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RESEARCH ARTICLE

Potential expanded pollinator distributions in North America under future climate

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Abstract

1. Pollinator species have declined globally during the last several decades due to a variety of factors, including habitat destruction and degradation, pesticides, disease and climate change.
2. To examine the effects of climate change on pollinator distributions, I modelled summer occurrences of pollinator species from North America under current climate (i.e. years 1981–2010) and predicted potential climate space for current, past (20, 10 and 6 thousand years ago) and future (six projections during 2071–2100, with North American warming of 4.3°C–8.8°C) climates.
3. Accuracies ranged in mean values from 0.93 for 12 fly species, 0.94 for 88 butterfly, 69 moth, and 17 wasp species, to 0.95 for 18 bee and 24 beetle species. Mean annual temperature was the most important variable for the greatest number of species. Centres of distributions moved about 500–650 km northwards during the interval from 20 ka to the current climate, which is similar to or less than shift distances, ranging from 500 km to 1350 km, predicted by end-of-century warming relative to the current climate. Generally, potential species losses, for these species overall centred in the United States, were indicated in Mexico, Central America, the Caribbean and most of the eastern half of the United States, relative to the number of species predicted under the current climate. The greatest absolute number of species was predicted to be lost in the eastern half of the United States. However, according to predictions, most pollinator species, including monarch butterflies (*Danaus plexippus*), may gain potential climate space in the future. Shifting to new locations is an additional challenge of climate change, particularly given current population declines under a range of stressors.
4. *Solution*. Management, restoration and citizen participation to provide resources and reduce stressors are ecological solutions to support declining pollinators and pollinator distribution shifts in response to climate change.

KEYWORDS
butterflies, climate change, insects, moths, paleoclimate, thinning

1 | INTRODUCTION

Animal pollination is necessary for the production of approximately 85% of flowering plant species (Ollerton et al., 2011). The degree to which animals pollinate depends on the movement of pollen through collection and deposition (Fishbein & Venable, 1996). Bees (Hymenoptera: Apoidea) are major pollinators due to intentional pollen collection. Flies (Diptera) may rank second as major pollinators, becoming more important pollinators at high latitudes (Larson et al., 2001; Orford et al., 2015). Beetles (Coleoptera) are bulk pollinators but imprecise, transporting pollen after eating flower parts (Larson et al., 2018). Wasps (Hymenoptera: Apocrita) are likely to be major pollinators, whereas butterflies and moths (Lepidoptera) and ants (Hymenoptera: Formicidae) may have minor roles in carrying pollen (Larson et al., 2018). Many insects may be at least accidental pollinators, through the use of flowers as substrates for perches, shelter, food and reproduction. For example, grasshoppers, locusts and crickets (Orthoptera) have been documented with pollen gathered on antennae and legs while feeding on flowers (Tan et al., 2017). The study of unconventional pollinators is in development, with challenges confirming pollination (Hassan et al., 2019).

Recently, rapid simultaneous declines of up to 40% of all pollinator species have occurred globally, with highly visible decreases in honeybees (*Apis mellifera*) and monarch butterflies (*Danaus plexippus*; IPBES, 2016; Koh et al., 2016; Potts et al., 2010; Winfree et al., 2009). Beginning in 2006, all or the majority of honeybees disappeared from some hives, a phenomenon known as colony collapse disorder (Winfree et al., 2009). Managed honeybees, which were domesticated at least 9000 years ago in Eurasia and introduced to North America during the early 1600s, are the most monitored pollinators (Roffet-Salque et al., 2015). However, native pollinators also have decreased. Monarch butterflies of eastern North America have declined about 85% since the mid-1990s, while the smaller western North American population has decreased 99% (Thogmartin et al., 2020).

Intensive research has not identified a single culprit that is responsible for general declines in pollinators and other animals, other than cumulative resource use by humans (IPBES, 2019; Koh et al., 2016; Potts et al., 2010; Winfree et al., 2009). Identified threats to pollinator populations include widespread habitat loss and degradation, reduced quantity and quality of floral resources, pesticides and associated chemicals, introduced diseases from non-native species, competition with non-native species, collisions with vehicles and climate change (Kantola et al., 2019; Potts et al., 2010; Vanbergen et al., 2013; Winfree et al., 2009). Nonetheless, examples may be found of pollinator declines in locations that are lacking one or more potential factors; for instance, much of the eastern United States has not warmed during the past 30 years, albeit precipitation has increased, and other climate components may have changed (Hanberry, 2022a).

Climate change will influence the growth, survival, and reproduction of plants and animals, as well as the timing and length of periodic events (i.e. phenology; Bartomeus et al., 2011; Bale & Hayward, 2010). Current climate change, driven by greenhouse gas emissions, encompasses warming temperatures and precipitation shifts, increased variation in precipitation resulting in droughts and floods, prolonged heat waves and reduced duration of snow cover (Karger et al., 2017). Heat and drought may reduce the quantity and quality of flower and nectar resources for pollinators, causing population declines (Ogilvie et al., 2017; Thomson, 2016). Climate change increasingly is affecting wildlife and ecosystems through interactions among extreme weather events, habitat and resource loss, phenological changes, physiological stress and increased vulnerability to disease. For example, a winter storm in 2002 combined with forest loss and degradation in the Monarch Butterfly Biosphere Reserve, the location of the concentrated overwintering monarch butterfly population in central Mexico, resulted in an estimated 75% mortality, up to 500 million monarchs, which is many times larger than the current North American monarch population (Brower et al., 2004). Interactions among climate change, land use and disturbances likely will result in a cascade of issues and perhaps change the direction of responses counter to expectations based on climate change alone (Chen et al., 2011).

