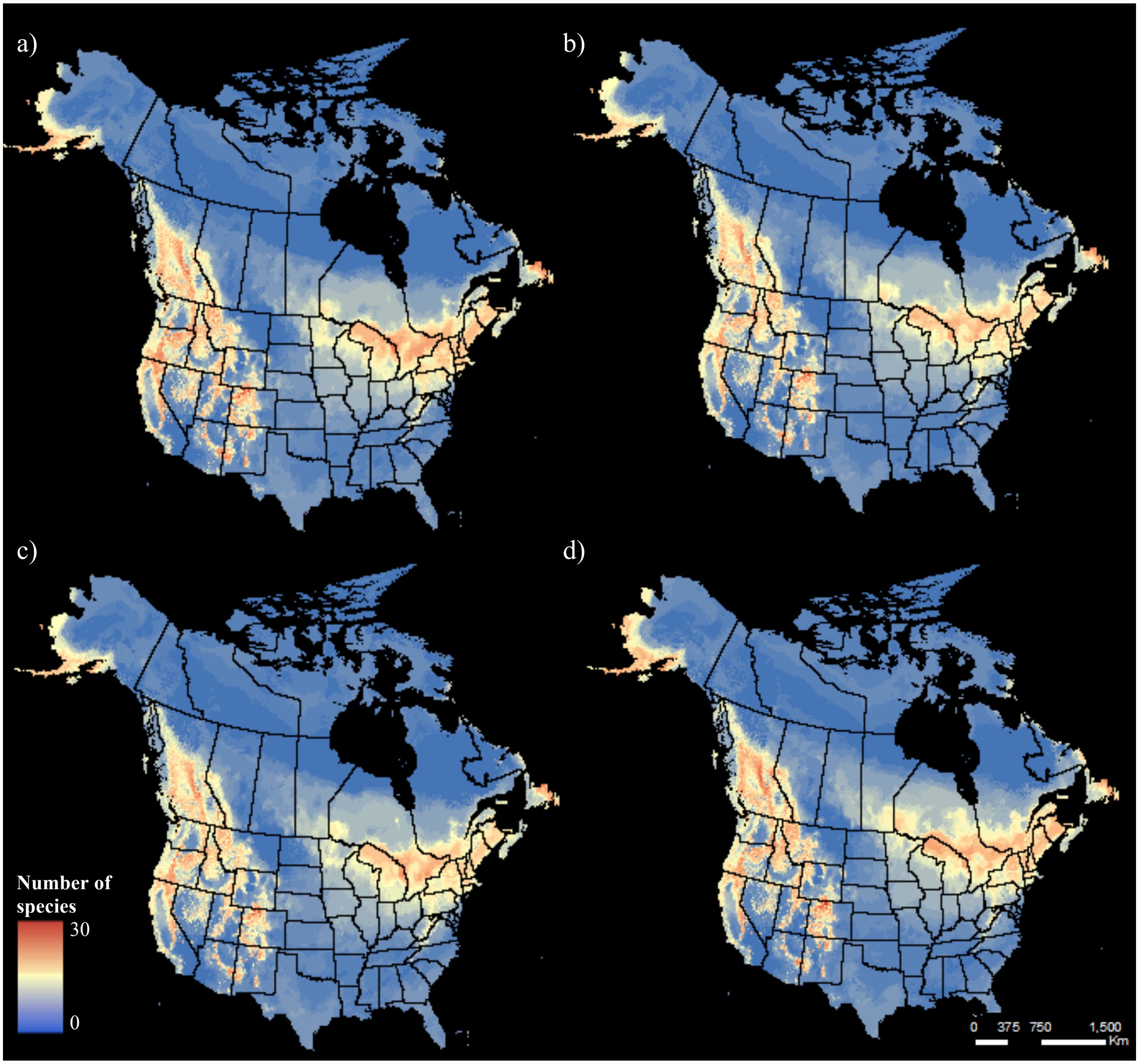

Figure A1: Species richness maps of North America for 30 bumblebee species under the RCP scenarios (a) RCP2.6, (b) RCP4.5, (c) RCP6.0, and (d) RCP8.5 in year 2050, assuming unlimited dispersal ability.

