


Potential regional declines in species richness of tomato pollinators in North America under climate change

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Abstract. About 70% of the world's main crops depend on insect pollination. Climate change is already affecting the abundance and distribution of insects, which could cause geographical mismatches between crops and their pollinators. Crops that rely primarily on wild pollinators (e.g., crops that cannot be effectively pollinated by commercial colonies of honey bees) could be particularly in jeopardy. However, limited information on plant–pollinator associations and pollinator distributions complicate the assessment of climate change impacts on specific crops. To study the potential impacts of climate change on pollination of a specific crop in North America, we use the case of open-field tomato crops, which rely on buzz pollinators (species that use vibration to release pollen, such as bumble bees) to increase their production. We aimed to (1) assess potential changes in buzz pollinator distribution and richness, and (2) evaluate the overlap between areas with high densities of tomato crops and high potential decrease in richness. We used baseline (1961–1990) climate and future (2050s and 2080s) climatic projections in ecological niche models fitted with occurrences of wild bees, documented in the literature as pollinators of tomatoes, to estimate the baseline and future potential distribution of suitable climatic conditions of targeted species and to create maps of richness change across North America. We obtained reliable models for 15 species and found important potential decreases in the distribution of some pollinators (e.g., *Lasioglossum pectorale* and *Augochlorella aurata*). We observed geographical discrepancies in the projected change in species richness across North America, detecting important declines in the eastern United States (up to 11 species decrease for 2050s). After overlapping the maps of species richness change with a tomato crop map for the United States, we found spatial correspondence between richness declines and areas with high concentration of tomato crops. Disparities in the effects of climate change on the potential future distribution of different wild pollinators and geographical variation in richness highlight the importance of crop-specific studies. Our study also emphasizes the challenges of compiling and modeling crop-specific pollinator data and the need to improve our understanding of current distribution of pollinators and their community dynamics under climate change.

Key words: bees; *Bombus*; bumble bees; buzz pollinators; climate change; crop production; ecological niche modeling; ecosystem services; Global Biodiversity Information Facility; Maxent; tomatoes.

INTRODUCTION

Insect pollinators provide key services to terrestrial ecosystems principally by assisting in the sexual reproduction of most wild plants and a wide range of crops (Klein et al. 2007, Ollerton et al. 2011). Growing evidence indicates a worldwide decline in insect pollinator diversity and populations (Goulson et al. 2008, Cameron

et al. 2011, Lebuhn et al. 2013) that threatens ecosystem service of pollination. Habitat loss and fragmentation, agrochemicals, invasive species, parasites, pathogens, light pollution, and climate change have been identified as contributing to these declines (Potts et al. 2010, Rundlöf et al. 2015, Forister et al. 2019). Recent climate change has already affected the distribution and abundances of numerous insect groups (Williams et al. 2007, Kerr et al. 2015), and future climate change is expected to become a major threat to crop pollination during the next decades (González-Varo et al. 2013). Climate change can be especially threatening to pollinator–host

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plant interactions, because phenological and spatial mismatches can occur as distributions of pollinators and host plants change (Memmott et al. 2007, Burkle et al. 2013). A better understanding of how climate change may contribute to declines in pollinator diversity and abundance that could lead to declines of plant species and crop productivity worldwide (Thomann et al. 2013), could help guide mitigation efforts.

Global declines in insect diversity and populations have raised concerns about the future of crop pollination (Klein et al. 2007, Lebuñ et al. 2013), especially regarding compromised pollinator groups, such as bees and butterflies (Wagner 2019). Crops depending on insect pollinators represent about 35% of the world's food supply (Klein et al. 2007), a number that is rapidly increasing due to agricultural expansion and the high demand for pollinator-dependent crops (Aizen et al. 2019). Currently, more than 70% of the 124 top global crop types are dependent directly on insect pollinators (Klein et al. 2007) and wild pollinators improve fruit set in at least 41 crop systems worldwide (Garibaldi et al. 2013). The global economic value of pollinator-dependent crops has been estimated at \$168.5 billion per year (Gallai et al. 2009). Furthermore, pollinator-dependent crops are, on average, 10 times more profitable than crops that are pollinated by wind, such as rice, wheat, or corn (Gallai et al. 2009). A decline in pollinator species would cause a decrease in the productivity of pollinator-dependent crops, translating to large economic losses.

Bees are the most important pollinators of food crops (Klein et al. 2007). In 2009, the total value of insect pollination to crops directly dependent on pollination services was estimated at \$15.1 billion in the United States, with wild pollinators (mainly wild bees) valued at \$8.7 billion (Calderone 2012). Managed bees, such as the honey bee, *Apis mellifera*, are bought or rented by crop growers as the primary pollinator of many crops (Aebi et al. 2012), though evidence suggests that where habitat is adequate, wild pollinators provide most of the pollination services (Winfree 2008, Venturini et al. 2017). Managed honey bees are not meeting agricultural demands due to the increases in cultivation of pollinator-dependent crops; additionally, they are sometimes less effective than wild pollinators and do not replace the contribution of diverse wild pollinators (Gallai et al. 2009, Garibaldi et al. 2013). While managed bees are the main pollinators in large monocultures, wild bees are essential to meet agricultural demands of pollination (Kerr et al. 2015) in croplands that present adequate habitat (Venturini et al. 2017), but threats such as climate change and land use change could cause important shifts in their distributions and compromise their populations (Kerr et al. 2015, Koh et al. 2016). Local extinction of bee species and decrease in bee species richness have been documented by revisiting sites sampled over a century ago and have been linked to deforestation and phenological changes influenced by temperature (Burkle et al. 2013). Climate and land use changes should

therefore be of concern especially for growing those crops that rely primarily on wild species.

Wild pollinators are especially important for crops whose flowers use buzz pollination, also known as sonication, to spread their pollen. Buzz pollination is a process in which the bees attach to the anther cone of the flower and contract their indirect flight muscles to produce vibrations. These vibrations are transferred to the flower by direct contact with the bee's body and, as a result, pollen is released from the anther (Vallejo-Marín 2019). Flowers that rely on buzz pollination have evolved multiple times, in 65 families (an estimated 15,000–20,000 species), including crops from the Solanaceae family, such as tomato, potato, pepper, and eggplant (Vallejo-Marín et al. 2010, De Luca and Vallejo-Marín 2013). Although these plants are capable of self-pollination as well, visitations by wild buzz pollinators increase pollen load, which increases fruit production and quality (McGregor 1976, Greenleaf and Kremen 2006, Silva Neto et al. 2013). Since honey bees cannot conduct buzz pollination, the plants are reliant on wild bees to increase their production. Common North American buzz pollinators include bumble bees, sweat bees, and carpenter bees (Winfree 2008, Cardinal et al. 2018). Because of the global decline in wild bees and because incorporating managed honey bees is not a viable solution to compensate the potential decrease in wild pollinator visits, the sustainability of those crops that rely on buzz pollination could be in jeopardy.

Although climate change is expected to have global effects on wild bee populations and therefore the productivity of crops dependent on pollination by wild bees, assessing the impacts on specific crops is challenging for multiple reasons. Most studied crops rely on a small number of pollinator species, such as the managed honey bee (Ashworth et al. 2009, Aebi et al. 2012, Saunders 2018), so the impacts of wild pollinators' declines might be greatly attenuated. Crops that rely on buzz pollinators, however, may be more sensitive to decreases in wild bees because managed honey bees may not pollinate these crops as effectively. Even when the diversity of wild bees within a region is acknowledged, the actual number of species that visit a certain crop is, in many cases, difficult to determine (Russo et al. 2015) or there may be little overlap in the composition of species visiting the same crop within a relatively small geographic region (a few thousand square kilometers; Adamson et al. 2012). Also, despite general trends indicating important decreases and distributional shifts in wild bees, the effects of climate change on wild bee communities show geographic differences, mainly due to the interaction with other threats such as land-use intensification (Kerr et al. 2015, Koh et al. 2016). Because optimal growing conditions vary by crop, climate impacts across crops and regions could be highly variable.