As temperatures increase, the geographic ranges of plant and wildlife species are predicted to move poleward, or upward for montane species, at unique rates and trajectories, resulting in disrupted ecosystem assemblages (Chen et al., 2011; Davis & Shaw, 2001). Species distributions are complex, comprised of various densities spatiotemporally. Leading and trailing distributional edges may be multidirectional and more complex than under past climate change, angled in different directions based on land-use gradients rather than along temperature gradients (Hanberry, 2022a). Land-use stresses in addition to climate change may particularly place pressure on ecosystem integration. Isolated species with limited connectivity of habitat, rare species after extirpations and habitat specialists may be particularly vulnerable (Crone & Schultz, 2021; Sáenz-Romero et al., 2012). Species may be vulnerable to climate change because their ecosystems are vulnerable, such as cold-limited ecosystems with substantial snowpack or tree species of high elevations, including *Abies religiosa* in the Monarch Reserve in Mexico, the overwintering site for most North American monarch butterflies (i.e. the eastern population; Sáenz-Romero et al., 2012). In response to climate change, monarchs may become non-migratory or locate to more northern overwintering sites (Crone & Schultz, 2021). Species may respond to habitat changes by shifting to new distributions in conjunction with phenotypic and genetic adaptations, adapting within their current range, or decreasing in isolated and increasingly contracting refugia, with different responses possible by population (Aitken et al., 2008; Comte et al., 2024; Davis & Shaw, 2001).

Traits are inconsistent predictors of species responses to climate change, in part because traits (e.g. given plasticity), exposure to climate change and range shifts are challenging to measure (Beissinger & Riddell, 2021; Hällfors et al., 2024). Generalist and non-native species typically have strong dispersal abilities, rapid

growth rates with short generation times, and great capacities to tolerate broad and changing environmental conditions, allowing both range shifts and adjustments in place (Berg et al., 2010; Chen et al., 2011; Comte et al., 2024). Equally, species that have specific tolerances may need to migrate to maintain a narrow range of climate relative to species with broader tolerances (Hällfors et al., 2024). Nonetheless, climate change may favour slower-growing, stress-tolerant species that can survive drought and extreme weather events rather than favouring generalist and non-native species, which have fast life-history stages (Minckley et al., 2013). While specialist pollinator species dependent on few plant species may be more sensitive to drought than generalist species (Settele et al., 2016), bees specialized to feed on drought-sensitive plant species may respond to low growing-season moisture cues by remaining in diapause (Minckley et al., 2013), thereby potentially avoiding unfavourable conditions and food shortages. Despite apparent vulnerabilities, species with slow life-history stages that are seasonally inactive, through aestivation or diapause, may be able to avoid unfavourable conditions that create water and food shortages.

Given unknowns about how taxa and species will respond to climate, bioclimatic models are applied to predict species distributions as a function of climate (Hanberry, 2023a). Although a singular focus on climate is transparent, many caveats exist related to species distributions and climate. Foremost, for declining species, such as some pollinators, recorded observations for contracted ranges will not encapsulate the entire climate space of the species (Hanberry, 2023a). During the extirpation process, some species may possibly lose traits for tolerance to climate of historical ranges because species are composed of populations, sometimes subspecies, genetically suited to the climate of their locations (Aitken et al., 2008). Species distributions based on climate are not equivalent to realized ranges, due to effects from land use and other human activities, competition, dispersal barriers and additional constraints (Coristine et al., 2016; Dennis et al., 2013; Hanberry, 2024a). Therefore, species may not express their full tolerances to climate until released from those limitations, as may occur when species are introduced outside of native ranges (Early & Sax, 2014). Additional modelling uncertainties in species distribution models arise from variations in climate general circulation models, differences in downscaling of climate data, and modelling choices in input climate variables and modelling algorithms that produce different prediction outputs (Hanberry, 2024a). Uncertainty occurs in modelling, which increases when modelling through time.

Relatedly, the major prerequisite for generating representative species distributions is that conditions of species distributions must be sampled to generate representative models (Gábor et al., 2020; Hanberry, 2024a; Thuiller et al., 2004) Any measurements and sampling involve errors, particularly for spatial distributions. For example, while human populations are well measured, multiple gridded population models distribute human densities with very different spatial dispersion patterns (Chen et al., 2020). Georeferenced records of species observations with tagged coordinate uncertainty in metres (<1 km) are the highest standard in accuracy. However, sampling will be concentrated in accessible areas, which is known as sampling bias, although predictive modelling is not statistical hypothesis testing (Gábor et al., 2020; Lamboley & Fourcade, 2024; McCarthy et al., 2012; Ten Caten & Dallas, 2023). Given enough samples of the climate amplitude for species ranges, indicated by at least 400 georeferenced records, modelling algorithms are able to generate representative species distribution models, gaining enough information to use, discard or discount errors and sampling bias (Gaul et al., 2020; McCarthy et al., 2012; Mitchell et al., 2017; Smith et al., 2023; Steen et al., 2021). While data processing should control basic inputs (i.e. missing and duplicated coordinates, locational uncertainty), routine removal of potential locational errors (e.g. outliers, records near administrative centroids and urban areas) and concentrated samples (i.e. thinning or filtering of sampling bias) is applied without evidence as a precaution to prevent poor models (Smith et al., 2023; Steen et al., 2021). However, deliberately withholding information by cleaning coordinates and other unsampling approaches, such as thinning, can create modelling uncertainty, overpredictions, underpredictions and unrepresentative models if the modelling algorithm does not have enough information to separate suitable conditions from unsuitable conditions (Gaul et al., 2020; Lamboley & Fourcade, 2024; Mitchell et al., 2017; Ten Caten & Dallas, 2023). Indeed, outlying records can help with likely undersampling of the climate amplitudes of the species ranges, reducing omission error (Smith et al., 2023). If enough information is available, reducing sampling bias by thinning samples may create slight differences by reducing precision due to concentrated samples and increasing the generality of models.