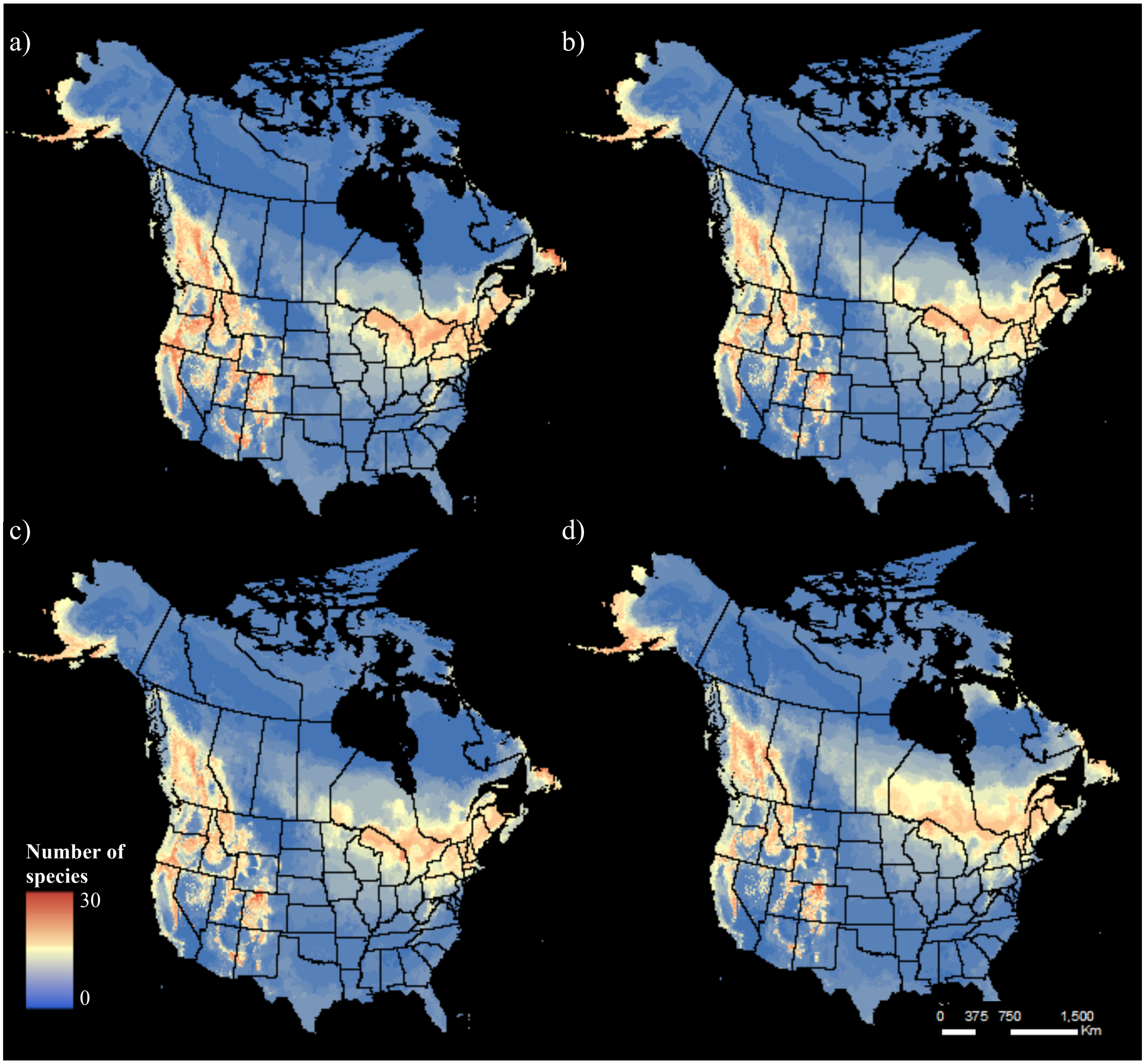

Figure A2: Species richness maps of North America for 30 bumblebee species under the RCP scenarios (a) RCP2.6, (b) RCP4.5, (c) RCP6.0, and (d) RCP8.5 in year 2070, assuming unlimited dispersal ability.