In this study, we use the case of buzz pollinators associated with tomato crops in North America to assess the potential impacts of climate change on a specific crop's

pollinator community. Tomato crops present an important economic revenue in North America and open-field tomato crops mainly rely on the pollination services of wild bees. We compiled information on bee species that buzz pollinate tomato crops in North America and estimated how climate change might affect their distributions. Our main objectives were to (1) assess potential future changes in distribution of individual buzz pollinators and patterns of species richness, and thereby identify regions with potentially high decreases in richness across North America, and (2) assess the overlap between areas with high density of tomato crops in the United States and a potential high decrease in pollinator richness. We compiled information on bee species identified as tomato pollinators in the literature and downloaded occurrence records of these species from the Global Biodiversity Information Facility (GBIF), an international open access biodiversity database. We used baseline (historical) and future projections of climatic conditions from four Global Circulation Models and two greenhouse gas emissions scenarios in ecological niche models to estimate the baseline and future potential distributions of suitable climatic conditions for the targeted species. We then aggregated those distributions to create maps of potential change in species richness across North America. Finally, we used a remote sensing derived crop layer to identify U.S. counties with high amounts of tomato crops, and overlapped these data with the maps of pollinator richness change in order to identify regions where the decrease in buzz pollinators might pose a higher impact on tomato production.

METHODS

Study area and species

We analyzed the potential change in climatic suitability under several future climate scenarios for 15 buzz pollinator species native to North America (Table 1). The species selected are known pollinators of tomato crops throughout North America, according to accounts published in peer-reviewed papers and other scholarly articles (Brewer and Denna 1980, Shelly et al. 1991, Kremen et al. 2002, Whittington and Winston 2004, Greenleaf and Kremen 2006, Klein et al. 2007, Winfree 2008, Winfree et al. 2008, Graham et al. 2015, Strange 2015, Aminatun and Putra 2017). From these resources, we compiled an initial list of 24 buzz pollinators of tomato crops; however, we eliminated nine species based on low occurrence data availability (see *Presence data*) and performance of initial ecological niche models (Appendix S1: Table S1).

Ecological niche models

Presence data.—Species' occurrence data necessary for training the ecological niche models were gathered at the extent of North America from the Global Biodiversity

TABLE 1. List of buzz pollinator species included in the study, with sample size of occurrences used to generate models, literature source associating species with pollination of tomatoes, and method used to split the occurrence data of each species into subsets for training and testing the models.

Species	Literature source	Number of occurrences	Method to subset occurrences
<i>Anthophora urbana</i>	Klein et al. (2007)	46	random seed
<i>Augochlora pura</i>	Winfree et al. (2008)	67	checkerboard
<i>Augochlorella aurata</i>	Winfree et al. (2008)	63	checkerboard
<i>Augochloropsis metallica</i>	Winfree et al. (2008)	86	checkerboard
<i>Bombus californicus</i>	Kremen et al. (2002)	62	checkerboard
<i>Bombus fervidus</i>	Winfree et al. (2008)	230	checkerboard
<i>Bombus griseocollis</i>	Winfree et al. (2008)	172	checkerboard
<i>Bombus huntii</i>	Strange (2015)	75	checkerboard
<i>Bombus impatiens</i>	Strange (2015)	243	checkerboard
<i>Bombus sonorus</i>	Brewer and Denna (1980)	29	random seed
<i>Bombus vosnesenskii</i>	Klein et al. (2007)	89	checkerboard
<i>Halictus confusus</i>	Winfree et al. (2008)	37	random seed
<i>Lasioglossum pectorale</i>	Winfree et al. (2008)	25	random seed
<i>Lasioglossum tegulare</i>	Winfree et al. (2008)	16	cross-validation
<i>Lasioglossum zephyrum</i>	Winfree et al. (2008)	5	cross-validation

Information Facility (GBIF), an open source of biodiversity data (GBIF: Global Biodiversity Information Facility 2019). We filtered the available species' records to include only museum specimen records, records within the species' known geographic range, and records from 1950 to 2000 to match the time span (± 10 yr) of the baseline (historical) climatic data set used to train the models (see *Environmental data*). Additionally, spatially duplicate records and records with missing latitude and longitude values, unknown georeferencing source, or unknown locality were removed.

Environmental data.—We downloaded raster climate data for North America with a spatial resolution of 1 km² from ClimateNA (AdaptWest Project 2015). Of the 27 bioclimatic variables available, we evaluated 26 for use in our ecological niche models for each species; we excluded one variable, mean annual solar radiation (MAR), because it did not extend south of the United States. ClimateNA houses climate variable data for

1961–1990, including seasonal and annual averages, minima and maxima temperatures, precipitation, moisture indices, and degree-days above and below certain temperatures. This time frame represented the baseline (historical) climate data used to train the ecological niche models. To reduce model complexity, we ran an initial modeling experiment in which we identified and removed from the final models the variables that contributed less than 5% to models for each of the 15 buzz pollinators. We did not use correlation analyses to decrease collinearity among variables because recent studies showed that Maxent's performance is not affected by collinearity (Tanner et al. 2017, De Marco and Nóbrega 2018, Feng et al. 2019). We trained the final models with subsets of variables that cumulatively contributed 95% to each species' ecological niche models (Appendix S1: Table S2).

Projections of future climate conditions are generated using General Circulation Models (GCMs) that incorporate global greenhouse gas emission scenarios. The most recent scenarios, known as Representative Concentration Pathways (RCPs), were developed as part of the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (2014). To capture variability and uncertainty of GCMs, we used three different GCMs downloaded from ClimateNA (AdaptWest Project 2015): GFDL-CM3, CCSM4, and INM-CM4. We chose these GCMs because they represent a high (GFDL-CM3), moderate (CCSM4), low (INM-CM4) change in temperature and precipitation for North America. We also used an ensemble GCM from ClimateNA, representing an average of 15 different GCMs (ACCESS1-0, CCSM4, CESM1-CAM5, CNRM-CM5, CSIRO-Mk3-6-0, CanESM2, GFDL-CM3, GISS-E2R, HadGEM2-ES, INM-CM4, IPSL-CM5A-MR, MIROC-ESM, MIROC5, MPI-ESM-LR, MRI-CGCM3). RCPs are scenarios that describe trajectories for greenhouse gas (GHG) emissions and concentrations (Van Vuuren et al. 2011). Our study included RCP4.5, where GHG concentration peaks in 2040, and RCP8.5, where GHG concentration rises continuously until 2100 (Intergovernmental Panel on Climate Change 2014). We downloaded and used in our analyses bioclimatic variables (the same as for baseline, above) for 2050s and 2080s, representing averages for years 2041–2070 and 2071–2100, respectively (AdaptWest Project 2015).

Maxent modeling.—Ecological niche models estimate the abiotic conditions associated with species' presence, under the assumption that climatic conditions are the main or one of the most important determinants of species' geographic ranges (Araújo and Peterson 2012). Thus, the model outputs are potential distributions that do not take into account other factors such as landscape heterogeneity, connectivity, or movement that affect species' distributions at regional to local scales. We used Maxent application version 3.4.1 to create ecological niche models based on baseline climate data and the

future climate projections. Maxent is a maximum entropy algorithm that models species' ecological requirements and estimates distributions using species' occurrence (presence) data and a random sample of 10,000 background (non-presence) locations from the landscape studied. The model is dependent upon constraints determined by the environmental conditions at the presence sites, contrasted with background sites (Phillips et al. 2017) and minimizes the relative entropy between the probability densities of the presence data and that of the landscape (Elith et al. 2011). Since our ecological niche models are limited to climatic data, we use the phrase “distributions of climatic suitability” to refer to potential distributions of species estimated with these models.

For the geographic extent at which to train the models, we used a minimum convex polygon approach. The polygons, generated in ArcMap 10.6 (Environmental Systems Research Institute 2013), surrounded the presence points of each species and extended out 10 km to account for possible undetected occurrences outside the boundary of recorded localities and local movements.