Baseline information about unmanaged pollinator populations is very sparse (Pollinator Research Action Plan, 2015). Here, my objective was to supply North American pollinator models of summer distributions based on current climate (1981–2010), with predictions to past climate of 20 thousand years ago (ka), 10 ka and 6 ka, and to six end-of-century climate general circulation models for moderate (SSP3-70) and high (SSP5-8.5) radiative forcing scenarios, which track realized emissions (Schwalm et al., 2020). I provided information about conventional pollinators of butterflies, moths and bees, and other potential pollinator species from wasp, beetle and fly families. In addition to generating models of potential climate space, my questions to answer with the modelled predictions were: How far will modelled distribution centres shift in latitudinal distance over time, relative to the past? Will species lose or gain climate space over time? What percentage of species will change over time by states or provinces (i.e. first level administrative divisions)? While species distribution models are not likely to be perfect, they can accurately model the samples and be representative of species if provided input samples from most of the climate amplitude of species ranges. Species distribution models supply a forecast about the magnitude of climate change in effects on species for biodiversity management.

2 | METHODS

2.1 | Extent, species data and pseudoabsences

Basic data processing controlled duplicated and missing coordinates, locational uncertainty, collection years, basis of record (i.e. observation type) and terrestrial coordinates. The modelling extent was the North American continent, encompassing Central America, the Caribbean and Greenland (Figure 1). From the Global Biodiversity Information Facility (GBIF; Global Biodiversity Information Facility, 2022), a centralized data repository containing 65,000 datasets of 2 billion species observations, I selected North American species (i.e. to the species level) that were observed or preserved specimens (not fossil records or with an unknown basis of record) since 1990 during the summer months of June, July and August, with coordinate uncertainty of less than 1000 m (GBIF occurrence downloads: https://doi.org/10.15468/dl.jhqkjh, https://doi.org/10.15468/dl.3trxwn, https://doi.org/10.15468/dl.9bv85f during March 2022). Additionally, I retained only species that had at least 1000 unique locations to achieve sample sizes necessary for representative models. Species occurrences that did not extract climate variables for the North American extent (i.e. terrestrial locations) were discarded. The selection process resulted in 88 butterfly species, 69 moth species, 18 bee species, 17 wasp species, 24 beetle species and 12 fly species with at least 1000 unique locations (Table S1). The GBIF database does provide reconciliation in synonyms and will retain older genera names (e.g. *Adelpha bredowii* and *Limenitis bredowii*), but inconsistencies still exist with synonyms (e.g. https://github.com/gbif/portal-feedback/issues/3427).

Due to concerns about proportional sampling and coordinate errors, I also performed a sensitivity analysis to determine effects

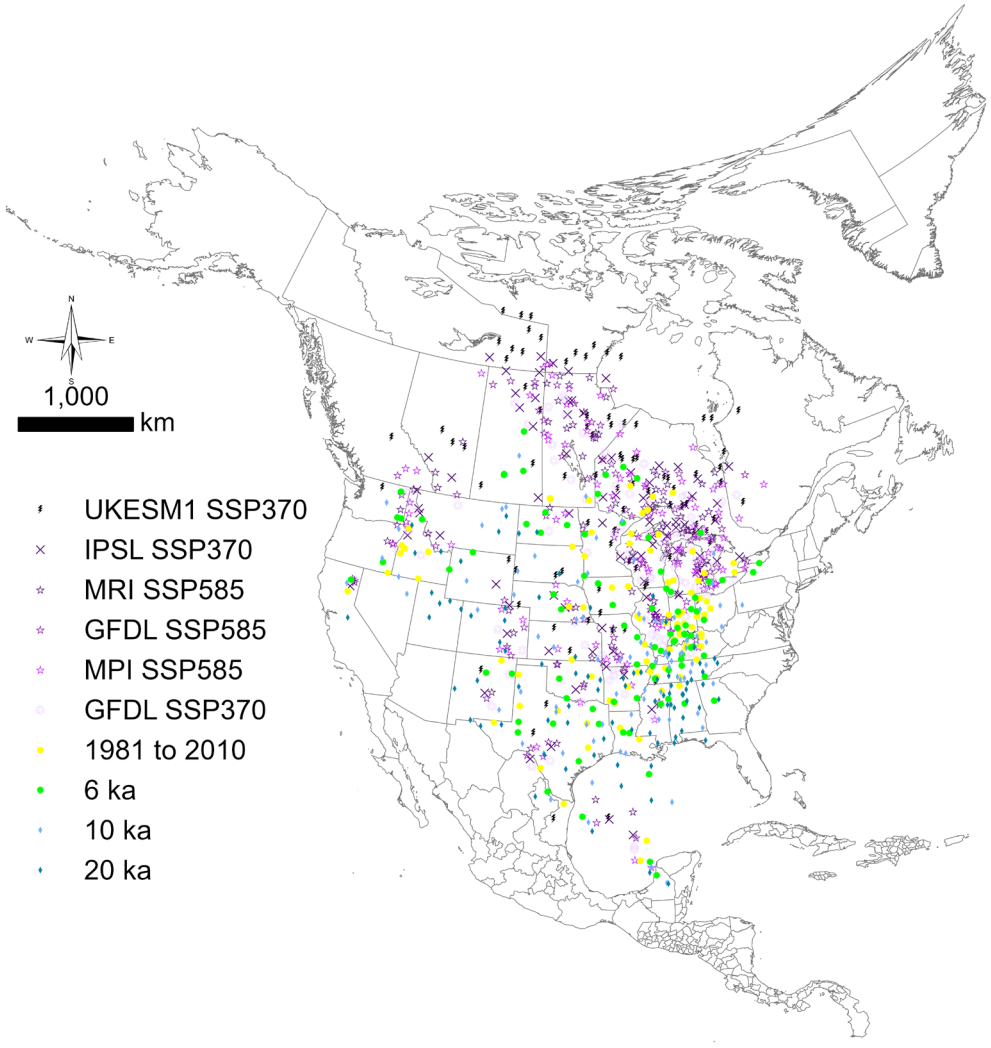

FIGURE 1 Study extent and centres of distribution during 20 ka, 10 ka, 6 ka, current (1981–2010) and six end-of-century (2071–2100) general circulation models for butterfly species. Future climates were the SSP3-7.0 (SSP370) scenario general circulation models GFDL-ESM4 (GFDL; Geophysical Fluid Dynamics Laboratory, USA), IPSL-CM6A-LR (IPSL; Institut Pierre Simon Laplace, France) and UKESM1-0-LL (UKESM1; Met Office Hadley Centre, UK) and the SSP5-8.5 (SSP585) scenario general circulation models GFDL-ESM4 (Geophysical Fluid Dynamics Laboratory), MPI-ESM1-2-HR (MPI; Max Planck Institute for Meteorology) and MRI-ESM2-0 (MRI; Meteorological Research Institute).