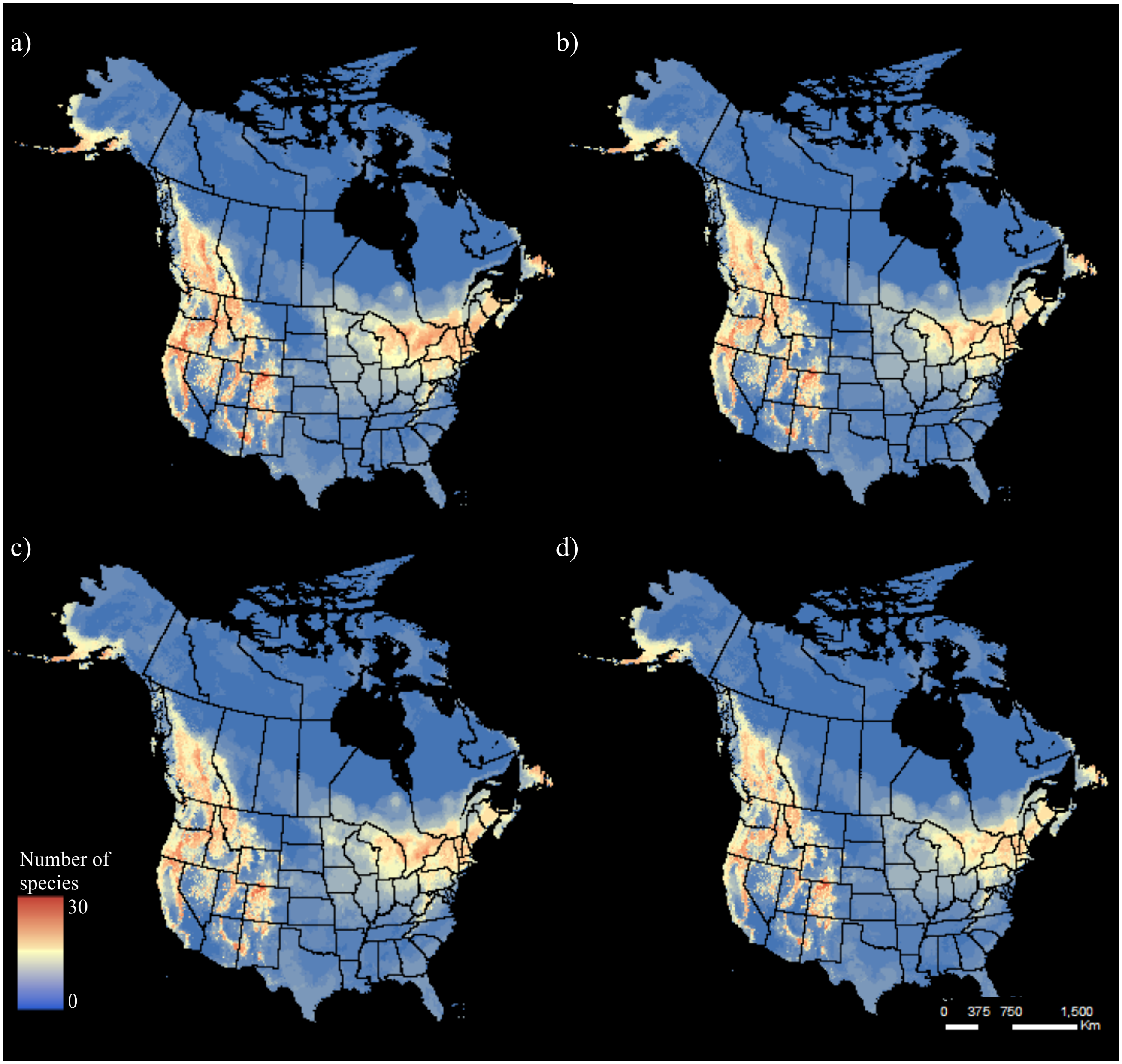

Figure A3: Species richness maps of North America for 30 bumblebee species under the RCP scenarios (a) RCP2.6, (b) RCP4.5, (c) RCP6.0, and (d) RCP8.5 in year 2050, assuming a high dispersal rate (10 km/year).