The occurrence data sets for each species were separated in training and testing samples using three different methods (Appendix S1: Table S3), based on number of presences available after applying the data filter described above in *Presence data*. For species with 50 or more occurrences, we used a checkerboard subsampling technique to reduce spatial bias (Muscarella et al. 2014). Spatial bias refers to the fact that survey efforts are generally dependent on accessibility (roads, proximity to populated places). We created a checkerboard by splitting our study area into 1-km² squares and randomly selected the presence data from half of the squares to train the Maxent models; the remaining presences were used to test the models. The checkerboard subsampling was performed in R 3.6 (R Development Core Team 2013). For species with 20–49 occurrences, we used a random seed method, where Maxent randomly chose 70% of the points as training data and 30% as testing. Models for species with less than 20 occurrences were five-fold cross-validated in Maxent by separating the data into five subsets and running five different model replicates, with each subset subsequently being used for testing. The five model replicates were converted to binary suitable-unsuitable predictions (see next paragraph) and the agreement among all five replicates was used as the final prediction. This is a conservative approach as it considers only areas that were predicted suitable by all replicates. Species occurrence data and testing method are presented in Appendix S1: Table S3.

The testing data were used to evaluate the model performance with two methods: area under the curve (AUC) of receiver operating characteristic and omission error (Fielding and Bell 1997). AUC evaluates the ability of the model to discriminate between presences and absences (Norberg et al. 2019); in the case of a presence-background algorithm like Maxent, AUC measures

ability to correctly predict presences relative to proportion of background samples predicted present; AUC values closer to 1 indicate most discriminant models, whereas values close to 0.5 correspond to models no better than random (Phillips et al. 2006). We considered models with an AUC of at least 0.7 to have an acceptable discrimination power (Elith et al. 2006). Omission error evaluates the model's inability to correctly predict known presences, thus it is a measure of model accuracy. To calculate omission error, model predictions are reclassified from suitability values ranging between 0 and 1 to binary predictions of suitable and unsuitable locations. We implemented a 10% training omission error threshold in Maxent, representing the suitability value at which 10% of our training presence points were predicted unsuitable (absent) for each species. Testing presence points corresponding to Maxent suitability values lower than the threshold value were considered incorrectly predicted unsuitable, thus omission error.

During the training process, Maxent calculates the cumulative contribution of each climatic variable to model accuracy gain across iterations generated, as a percent of the total contribution from all variables. We used the percent contribution values from an initial Maxent modeling experiment to select the variables that contributed cumulatively 95% to each species' model. We then used these subsets of variables (Appendix S1: Table S2) to run the final models and projected these models on future climatic conditions, from three GCMs and one ensemble GCM, two RCPs, and two time frames (2050s and 2080s).

Changes in distributions of pollinators

To study the differences in the potential distribution of climatic suitability estimated using different GCMs and RCPs, we generated binary maps for each buzz pollinator species using the 10% omission threshold (see *Maxent modeling*) for the baseline (1961–1990) and future time periods (2050s and 2080s) for the four GCMs and two RCPs. From binary maps, we calculated, for each species, the change in total suitable area (hereafter, total area change) and the decrease of the baseline suitable area (hereafter, baseline distributional loss). Total area change summarizes increase or decrease in area from baseline suitability to future suitability, regardless of geographic location (or spatial shift), whereas baseline distributional loss identifies future loss of suitability within the baseline suitable prediction, thus it is geographically explicit. Total area change and baseline distributional loss were calculated for each species, under each RCP and GCM, for 2050s and 2080s separately (Appendix S1: Tables S4, S5). To concisely illustrate trends in distributional changes of potential climatic suitability, we used box plots to summarize the variation among all GCMs and RCP for each species for the 2050s. We chose to highlight projections for the 2050s, because this time frame is temporally closer to

present conditions and may be of greater interest to resource managers and policy officials.

Last, we compared potential changes in species richness of buzz pollinators over time. We first compiled two sets of richness maps: one for the baseline distribution and one for the future predictions of climatic suitability. We did this by adding each pixel predicted suitable for our 15 species of pollinators, which resulted in a gridded map with values ranging from zero to 15, zero indicating lack of suitability for any species and 15 indicating suitability for all species. We also generated a map indicating change in richness by subtracting the richness map for the baseline climate conditions from the prediction of richness for future climatic conditions (for each GCM, RCP, and period). All maps were generated in ESRI ArcMap 10.6 (Environmental Systems Research Institute 2013).

Distribution of tomato crops in the U.S.

In order to identify potential impacts on U.S. crops from a predicted decrease in richness of buzz-pollinating species, we analyzed the overlap between species richness predictions and the current distribution of tomato crops. We created a tomato crop distribution map using the U.S. CropScape–Cropland Data Layer (USDA National Agricultural Statistics Service 2019). CropScape is an agricultural land use data set, revised annually, that covers the continental United States. CropScape is created from a combination of remote-sensing and ground-truth data and provides crop-specific georeferenced rasters with a spatial resolution of 30 m. Buzz pollinators can be brought into greenhouses for pollinating tomato flowers (Whittington et al. 2004) so we focused on field crops only, where pollination relies mainly on wild species. The CropScape data set is based principally on the classification of remote sensing imagery, thus our analysis excluded areas with greenhouse-cultivated tomatoes. Note that the distribution of field-grown tomato production across the United States is much broader than shown by CropScape, which includes only larger scale production that can be captured in satellite imagery.

We aggregated the area of tomato crops at the county level for the continental United States. To do that, we combined the tomato crop distribution map with the U.S. County Boundaries data set (U.S. Bureau of the Census 2000) and calculated the total tomato crop area, the proportion of tomato crops relative to the county area, and the proportion of tomato crops relative to the total cultivated area at the county level. Finally, we overlapped the distribution of tomato crops with the distribution of mean species richness change at the county level in order to identify areas in the United States where important tomato production coincided with projected severe decreases of pollinator species richness. We used R 3.6 to perform the calculations.

RESULTS

Performance of ecological niche models

Based on presence data (occurrences) available for each species, we used three methods to separate the data sets into training and testing subsets: checkerboard for nine species, random seed for four species, and cross-validation for two species (Appendix S1: Table S6). The choice of subsetting method had a small effect on the model discrimination metric, AUC (Fig. 1). Our Maxent models had relatively high discrimination power, indicated by the mean AUC value of 0.83 for all species; the minimum AUC value was 0.71, for *Bombus vosnesenskii* models, and maximum AUC was 0.93, for *Lasioglossum pectorale* models (Appendix S1: Table S6). The accuracy of models, measured with omission error, was moderate, with a mean omission error of 0.14 for all species and minimum of 0 for *L. pectorale* (most accurate model) and maximum of 0.32 for *B. vosnesenskii* (least accurate model; Appendix S1: Table S6).

Of the 26 bioclimatic variables considered in our analysis, 23 contributed to the models for at least one species; the three variables that did not contribute to any of the models were degree-days below 18°C, mean temperature of the warmest month, and mean annual

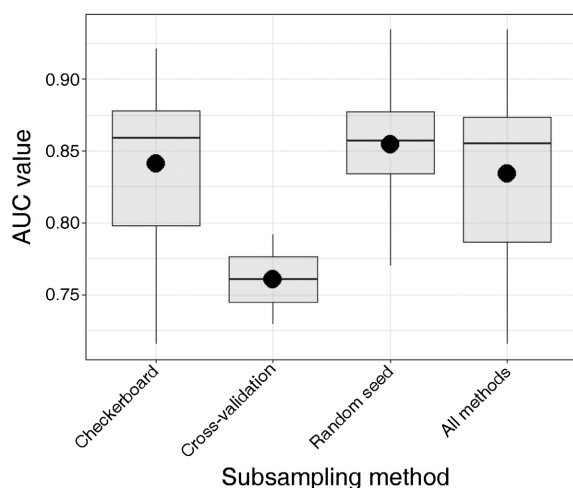


FIG. 1. Performance of ecological niche models measured as discrimination power with Area Under the Curve (AUC). Species' presence data sets were separated into training and testing subsets based on size of data set. Checkerboard subsampling includes nine species with 50 or more occurrences, cross-validation two species with less than 20 occurrences, and random seed four species with 20–49 occurrences. The discriminant power is considered acceptable at AUC > 0.7. The category all methods represents the total AUC value distribution over the three methods. Box plots illustrate the distribution of AUC values within each subsampling method. The length of the box represents the distance between the 25th and 75th percentiles. The point is the mean AUC value and the horizontal line is the median AUC value. The vertical lines extend to the minimum and maximum AUC values.

temperature (Appendix S1: Table S2). The lack of contribution of mean annual temperature to our models diverges from the results of Sirois-Delisle and Kerr (2018) in which this variable was one of four used to calibrate models for North American bumble bee species. However, several differences in environmental data (e.g., resolution, extent, interpolation method) preclude us from comparing our variable contribution results to those of Sirois-Delisle and Kerr (2018). The most frequently used variable, included in the models of 12 species, was precipitation as snow (mm), and the least used variables (for one species' model, three different species) were frost-free period, degree-days above 5°C, and summer (June–August) mean temperature (Fig. 2). The median number of variables used to generate models for each species was seven, the minimum was four (models of *B. sonorus*, *L. tegulare*, and *L. zephyrum*), and maximum number of variables was 11 (models of *B. californicus* and *B. fervidus*; Appendix S1: Table S2).