on butterfly species models by (1) thinning records (i.e. removal of clustered records within the same climate pixels), (2) removing urban records, (3) thinning and removing urban records, and (4) thinning, removing urban records and removing records flagged as outliers or within 1 km of country and province centres or biodiversity institutions (dismo package for R; Hijmans et al., 2011; CoordinateCleaner package for R; Zizka et al., 2019). The most extreme removal of samples resulted in sample sizes ranging from 481 records to 13,046 records. After modelling (see methods below), I calculated niche overlap (i.e. geographic distance or similarity index) between predictions from species distribution models with removed errors and the baseline species distribution models from unthinned georeferenced records. For niche overlap, I selected the Hellinger distance similarity index scaled from 0 to 1 to match the range of predicted probabilities (dismo package for R; Hijmans et al., 2011) but only compared areas where either model predicted ≥0.5 probability of presence.

In addition to non-native honeybees (*Apis mellifera*), some of the abundant 228 modelled species had a status that was non-native, at least in parts (Pagad et al., 2022). *Bombus impatiens* was native to the United States and Canada, but not considered native in Mexico. Equally, some species were native to parts of the United States, but not others, such as the monarch in Hawaii. Lady beetles (Coccinellidae) of *Coccinella septempunctata*, *Harmonia axyridis* and *Propylaea quatuordecimpunctata* have been established intentionally in North America as biological control agents of aphids (Aphidoidea). *Lymantria dispar* is a forest health concern. *Exomala orientalis*, *Pieris rapae*, *Polydrusus formosus*, *Popillia japonica* may damage cultivated plants. *Anthidium manicatum*, *Eristalis tenax*, *Noctua pronuba*, *Polistes dominula*, *Rhagonycha fulva*, *Syritta pipiens* and *Thymelicus lineola* are non-native species.

For pseudoabsences, where species are not known to occur, I generated an equal number of random points from the study extent, or background, as the number of occurrences for each species (after filtering coordinates and extracting climate data; Barbet-Massin et al., 2012; Menardi & Torelli, 2014). Therefore, the modelling prevalence of the number of presences and pseudoabsences was equal, which allows model standardization and also ensures that the modelling algorithm equally models the presence and absence classes, rather than favouring one class. This provides a consistent modelling basis to use modelling prevalence values as the threshold to convert continuous predicted probabilities back to discrete presence and absence classes (i.e. Hanberry & He, 2013). Indeed, the default probability threshold for binary classification, of presence and absence, is 0.5 (Kuhn, 2008).

Pseudoabsences were from the full study extent, in this case, a continent for continental distributions. Just as species occurrences need to cover the full environmental range of the species, or the model will not be able to identify suitable conditions for species, so should background samples cover the entire study extent to provide a full range of environmental values so the models can differentiate unsuitable conditions (Barbet-Massin et al., 2012; Thuiller et al., 2004). Constraining pseudoabsences to the presence environmental space will underpredict presences within the species distributions; that is, it will interfere with modelling the known observed space so that predictions of presence do not match occurrence points (Hanberry et al., 2012). Indeed, more representative models of ranges occur if pseudoabsences occur outside of the presence environmental space (Hanberry, 2023a). In addition, ensemble or machine learning algorithms, such as random forests (see below), cannot extrapolate outside of the training data. Withholding the full range of climate values, extending from boreal to hypertropical zones, from the modelling process will degrade delineation of the species distribution boundaries when predicting to climates of the future or past (Thuiller et al., 2004).

2.2 | Climate data

Regarding climate, I obtained 30-year climatologies for 1981–2010 and 2071–2100 and 100-year climatologies for 20 ka, 10 ka and 6 ka (resolution: 30 arc seconds and future climate: downscaled and debiased; Karger et al., 2017, 2018, 2020, 2021). For future climate, from the latest phase of climate simulations, Coupled Model Intercomparison Project Phase 6, I used a range of climate for the moderate SSP3-7.0 scenario: GFDL-ESM4 (GFDL; Geophysical Fluid Dynamics Laboratory, USA), which projected an increase of 4.3°C mean annual temperature for North America (excluding Greenland), IPSL-CM6A-LR (IPSL; Institut Pierre Simon Laplace, France) with an increase of 6.3°C mean annual temperature and UKESM1-0-LL (UKESM1; Met Office Hadley Centre, UK) with an increase of 8.8°C mean annual temperature. Additionally, I used similar climates, with increased temperatures of 5.2°C–5.9°C in North America, from the fossil fuel-driven SSP5-8.5 scenario general circulation models GFDL-ESM4 (Geophysical Fluid Dynamics Laboratory), MPI-ESM1-2-HR (MPI; Max Planck Institute for Meteorology) and MRI-ESM2-0 (MRI; Meteorological Research Institute).

For variables, I selected 13 bioclimatic variables that quantify temperature and precipitation at annual, seasonal and monthly intervals (i.e. mean annual temperature, maximum temperature of the hottest month, minimum temperature of the coldest month, mean temperature of the coldest and hottest 3 months, mean temperature of the driest and wettest 3 months, annual total precipitation, precipitation during the driest month and driest 3 months, precipitation during the wettest month, and precipitation during the coldest and warmest 3 months). I extracted climate values at each of the species occurrence coordinates. I likewise extracted climate variables for the pseudoabsence points.