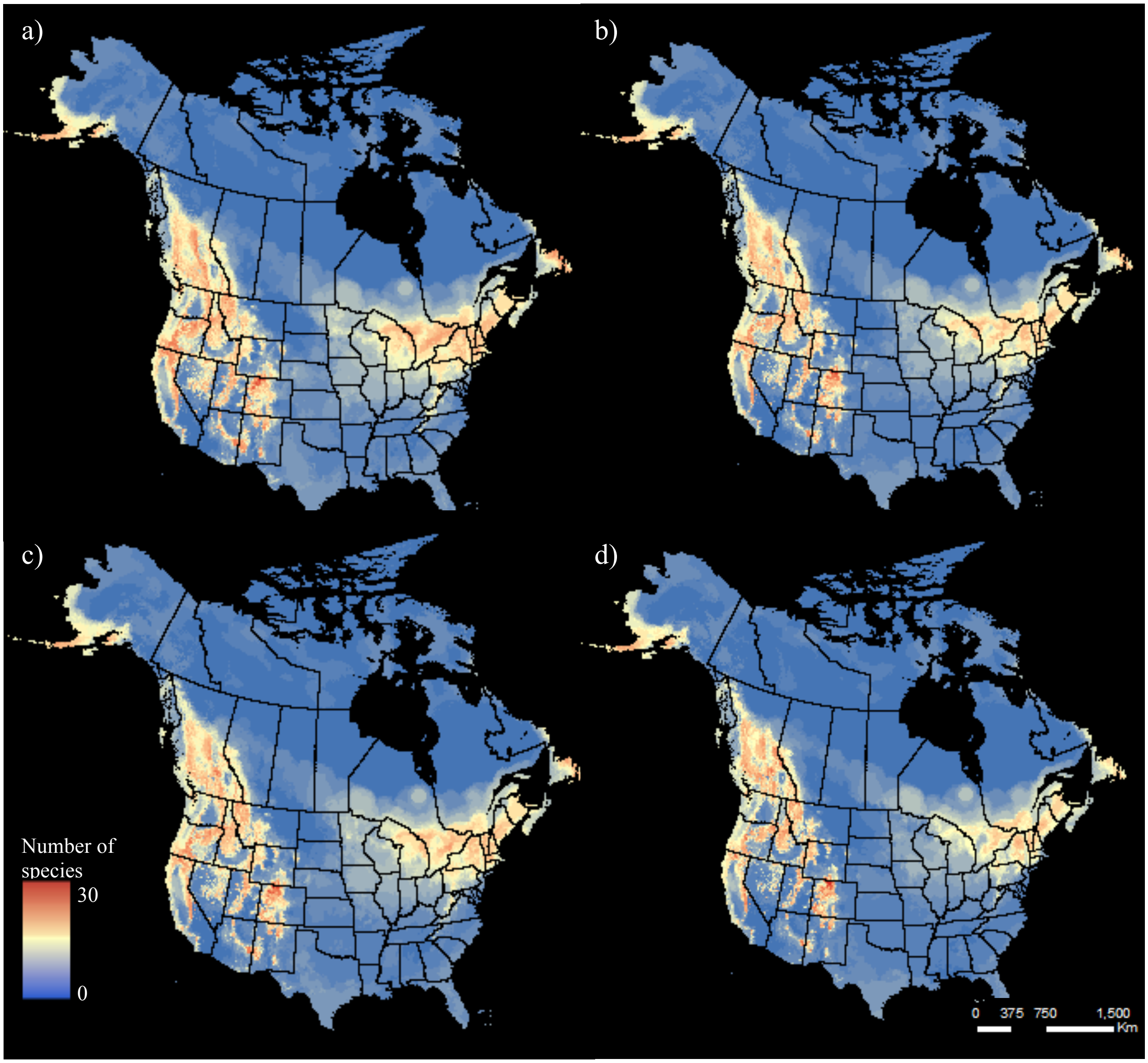

Figure A4: Species richness maps of North America for 30 bumblebee species under the RCP scenarios (a) RCP2.6, (b) RCP4.5, (c) RCP6.0, and (d) RCP8.5 in year 2070, assuming a high dispersal rate (10 km/year).