Species distribution projections

As expected, the forecasts of climatic suitability for individual species varied across the four GCMs and two RCPs considered, for each of the two time frames (Fig. 3). Differences in baseline potential suitability and future suitability forecasts for each species were summarized as total area change (gain or loss in total area predicted suitable, Appendix S1: Table S4) and as baseline distributional loss under future climate scenarios (Appendix S1: Table S5).

Total area change ranged across species, RCPs, and GCMs from 69% loss (*B. sonorus*) to 98% gain (*L. zephyrum*) in 2050s and 81% loss (*B. sonorus*) to 106% gain (*L. zephyrum*) in 2080 (Appendix S1: Table S4). For two species of *Bombus*, *B. impatiens* and *B. vosnesenskii*, estimates of future suitability increased (area gain) relative to baseline suitable area under most combinations of GCMs, RCPs, and time period; area loss was predicted only for *B. vosnesenskii*, 33%, under RCP 8.5, GFDL-CM3 GCM, for 2080s. Within an RCP and time period, the range of area gain varied greatly, for example 4–31% for *B. impatiens* across the four GCMs, under RCP8.5, for 2050s. For the remaining five species of *Bombus*, the forecasts of suitability decreased (area loss) under most GCMs, RCPs, and time period, relative to area estimated as suitable with baseline climate data; the largest area loss ranged across GCMs from 19% to 81% for *B. sonorus* under RCP 8.5, for 2080s. In the case of *Lasioglossum* species, the models projected the largest variation in total area change for *L. zephyrum*; within a time period and RCP, both suitability loss (maximum 41%) and gain (maximum 106%) were predicted across the four GCMs (Appendix S1: Table S4). These results indicate that the agreement among suitability estimates obtained with the four GCMs within an RCP and time period was low for some

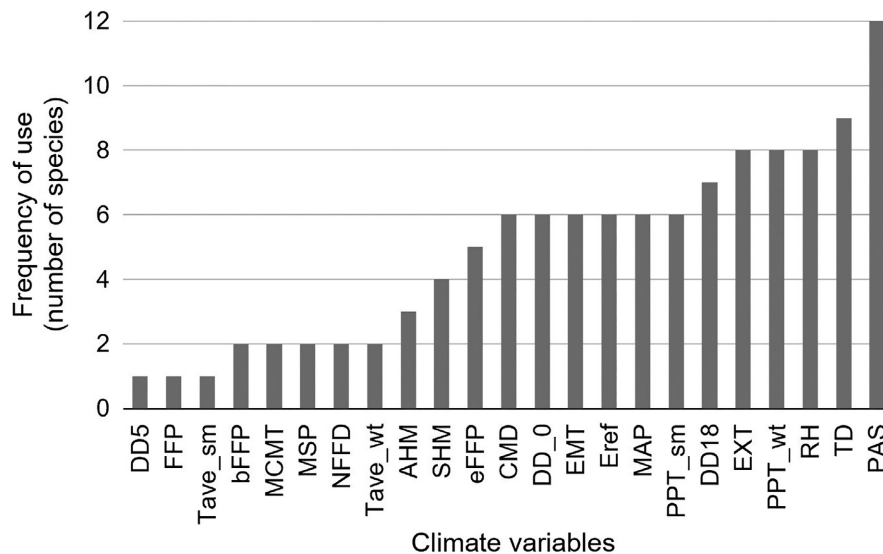


Fig. 2. Frequency of climate variables selected for ecological niche models of 15 buzz pollinator species. Frequency represents the number of species for which the models incorporated each variable. Variable abbreviations are DD5, degree-days above 5°C (growing degree days); FFP, frost-free period; Tave_sm, summer (June–August) mean temperature (°C); bFFP, the day of year (with 1 January = 1) on which the frost-free period begins; MCMT, mean temperature of the coldest month (°C); MSP, mean summer (May–September) precipitation (mm); NFFD, the number of frost-free days; Tave_wt, winter (December–February) mean temperature (°C); AHM, annual heat moisture index, calculated as $(MAT + 10)/(MAP/1000)$; SHM, summer heat moisture index, calculated as $MWMT/(MSP/1000)$; eFFP, the day of year on which the frost-free period ends; CMD, Hargreave's climatic moisture index; DD_0, degree-days below 0°C (chilling degree days); EMT, extreme minimum temperature over 30 yr; Eref, Hargreave's reference evaporation; MAP, mean annual precipitation (mm); PPT_sm, summer (June–August) precipitation (mm); DD18, degree-days above 18°C; EXT, extreme maximum temperature over 30 yr; PPT_wt, winter (December–February) precipitation (mm); RH, mean annual relative humidity (%); TD, difference between MCMT and MWMT, as a measure of continentality (°C); PAS, precipitation as snow (mm).

species (e.g., *Augochlorella aurata*, *B. sonorum*, and *L. zephyrum*).

We observed baseline distributional loss of climatic suitability (i.e., part of baseline suitable area projected as unsuitable in the future) for all 15 species studied, ranging, on average, from 17% for *Anthophora urbana* to 92% for *L. zephyrum* over GCMs, RCPs, and time periods (Appendix S1: Table S5). One of the GCMs, GFDL-CM3, consistently predicted higher baseline distributional loss, for all species, under both RCPs, and both time periods. The estimates obtained for the other three GCMs were comparable within a species, RCP, and time period. The extent of distributional loss estimated for each species was consistent, except for *L. tegulare*, for which estimated suitability loss varied more among GCMs (Appendix S1: Table S5).

Focusing on the distributional changes predicted for the nearer time frame, 2050s, comparisons across all GCMs and two RCPs (Fig. 3) showed that the climatic suitability for only five species was estimated to increase in the future (*Halictus confusus*, *L. tegulare*, *B. impatiens*, *B. vosnesenskii*, and *A. urbana*); one species, *L. zephyrum*, was estimated to experience little change in total suitable area; and the remaining nine species were estimated to experience loss in total area suitable. The variability in area loss estimates was large for

L. pectorale and *Augochlorella aurata*, two species for which the models also estimated the highest total area loss and baseline distributional loss of climatic suitability. Similarly, baseline distributional loss of climatic suitability was high for *Augochloropsis metallica*. In contrast, smaller losses of baseline distribution of climatic suitability were estimated for *L. zephyrum*, *L. tegulare*, *B. impatiens*, *B. vosnesenskii*, and *A. urbana* (Fig. 3). Because changes associated with GCM CCSM4 in the 2050s were relatively close to the mean, for the remainder of the paper we will present results and discuss species projections for CCSM4 climatic forecasts, unless specifically stated otherwise.