2.3 | Modelling

For modelling each species, I applied an iterative process to reduce the number of current climate variables to the most important variables with the random forests classifier, an ensemble non-linear model, and 10-fold cross validation repeated three times

for hyperparameter tuning, and then used the final model to predict potential distributions for each climate interval (caret package; Hanberry, 2024a; Kuhn, 2008; R Core Team, 2022). Ensemble non-linear models distinguish correlated strong predictors (i.e. temperature variables) rather than splitting the explanatory value into intermediate importance (Hanberry, 2023b, 2024a). Elimination of important variables can result in biased models that do not fit well, but parsimony in the number of climate variables increases generalization (i.e. instead of overfitting with too many rules) and insight about variable importance (Hanberry, 2023b, 2024a). A variable reduction process provides some balance between underfitting due to not enough important variables and overfitting due to constraints from numerous variables.

Therefore, modelling occurred in a series of steps, starting with variable reduction. First, I used random forests recursive feature elimination, which builds a model based on all variables, rank-orders variable importance, and removes variables with the least importance based on accuracy, to reduce the number of variables to eight. Then, with random forests and 10-fold cross validation, repeated three times, I iterated through the modelling process twice. The first time was to retain only variables that carried an importance value ≥10 (out of 100 scale; note that other classifiers will assign weights differently) to end up at about half of the input variables, varying by species, but added back annual precipitation if no precipitation variable was important. The second time was to determine the importance of retained variables. Then, I directed these modelled variables to two different pathways. With all the samples, I predicted distributions with the different climate intervals. For samples partitioned into training (75% of samples) and test (25% of samples), I calculated accuracy metrics of sensitivity, specificity and balanced accuracy or the mean of sensitivity and specificity, given that single score evaluation statistics have come in and out of favour (Fernandes et al., 2019).

2.4 | Changes in distributions

As for distance and area summaries, layers were projected to the Albers projection (Snyder, 1987). Species were considered present if the predicted probability was ≥0.5, which matches the modelling prevalence and allows for consistency in comparisons. I located the centres of each distribution and determined the latitudinal distances of each past and future interval relative to the centroids of current climate. For results by species, I used the ratio of mean total area of distributions predicted by six future climates to the area predicted under current climate. For relative species losses and gains by first-level internal administrative country divisions, I used ratios of the future number of species compared with the current number of species. Specifically, a species loss occurred if present under current climate and absent under five of six future climates (i.e. supported by most climate projections) and a species gain occurred if a species was absent under current climate and present under five of six future climates. The total area for a species to be counted as present had a threshold of ≥250 km^2 by administrative unit to prevent the inclusion of unlikely potential distributions in disjunct yet appropriate climate space.

3 | RESULTS

3.1 | Accuracy and the most important variables

For the 88 butterfly species, the accuracy of samples withheld from modelling was 0.94 (0.95 sensitivity and 0.92 specificity) with an average of 5.8 retained variables (see Table S2 for important variables). Mean annual temperature was the most important modelling variable for the greatest number (42) of species. Mean temperature of the coldest quarter, mean temperature of the warmest quarter and precipitation of the driest month each were most important for 10–13 species.

For the 69 moth species, accuracy was 0.94 (0.96 sensitivity, 0.91 specificity) with an average of 6.0 retained variables (see Table S2 for important variables). Precipitation of the driest month and mean annual temperature were the most important modelling variables for 28 species and 20 species each, respectively. The next important variable, mean temperature of the warmest quarter, was important for 10 species.

Accuracy was 0.95 (0.97 sensitivity, 0.93 specificity) for both the 18 bee and 24 beetle species; accuracy was 0.94 (0.97 sensitivity, 0.91 specificity) for 17 wasp species, and accuracy was 0.93 (0.95 sensitivity, 0.91 specificity) for 12 fly species. The mean number of retained variables ranged from 5.6 to 6.1 for each pollinator type (see Table S2 for important variables). Mean annual temperature was the most important modelling variable for nine bee species, including the honeybee, 10 beetle species and 7 fly species. For wasps, mean annual temperature was the most important variable for six species, and mean temperature of the warmest quarter was the most important variable for eight species.

3.2 | Sensitivity analysis

Compared with 88 butterfly models from unthinned records, mean niche overlap was 0.992 (out of a maximum value of 1) for butterfly models from thinned records; mean niche overlap was 0.993 for butterfly models without urban records, 0.990 for butterfly models from thinned records without urban records and 0.986 for butterfly models from thinned records without urban records and flagged records of outliers and potential locational errors (i.e. biodiversity centres and administrative centroids). While these were very similar models, the most extreme removal of samples (thinned records without urban records and flagged records) produced the least niche overlap values of 0.920 for *Euptychia cymela* and 0.924 for *Eresia aveyrana*. Maps of predicted probabilities for these species demonstrated the generalized predictions resulting from reduced information, including apparent commission error outside of species ranges, relative to precise predictions from models of all records (Figure S1).

3.3 | Centroid distances

The mean centres of all species distributions shifted north over time from past to current climate, with past and current distribution centres located in the United States and future distributions centred in the northern United States or Canada (Figure 1; not all species were present 20 ka in North America, but distances supply a simple index of climate change effects and inclusion of all species allows consistent comparison; Suchan et al., 2024). Relative to the climate of 1981–2010, centres of distributions for the butterfly species moved an average of 505 km north in latitude since the climate during 20 ka. Due to a region of warm climate in Alaska during 20 ka (Hanberry, 2022b), two species had potential distribution centres that shifted southwards between 20 ka and current climate. For moth species, centres of distributions moved an average of 642 km in latitude since the climate during 20 ka. For the 71 bee, fly, beetle and wasp species, centres of distributions moved an average of 618 km in latitude since the climate during 20 ka. One species had a distribution centre that shifted southward between 20 ka and current climate.

According to the warming of each general circulation model for end-of-century climate relative to the current climate, mean butterfly distribution shifts in latitude were 492 km for GFDL SSP3-7.0, 624–711 km for the three SSP5-8.5 general circulation models, 760 km for IPSL SSP3-7.0 and 1115 km for UKESM1 SSP3-7.0. For moth species, distribution shifts in latitude were 564 km for GFDL SSP3-7.0, 659–810 km for the three SSP5-8.5 general circulation models, 847 km for IPSL SSP3-7.0 and 1243 km for UKESM1 SSP3-7.0. For the 71 bee, fly, beetle and wasp species, distribution shifts in latitude were 582 km for GFDL SSP3-7.0, 568–695 km for the three SSP5-8.5 general circulation models, 865 km for IPSL SSP3-7.0 and 1351 km for UKESM1 SSP3-7.0.