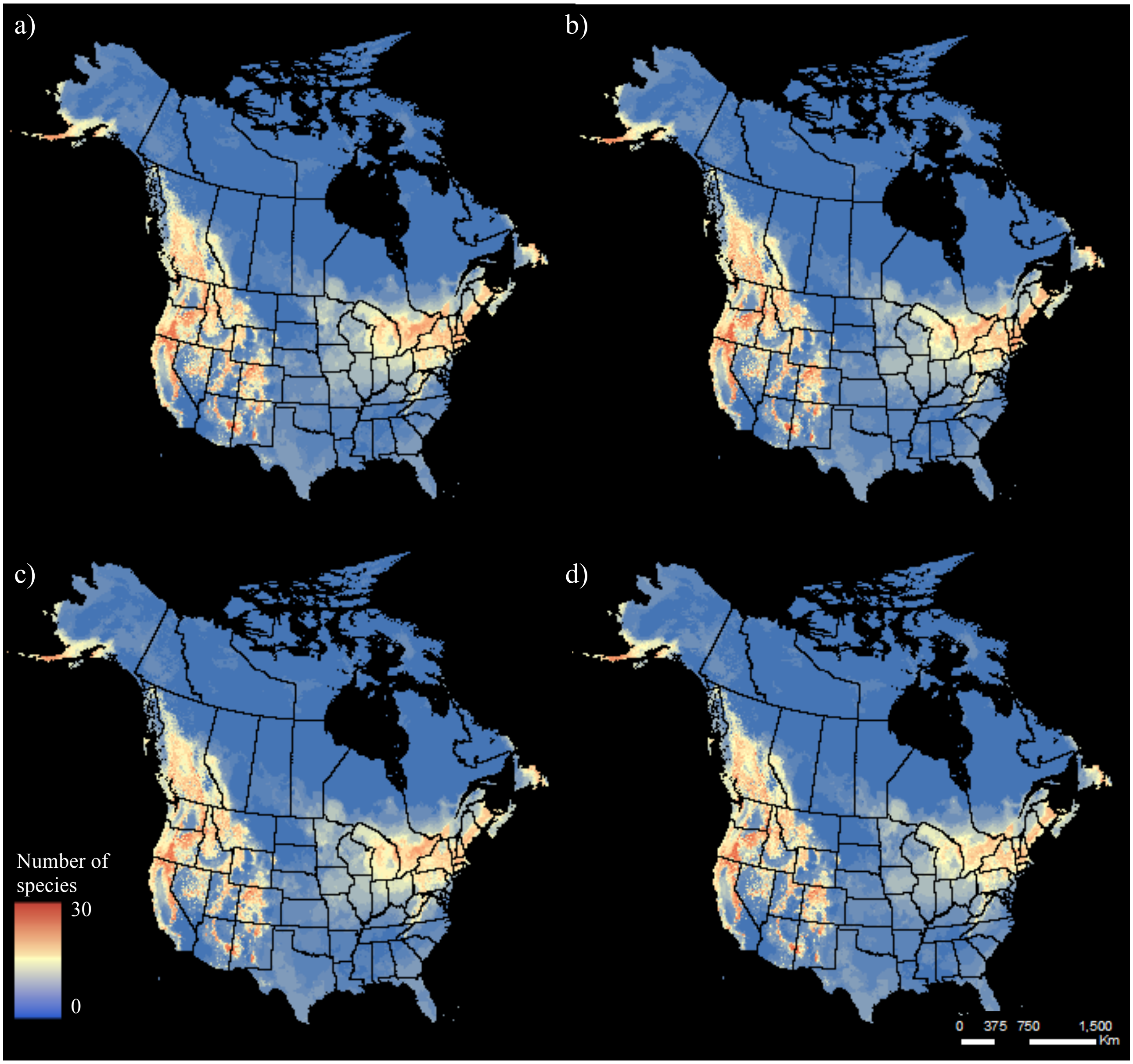

Figure A5: Species richness maps of North America for 30 bumblebee species under the RCP scenarios (a) RCP2.6, (b) RCP4.5, (c) RCP6.0, and (d) RCP8.5 in year 2050, assuming a dispersal rate of 0 km/year.