For most species, the projected patterns of climatic suitability obtained with CCSM4 were comparable between RCPs and time periods (Appendix S1: Fig. S1). For some species (*Augochlora pura*, *A. aurata*, *A. metallica*), the projected area loss was much larger than projected area gain (climatic suitability expansion northwards) for both RCPs and time frames (Appendix S1: Fig. S1). In addition to area loss, latitudinal shift in potential climatic suitability was observed for several species, compounding high area loss with high distributional shift, as was the case for *A. aurata* (Fig. 4). A combination of high area loss and low distributional shift was observed for *A. metallica*. In contrast,

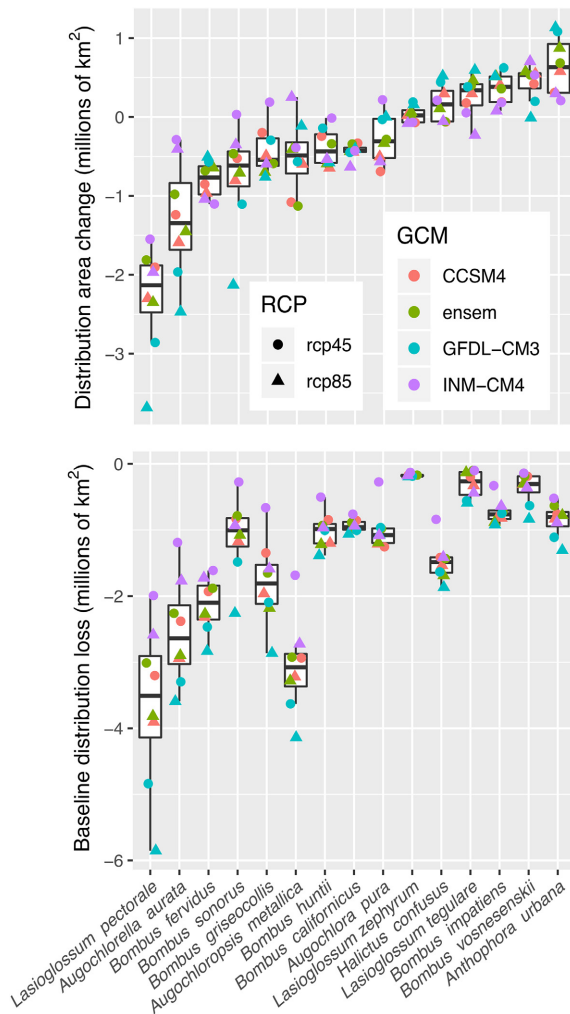


FIG. 3. Changes in individual species' distribution area for different General Circulation Models (GCMs) and Representative Concentration Pathways (RCPs) for the year 2050. The upper panel shows the total area change between suitability under the baseline (historical) climate and suitability estimated under future climate projections. The lower panel shows the projected loss in climatic suitability under future climate compared to baseline distribution. Box plots illustrate the median area change values across all GCMs and RCPs. The ends of the whiskers represent the lowest/highest values within 1.5 interquartile ranges (IQR) of the lower/upper quartile. Results for the rest of GCMs, RCPs, and for 2080s are shown in Appendix S1: Tables S4, S5.

a best case scenario would be low area loss and low distributional shift, such as for *B. vosnesenskii* (Fig. 4). A low area loss combined with high distributional shift was obtained for *B. impatiens*. The most pronounced northwards expansion of potential climatic suitability was projected for *A. metallica*, for 2080s under RCP 8.5; for two species, *A. metallica* and *A. pura*, this expansion was not coupled with contraction or shift of the southern limit of area predicted suitable under baseline climatic conditions, but with a considerable loss of the

central region compared to baseline potential of climatic suitability. Two *Bombus* species (*B. fervidus* and *B. impatiens*) were projected to shift their distribution northwards, without much overlap between baseline potential of climatic suitability and CCSM4 projected suitability (for both RCPs and time frames).

Changes in species richness

All future predictions using CCSM4 suggested net losses of pollinators in North America when compared to baseline pollinator species richness estimates (Fig. 5; Appendix S1: Fig. S2). On average, across all North America (all raster cells), under RCPs 4.5 and 8.5, species richness was predicted to decline in the 2050s by 0.2968 and 0.3010, respectively, and in the 2080s by 0.2184 and 0.2099, respectively. The largest contiguous areas of greatest species declines were predicted in the eastern and northeastern United States, with some areas losing up to 11 pollinator species by the 2080s under RCP 8.5 (Fig. 5); this pattern was predicted under all GCMs used in this study (Appendix S1: Fig. S2).

Despite models showing overall species richness declines, gains in suitable climate conditions for buzz pollinators were predicted in new areas at northern latitudes and in mountainous regions of western North America (up to 10 species gained) for all climate projections. While some of these gains reflect the forecast of climates at higher elevations becoming more suitable, other areas of predicted gain in the southern half of the United States, such as parts of Arizona, New Mexico, and Texas, may reflect climate conditions becoming more suitable for species with distributions primarily south of those states (Fig. 5).

Species richness changes in tomato-producing U.S. counties

We identified 394 U.S. counties with tomato cultivation documented in CropSpace (Appendix S1: Figs. S3, S4). For 29 of those counties, more than 1% of their total cultivated land was represented by tomato crops. Buzz pollinator richness within U.S. tomato-producing counties was predicted to decrease, on average, by 2.26 species, while the average decrease predicted for the continental United States (excluding Alaska) was 1.25 species (using the CCSM4 for 2050s and RCP4.5, Table 2; Appendix S1: Fig. S5). Predicted changes in species richness within tomato-producing counties for other GCM, RCPs, and projected time frames are shown in Table 2. In Appendix S1: Table S7 we present the CropSpace estimate of tomato crop area, total cultivated area, tomato crop proportions relative to the county area and relative to the total cultivated area, and change in pollinator species richness at the county level.

Large scale tomato crop production is unevenly distributed across the United States. We identified counties with high production of tomatoes on the west coast

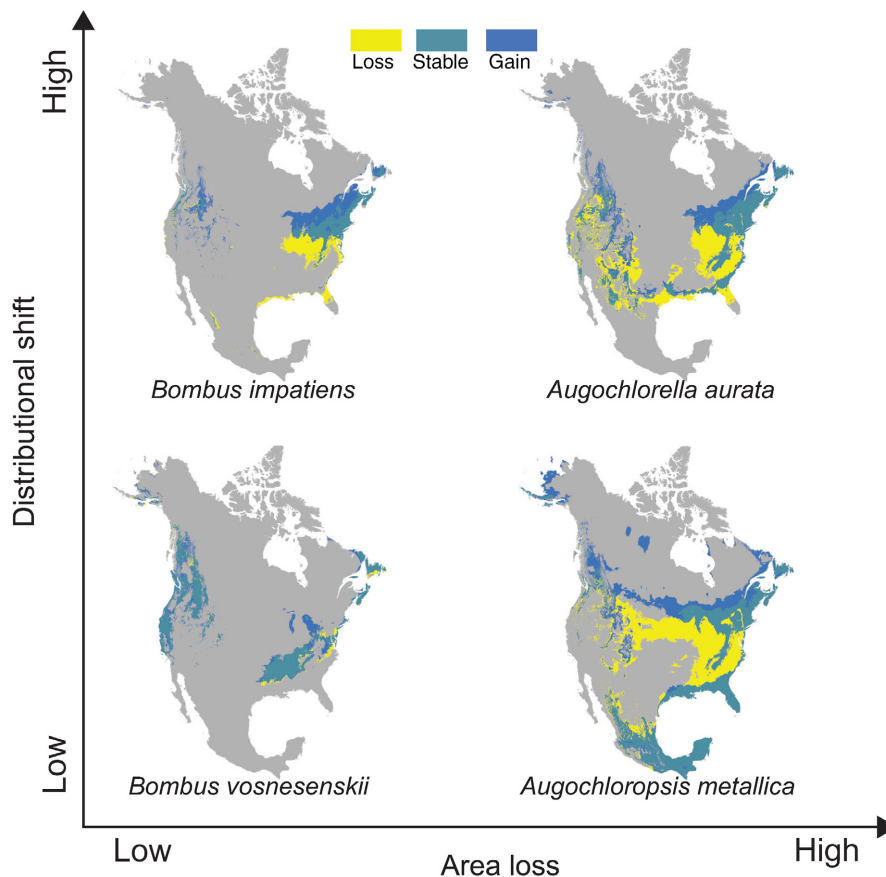


FIG. 4. Examples of area loss of projected climatic suitability and potential distributional shift under future climate conditions. The examples of species projections presented were generated using GCM CCSM4 and RCP 4.5 for the 2050s.

(mainly in California), south of the Great Lakes (e.g., Indiana and Ohio), and in the eastern United States (e.g., Pennsylvania, Tennessee, North Carolina, and Florida; Appendix S1: Fig. S3). Based on tomato production and potential change in pollinator richness, the potential impacts of richness decrease might vary greatly between regions (Fig. 6). Indeed, the largest areas predicted to have marked decreases in buzz pollinator richness are located mainly in the central and eastern United States. Counties in Indiana and Ohio constitute a large contiguous expanse of tomato crops with predicted decreases of more than five pollinator species for 2050s. For example, we estimated that the county of Putnam (Ohio) cultivates around 692 ha of tomatoes (0.6% of total cultivated land in the county) and our models predict a decrease of seven tomato pollinator species. Although with lower total crop area compared to other states, some counties in Tennessee and North Carolina present a high percentage of cultivated land as tomato production (Cocke, Tennessee, 4.4%; Henderson, North Carolina, 1.1%) are predicted to lose species richness (Cocke, Tennessee, 2.7 species decrease; Henderson, North Carolina, 2.6 species decrease).