3.4 | Changes in the relative number of species

The GBIF database primarily has records of pollinator species that were centred in the United States, with the greatest number of species predicted in the United States and southern Canada (Figures 1 and 2). For these modelled species, the generally relative potential species loss in the future, by location, was indicated in Mexico, Central America, the Caribbean and most of the eastern half of the United States, based on ratios of the number of species expected by five of six end-of-century climates to the number of species predicted under the current climate (Figure 2 displays changes in butterfly species). However, in absolute numbers, the eastern half of the United States was predicted to lose the greatest number of species. Canada and Greenland were likely to gain

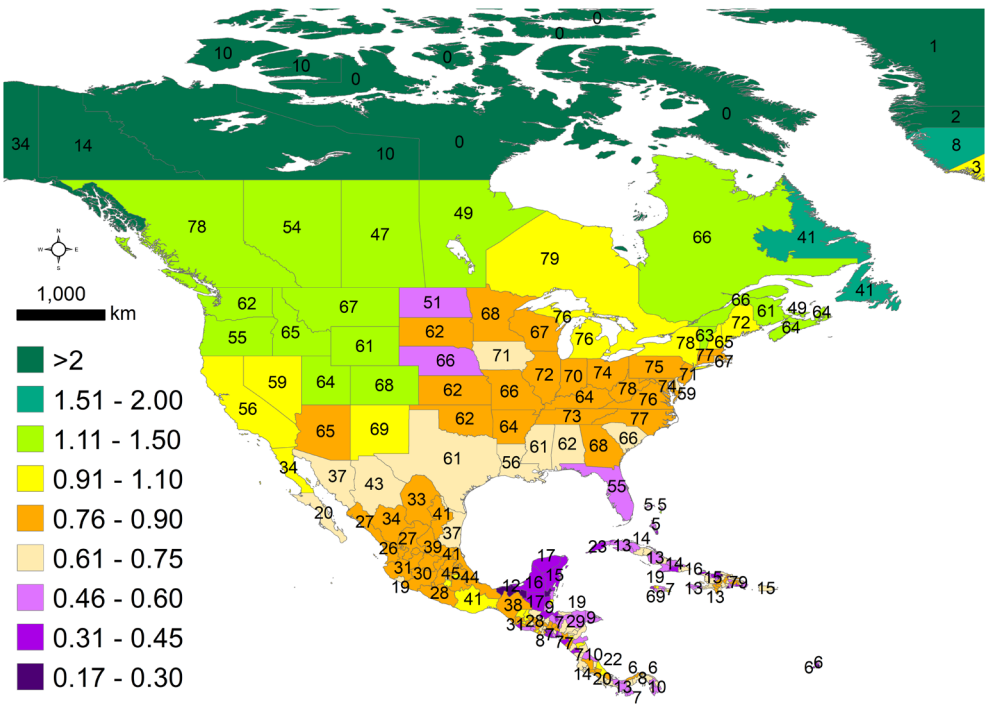

FIGURE 2 For the example of butterflies, ratios of future numbers of predicted species compared with current numbers of predicted species (i.e. a ratio of 1 means that the number but not identity of species remained the same, whereas a ratio >1 indicates gains in number of species and ratio <1 indicates loss in number of species), with the current predicted numbers of species listed for the internal administrative country division. Due to the greatest number of the modelled species in the United States, the eastern United States is predicted to lose the greatest number of species.