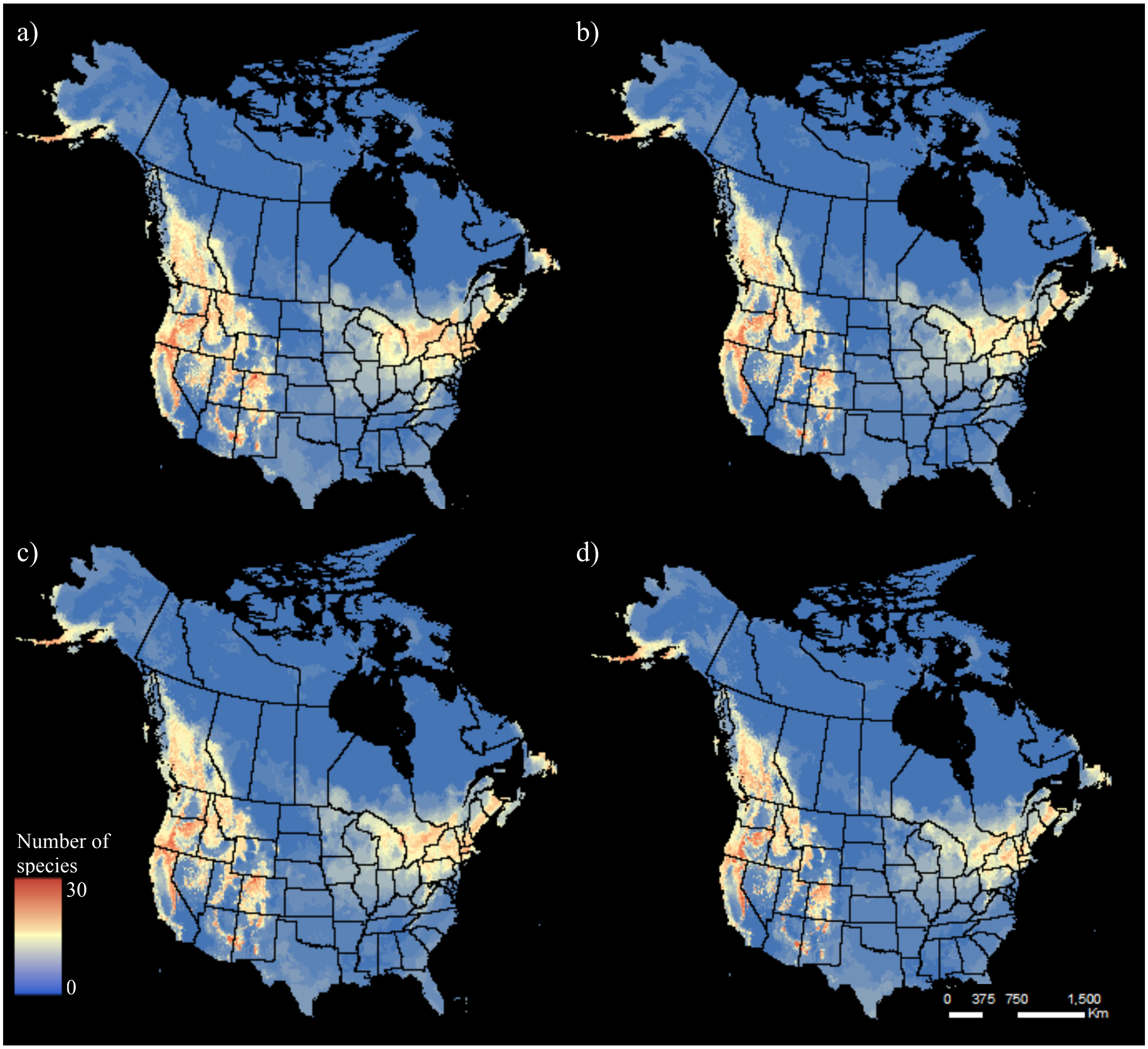

Figure A6: Species richness maps of North America for 30 bumblebee species under the RCP scenarios (a) RCP2.6, (b) RCP4.5, (c) RCP6.0, and (d) RCP8.5 in year 2070, assuming a dispersal rate of 0 km/year.