On the other hand, some counties in California and other parts of the United States (e.g., Idaho and Arkansas) contain considerable expanses of tomato crops, but the predicted change in bee species richness is low. For example, a total of 33,538 ha of tomato crops is found Fresno county (6.2% of the cultivated area) in California, but the predicted change in species richness is near zero. In the county of Bradley, Arkansas, 48% of cultivated land is tomato crops (185 ha), and pollinator richness is predicted to increase by 0.8.

DISCUSSION

Despite mounting evidence suggesting that pollinator populations are decreasing and shifting their distributions worldwide (Cameron et al. 2011, Burkle et al. 2013, Lebuhr et al. 2013, Soroye et al. 2020), the potential impacts of these declines on specific crops are still poorly understood (Garratt et al. 2014). In this study, we considered several scenarios of climate change for the 2050s (2041–2070) and 2080s (2071–2100) and showed important potential decreases in the projected distribution of buzz pollinator species (e.g., *L. pectorale*, *A. arata*)

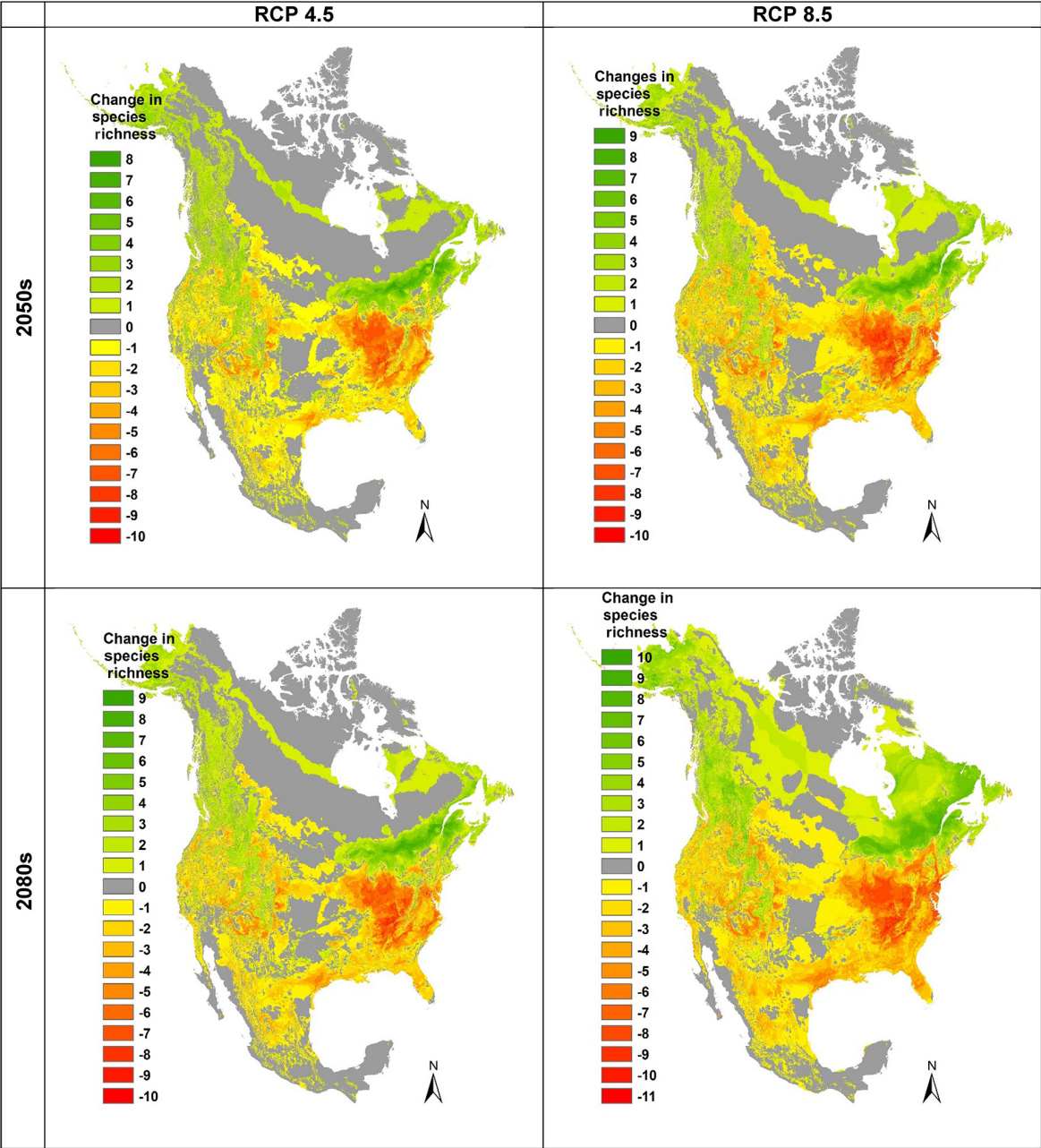


FIG. 5. Projected changes in pollinator species richness due to climatic changes calculated with General Circulation Model CCSM4, under moderate (4.5) and high (8.5) emission scenarios (Representative Concentration Pathway, RCP) and two future projection times (2050s and 2080s).

associated with tomato crops, in North America. Aggregated, our model outputs predict substantial species richness declines under future climates modeled for North America, especially in the eastern United States (up to 11 species decrease predicted for the 2050s), and we observed spatial correspondence between those declines and areas where tomato crop production is concentrated in the United States. In our view, this decrease in

potentially suitable climate conditions for buzz pollinators and associated bee richness could greatly affect tomato crop production and other buzz-pollinated crop production. We highlight the importance of crop-specific pollinator studies and discuss the challenges of modeling crop-specific pollinator distribution with limited presence data for developing reliable ecological niche models to project future distributions.

TABLE 2. Projected mean change in species richness within continental United States (excluding Alaska) and within counties that contained tomato crops.

GCM, RCP, and Year	Change in species richness	
	All counties	Tomato counties
CCSM4		
4.5		
2050	−1.25 (−23.1%)	−2.26 (−28.3%)
2080	−1.22 (−21.6%)	−2.28 (−30.1%)
8.5		
2050	−1.48 (−29.9%)	−2.60 (−34.5%)
2080	−2.04 (−40.5%)	−3.56 (−48.2%)
GFDL-CM3		
4.5		
2050	−1.63 (−27.4%)	−2.69 (−36.1%)
2080	−2.04 (−38.4%)	−3.17 (−42.9%)
8.5		
2050	−2.09 (−38.9%)	−3.35 (−45.0%)
2080	−2.77 (−58.0%)	−4.24 (−57.1%)
INM-CM4		
4.5		
2050	−0.53 (−10.1%)	−0.79 (−9.4%)
2080	−0.92 (−16.6%)	−1.72 (−21.6%)
8.5		
2050	−1.09 (−23.1%)	−1.73 (−20.4%)
2850	−1.44 (−28.0%)	−2.22 (−30.9%)
Ensemble		
4.5		
2050	−1.16 (−21.3%)	−2.13 (−27.9%)
2080	−1.35 (−25.2%)	−2.49 (−33.1%)
8.5		
2050	−1.50 (−29.0%)	−2.69 (−35.8%)
2080	−2.06 (−40.4%)	−3.50 (−47.5%)

Notes: Results for projected change in species richness are presented for four different global circulation models (GCMs), two emission scenarios (representative concentration pathways, RCPs), projected for 2050s and 2080s. Percentages of change in species richness are presented in parentheses.