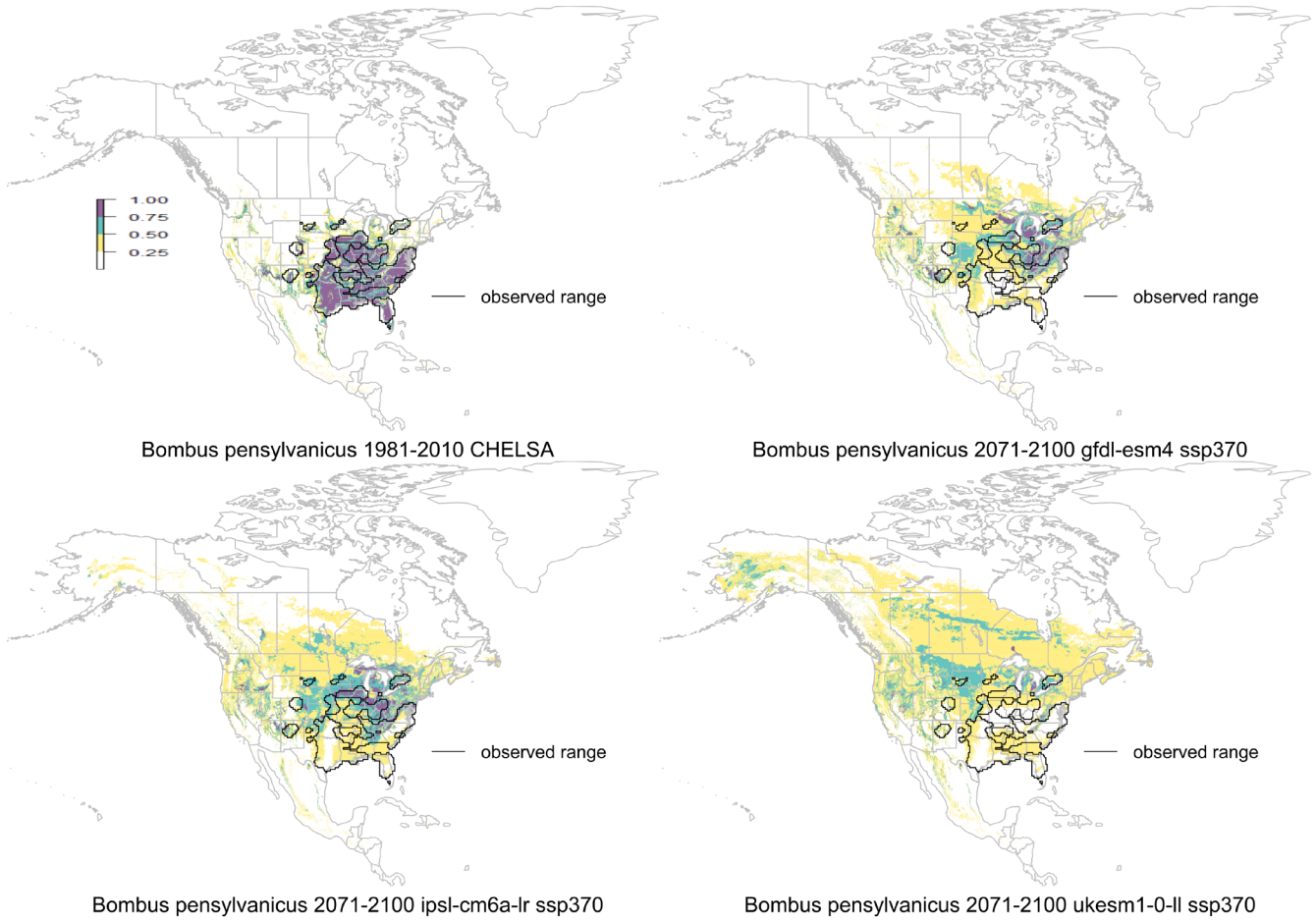

FIGURE 3 American bumblebees are one of the few species predicted to lose potential climate space in the future (2071–2100) compared with current potential climate space (1981–2010) for summer distributions. The observed range encompassed 95% of records. Predicted probabilities were divided into three colour classes of yellow (0.25 to <0.5, not classified as present); green (≥0.5 to <0.75, present); and purple (≥0.75, present). Three end-of-century (2071–2100) climates were the SSP3-7.0 (ssp370) scenario general circulation models GFDL-ESM4 (GFDL; Geophysical Fluid Dynamics Laboratory, USA), IPSL-CM6A-LR (IPSL; Institut Pierre Simon Laplace, France) and UKESM1-0-LL (UKESM1; Met Office Hadley Centre, UK).

species. Stability or even slight gains in the relative number of butterfly and the other pollinator species may occur in the western half of the United States and the Northeast (i.e. the eastern part of the northeastern United States). Potential gains in moth species may occur in the western United States, and stability in the northern and eastern states of the eastern half of the United States, with potential losses in the interior and southern states of the eastern half of the United States However, due to the greatest number of the moth species in the United States, from the database, in absolute terms, the eastern United States was predicted to lose the greatest number of species.

For species losses by area in the future, nine butterfly species out of 88 (or 10%) may lose area in the future, based on ratios of 0.53–0.89 mean area of six end-of-century climates compared with area of current climate space during summer (Tables S1 and S3; ratios ≥1.1 refer to gain in predicted distributional area relative to current predicted distributional area and ratios <0.9 refer to loss in predicted distributional area relative to current predicted distributional area). Regarding moth species, *Eacles imperialis* (imperial moth; or 1 out of 69 species) potentially may have a loss of area in the future (ratio of 0.78). As for the other pollinator species, five species out of 71 (6% of all species) potentially may experience loss of area in the future, according to ratios of 0.85–0.87, including four bee species, such as *Bombus pensylvanicus* (American bumblebee; Figure 3).

In contrast to the predicted contraction of distributions in the future, 73 butterfly species out of 88 species may increase in potential climate space in the future compared with current potential climate space during summer (Tables S1 and S3; i.e. ratios ≥1.1). The monarch had a ratio of future climate space to current climate space of 1.4, with an attendant area increase of 1 million km^2 (Figure 4). *Phyciodes phaon* (Phaon crescent) and *Limenitis archippus* (viceroy) had ratios ≥2.0. Sixty-three moth species out of 69 species may have gains in future climate space, according to ratios of 1.11–1.97. *Haematopis grataria* (chickweed geometer) had the maximum relative gain in potential distribution, with a ratio of 2.57. Lastly, for the other pollinators, 57 species out of 71 species had ratios from 1.1 to 1.85.