We modeled the ecological niches based on suitable climatic conditions of 15 species of buzz pollinators, yet we initially considered a wider pool of candidate species. Several species were excluded due to lack of documentation regarding roles as regular pollinators. Data availability poses challenges for pollinator investigations in general (Bartomeus et al. 2019) and our set of well-documented buzz pollinators of tomatoes (24 species; see Appendix S1: Table S1) was reduced for modeling based on limited availability of occurrence points. In our initial pollinator set, six species had very few occurrence data points (four to five presence points), inadequate for building reliable models, thus we excluded these species (*Lasioglossum admirandum*, *L. albipenne*, *L. nymphaeae*, *L. pilosum*, *L. rohweri*, and *L. versatum*). Some of these species may be important pollinators of tomatoes, despite a dearth of occurrence data and may merit further investigation. We were able to obtain a reliable model with such a small sample size

(five presences) only for one species, *L. zephyrum* (Appendix S1: Table S1).

The small sample sizes in our study are in part due to our criteria for including occurrence data for each species. From the occurrence data available in GBIF, we used only museum specimen records to limit identification errors, and only latitude and longitude coordinates that had associated georeferencing sources listed to ensure reliability of the data. In our models we did not include GBIF occurrence data from iNaturalist, which are collected through citizen science efforts. Pollinator communities can be effectively monitored by citizen scientists, generating valuable data on species' richness and abundance; however, species that have low abundance or are hard to identify can introduce error in citizen science data (Kremen et al. 2011). Using records from such sources as iNaturalist, along with accompanying photos for identification confirmation and/or correction, could enhance the occurrence sample sizes and facilitate inclusion of more pollinator species in modeling studies (Suzuki-Ohno et al. 2017).

Our criteria for selecting presence records reduced the sample sizes used to refine ecological niche models, and for several species this required different methods of subsetting the data for model training and testing (random seed for four species, sample size 25–46 occurrences; cross-validation for two species, sample sizes of 5 and 16 occurrences; Table 1). Larger sample sizes (above 50 occurrences, for nine species) ensured a spatial subsetting of data, thus a stronger test of our models. The model discrimination metric (AUC) was lowest with the lowest sample sizes and cross-validation, but still above the value of 0.7, indicating reliable models (Fig. 1). However, we did not obtain reliable models for two species with moderate sample sizes (*Xylocopa varipuncta*, 22 occurrences; *L. imitatum*, 27 occurrences) and thus we did not include these species in our study. This result indicates that sample size requirements are different for different species, probably related to the species' prevalence and heterogeneity of climatic space. Generally, low prevalence (spatial distribution) produces more performant models (higher AUC) than high prevalence, for the same sample size (van Proosdij et al. 2016). In other words, models trained with the same number of occurrences will perform worse if trained on smaller geographic extent. We observed this pattern for *L. imitatum*, for which we obtained a low performance model with 27 occurrences over an area of approximately 663,000 km², and *L. pectorale*, with 25 occurrences over about 5.1 million km² generating a performant model, according to discriminant metric (AUC) and accuracy metric (omission error). The range of AUC values of the ecological niche models for the species in this study (Fig. 1) is comparable to that for models of *Bombus* species in Sirois-Delisle and Kerr (2018).

Overall, we chose a “cautious” methodological approach: our ecological niche models were trained on a

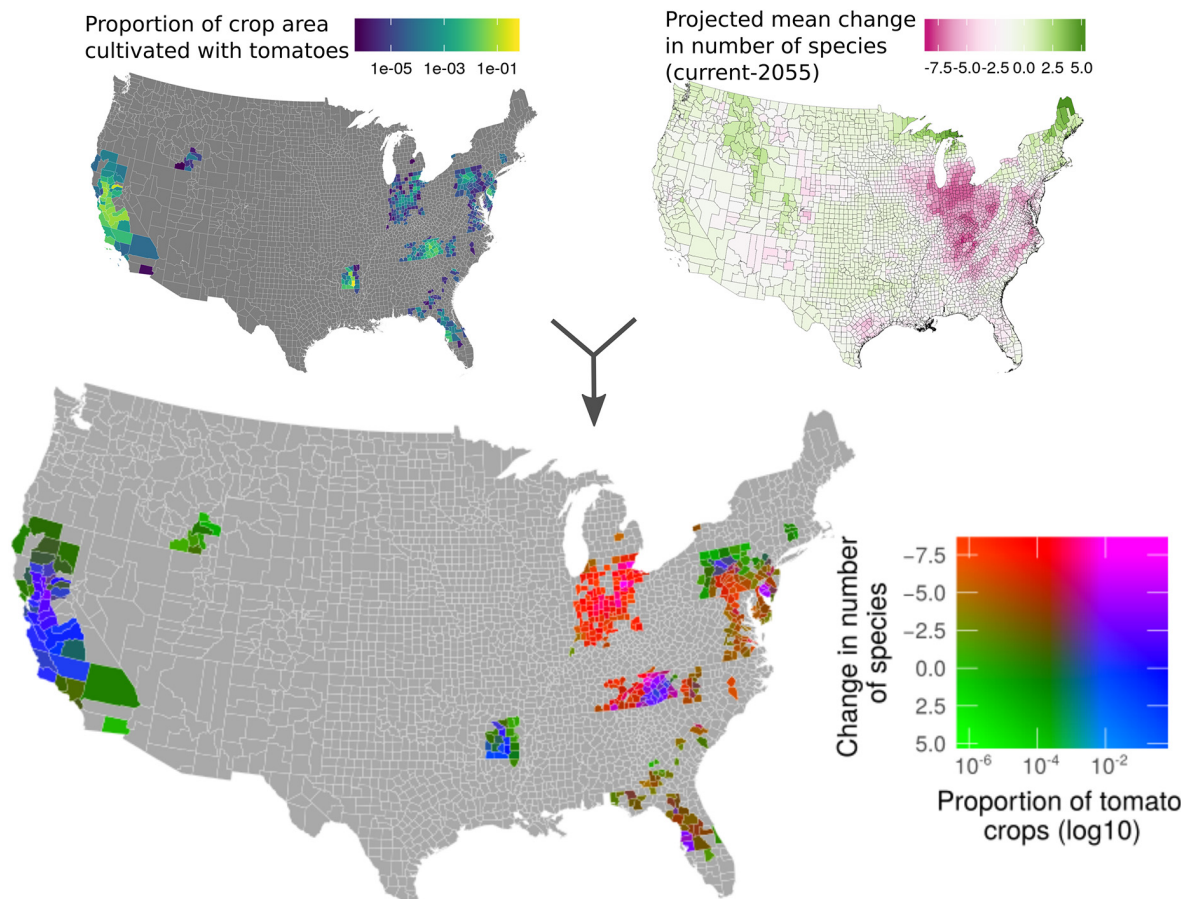


FIG. 6. Overlap between the proportion of tomato crops and projected change in pollinator species richness (for the year 2050; CCSM4, RCP4.5) at the county level. The top-left panel shows the proportion of tomato crops relative to the total amount of cultivated lands at the county level. The top-right panel shows the mean change in pollinator species richness at the county level.

quality-controlled subset of species' occurrence data downloaded from GBIF, we considered only agreement among model replicates from cross-validation to identify potentially suitable areas, we examined the distributional projections from each future climate scenario separately (rather than averaging modeling outputs), and we focused on distributional estimates obtained with the GCM forecasting moderate changes in temperature and precipitation (CCSM4). Thus, our calculations of total area change and baseline distributional loss may represent conservative estimates of distributional change for potentially suitable climatic conditions for some species. Estimated total area loss in 2050s increased for example for *A. aurata* from -35% to -54% and for *B. sonorus* from -26% to -69% under the climatic projections of high changes GCM (GFDL-CM3) and RCP 8.5 (high emissions scenario). However, for *B. impatiens*, these future climatic conditions predicted more area gain (31%) than CCSM4 conditions (24%). The estimated positive trend in total suitable area for *B. impatiens*, regardless of climate change scenario, is not surprising given work by Cameron et al. (2011) that showed that

this species has been stable across the United States in the past 100 yr, remaining abundant and widespread at over 3,000 sites sampled. We observed similar concordance between our estimates of future total area gain in suitability for *B. vosnesenskii* and long-term stability at the site level shown in Cameron et al. (2011). Last, our future potential distribution estimates are subject to the uncertainties associated with model transfer across different environmental conditions. Several studies have shown that model performance decreased when transferred to new environmental conditions (Owens et al. 2013, Feng et al. 2019, Qiao et al. 2019).

Our models projected decreases in pollinator species richness for all RCPs, GCMs, and time frames in the United States and overall in North America (although we did not consider non-native species). We found similar regions of richness decline for our suite of buzz pollinators as observed by other studies examining bumble bees (*Bombus* spp.) in North America (Sirois-Delisle and Kerr 2018, Soroye et al. 2020). The areas with the greatest projected decrease in species richness (in our study, from 13 to 2 species under some climate change

scenarios) were also the areas with the greatest baseline species richness. This may indicate that some pollinator species are sensitive to even moderate changes in climate.

Despite the overall decreases in species richness observed on a continental scale, gains in species richness were predicted in certain areas of the continent, primarily in mountainous regions and northern areas of North America. The trends of future climate projections driving species to higher elevations and/or poleward have been observed in projections for numerous species (Parmesan and Yohe 2003, Root et al. 2003, Hickling et al. 2006, Thomas 2010, Chen et al. 2011). However, small decreases, or even gains, in total area change may be misleading when considering future distributions of pollinators, if the distributional area of these projections is a result of elevational or latitudinal shifts. Although projected distributions that include new areas of suitable climate may be comparable in size to current distributions, it is uncertain if pollinator species will indeed readily colonize these new areas. In both North America and Europe, bumble bees have not expanded their northern range limits, yet ranges of some species have contracted significantly (up to 300 km) along their southern limits; these changes are attributed primarily to changing climates (Kerr et al. 2015, Soroye et al. 2020). Bumble bees and other bees may not migrate readily to regions of newly suitable climates, as simulations using high dispersal rates for bumble bees still predicted range contractions in North America (Sirois-Delisle and Kerr 2018). Even if colonization does occur in newly suitable areas, it could take decades or longer for species richness to approach that of regions with historically similar climate, especially for specialist bees since they depend on plant presence and phenological matching (Gauthier 2019, Rasmussen et al. 2020). Thus, regions of high species loss should be the focus of conservation efforts to mitigate some losses of bee species by enhancing bee habitat and creating dispersal corridors or “stepping stone” habitat patches (Settele et al. 2016, Gutiérrez-Chacón et al. 2020).

We observed geographical disparities in the projected change in species richness across North America, with implications to the potential impacts on tomato crops in the United States. For example, the number of tomato pollinator species is not projected to decrease significantly during this century in California, the leading tomato-producing state in the United States and the second largest producer of fresh market tomatoes (National Agricultural Statistics Service 2017). The largest fresh market tomato producer in the United States is Florida (National Agricultural Statistics Service 2017), but only slight decreases in pollinator richness are projected for some central and western areas of the state, and therefore the impacts might be limited. However, we detected sharp decreases of potential richness in central and eastern United States that overlapped with important tomato-producing states (e.g., Ohio, the third largest

fresh market tomato-producing state, with 56,000 tons of fresh tomatoes per year). Tomato plants are capable of self-pollinating, but the productivity decreases substantially in the absence of wild pollinators (Greenleaf and Kremen 2006, Bergamini et al. 2013). Bergamini et al. (2013) showed how native buzz pollinators increase the pollen load on the tomato flowers stigma, increasing productivity and quality. Consequently, a decrease in wild pollinators might have severe economic impacts for the U.S. tomato industry, especially for fresh market tomatoes, with an annual revenue (in 2018) of 814 million dollars (National Agricultural Statistics Service 2017). Currently, it is extremely difficult to calculate the exact economic loss derived from pollinators declines in abundance and diversity, although some studies have tried to quantify the ecosystem services of pollinators for individual crops (Lonsdorf et al. 2009). The potential richness loss described in this study could severely affect the economy of regions that rely heavily on tomato production. If recent trends of introducing captive buzz pollinator species (Evans 2017, Dabak and Özenirler 2018) are continued, the transition to greenhouse crops and the development of pollination strategies around captive species could mitigate potential economic losses associated with the loss of bee species richness.

Other economically important crops grown in North America benefit from buzz pollination, especially crops in the Solanaceae (e.g., potatoes, eggplants, peppers, or tobacco; Al-Abbadi et al. 2009, Dar et al. 2017) and Ericaceae families (e.g., blueberry crops; Button and Elle 2014, Gibbs et al. 2016). Our study could be informative to researchers and stakeholders working with those crops because some of the species analyzed here are also their primary pollinators. For example, *Bombus* spp. are well known pollinators of peppers and eggplants (Dar et al. 2017), and we show that species such as *Bombus impatiens* (one of the most common bumble bees in eastern North America) might lose the southern half of its distribution in the coming decades. *Anthophora* spp. are known pollinators of watermelon and canola (Kremen et al. 2002, Ricketts et al. 2008). Although we did not assess the whole suite of pollinators that visit these other crops, or the overlap between these crops and our maps of richness change, it is reasonable to assume that the production of crops that partly rely on the studied pollinators might be impacted, especially in the Northeast of the United States. For some crops, however, the presence of a common species could be more important than bee diversity (Adamson et al. 2012), so in these cases the projected climatic suitability for certain species could be more useful to assess potential impacts. Our richness change maps also can be useful to assess impacts on tomato or other crops that benefit from buzz pollinators in Canada and Mexico.

Studies that target specific crops and their associated specialized pollinators are important because they reduce the number of species to model. This simplifies the study system and decreases the accumulated

uncertainty associated with combining projected distributions for multiple species. Crop specific studies also help us target mitigation efforts to the most threatened areas, where crop distribution and a potential decrease of pollinator services overlap, and help us target the conservation of specific pollinator taxa (Garratt et al. 2014). Managing the habitats that surround the crops is one effective, local mitigation strategy (Garibaldi et al. 2011), mainly because the diversity of the surrounding floral resources increases pollinator richness (Kennedy et al. 2013, Garibaldi et al. 2014). For example, *A. ur-bana* and *B. vosnesenskii* abundance was affected by the landscape surrounding tomato crops in California (Greenleaf and Kremen 2006). Gemmill-Herren et al. (2008) studied the benefits of adjacent wild plants on eggplant production mediated by wild buzz pollinators.

Studies like ours, targeting pollinators of specific crops and estimating pollinator richness declines under climate change scenarios have, however, several inherent limitations. First, data on pollinator visits for specific crops are scarce (as discussed above), especially for large regions, which could lead to an underestimation of the pollinator community richness. Some species are less abundant or are only occasional visitors of certain plants so some pollinator–plant interactions might not be described in the literature. Additionally, presence data on some species are limited, potentially leading to an underestimation of current and future distribution ranges. Second, studies focusing on the decrease of targeted pollinator richness do not inform us about the population dynamics of the remaining species. Local community assemblages might change under local extinctions, and some species with lesser abundances could become primary visitors, establishing the ecosystem services. Also, bee phenology varies by species, so a model that includes species changes through the growing season would be more realistic. However, pollinator richness contributes to crop pollination efficiency even in the presence of highly abundant species (Garibaldi et al. 2014). Winfree and Kremen (2009) showed how the increase in abundance of some species does not replace the services provided by highly diverse pollinator assemblages. A decrease in richness may be therefore detrimental to crop production even under potential rearrangements of pollinator community assemblages. In any case, without better documentation of species richness, impacts of large scale species loss may be difficult to determine.

In summary, we projected ecological niche models for tomato pollinators on future climatic conditions and predicted important distributional shifts of several species, even with scenarios projecting moderate changes in future climate conditions and with a conservative modeling approach for some species. Our models indicate that substantial changes in pollinator species richness could occur during the next decades across North America. However, changes in species richness are projected to greatly differ for different regions, with eastern U.S.

experiencing the highest losses and eastern Canada experiencing gains. Tomato production in central and north-eastern U.S. counties might be at high risk due to climate-change-induced decrease in buzz pollinator richness. Our methodology and results could be applied to assess the threat to other tomato-producing areas in Canada or Mexico, and also to study other crops that benefit from this suite of buzz pollinators. Climate change will likely have distinct effects on pollination services across different regions and across different crops, and our study emphasizes the importance of assessing impacts on specific crops. However, it also highlights the challenges of compiling data and modeling climatic suitability for bee species associated with a particular plant. Our study could serve as a guide for future crop-specific studies. In order to decrease the uncertainty of climatic suitability models for crop pollinators, future work will need to focus on incorporating species population dynamics and phenological mismatches, and on improving our understanding of the current distribution of wild pollinator species.

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