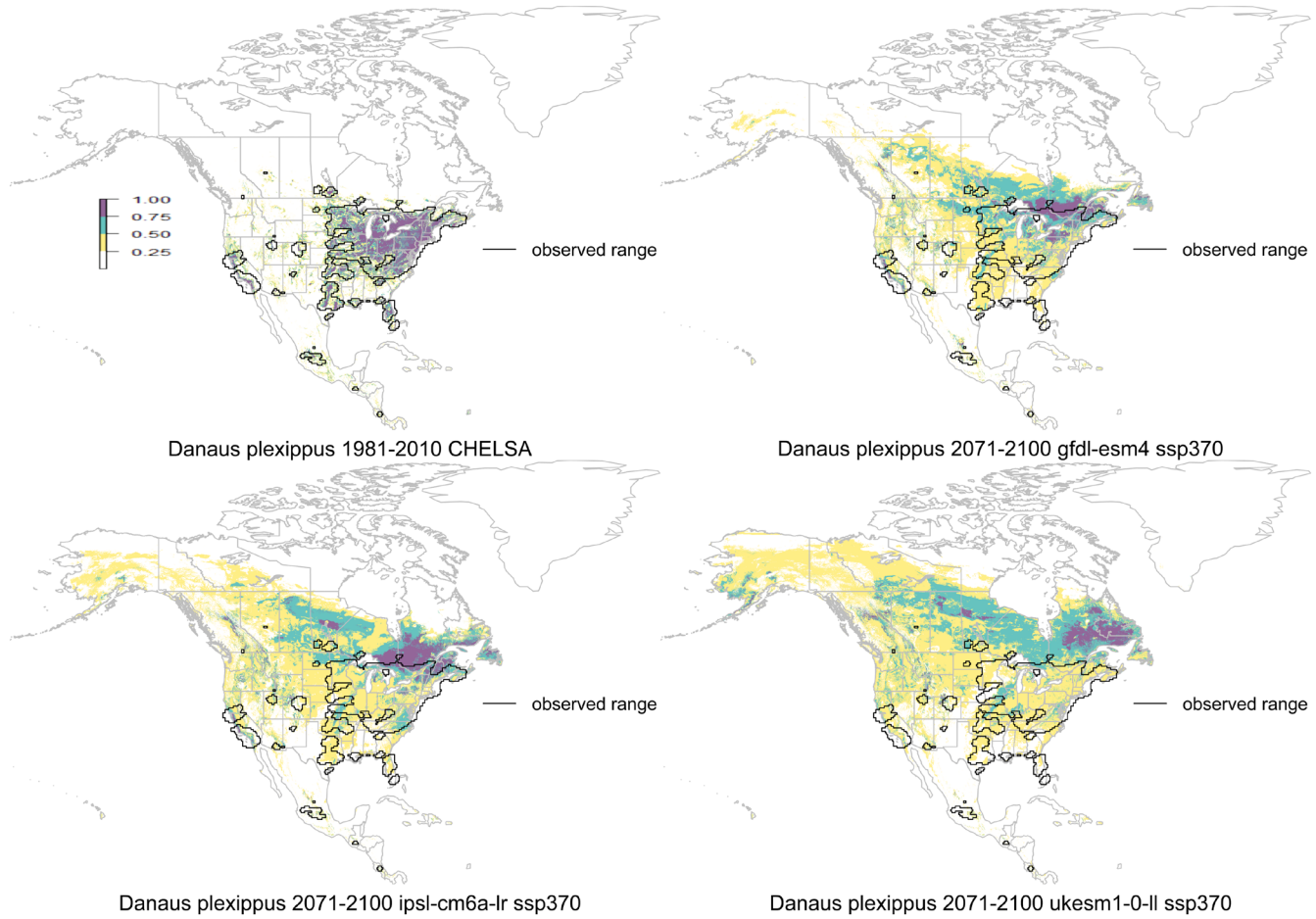

FIGURE 4 Monarch butterflies are predicted to gain potential climate space in the future (2071–2100) compared with current potential climate space (1981–2010) for summer distributions. The observed range encompassed 95% of records. Predicted probabilities were divided into three colour classes of yellow (0.25 to <0.5, not classified as present); green (≥0.5 to <0.75, present); and purple (≥0.75, present). Three end-of-century (2071–2100) climates were the SSP3-7.0 (ssp370) scenario general circulation models GFDL-ESM4 (GFDL; Geophysical Fluid Dynamics Laboratory, USA), IPSL-CM6A-LR (IPSL; Institut Pierre Simon Laplace, France) and UKESM1-0-LL (UKESM1; Met Office Hadley Centre, UK).

4 | DISCUSSION

4.1 | Ecological evidence

General declines in pollinators may be related to climate change, particularly in the future (Koh et al., 2016; Potts et al., 2010; Winfree et al., 2009). Decreases in the abundance and diversity of pollinators and pollination services may ultimately lead to pollen limitations, reductions in seed production and subsequent declines in flowering plants, which in turn will reduce floral resources for pollinators (Brosi & Briggs, 2013; Thomann et al., 2013). I modelled distributions of pollinator species occurrences during summer throughout North America at a scale to capture entire ranges, and then predicted potential climate space to past (i.e. 20, 10 and 6 ka), current (i.e. 1981–2010) and future (i.e. six projections of climate during 2071–2100) climates. Model accuracies ranged in mean values from 0.93 to 0.95 by taxa. Mean annual temperature was the most important variable for the greatest number of species. As an indicator of climate effects on distributions, centres of distributions moved about 500–650 km in latitude since climate during 20 ka, which were similar to distances expected in response to most of the end-of-century projections. Generally, for these species distributions, which were centred in northern North America, potential losses were predicted under future climate change in Mexico, Central America, the Caribbean and most of the eastern half of the United States, relative to the number of species predicted under current climate. Nonetheless, based on the models of potential distributions and with many uncertainties related to modelling and predictions under future climate, most pollinator species may gain potential climate space in the future due to greater land area in northern North America (i.e. widening at higher latitudes, where Canada is the second largest country at 10 million square kilometres). Realized ranges under current and future change will not match modelled species distributions, which are of potential climate space only. Current observations may be incomplete representations of species tolerances, future climate may not match any climate projections, and land use and disturbances dislocate distributions.

These models offer information about the magnitude of change in species distributions necessary to maintain the climate space of recorded observations. Even though these are estimates of the distances species will need to shift to maintain climate space by the end of the century, most species probably will not shift at the same rate as climate change. The rate of climate warming during the next 80 years may require that species cover distances (i.e. 600 km) equivalent to thousands of years of movement to keep pace with climate change. The fates of pollinators and flowering plants are fundamentally linked, and shifts in pollinator distributions may depend on the pace of shifts in the availability and abundance of flowering plants (Wilson et al., 2021). These rates overall are not attainable for immobile plants that depend on dispersal agents for movement of propagules, at least under conditions of natural regeneration rather than human vectors (Hanberry, 2023b). Until shifts of flowering plants occur, suitable plants may not be available north of current ranges for some pollinators. Some species will be able to use new resources, but most species may continue to rely on familiar resources and shift location, behaviour and plastic life history traits if possible (Coristine & Kerr, 2011; Lancaster et al., 2017).

Land use interacts with climate change to affect species responses, which is unlike species shifts under past climate change, and creates additional obstacles for both pollinator movement and conservation (Coristine & Kerr, 2011; Hanberry et al., 2021). Climate change effects are wide-ranging and compounded by interactions with land use and human activities, including the introduction of non-native species and insecticide applications. Heat waves and varying precipitation may reduce the quantity or quality of flower and nectar resources for pollinators (Ogilvie et al., 2017; Thomson, 2016), resulting in stressed and poorly nourished animals that are less resistant to drought, temperature fluctuations, fire, land use pressure, insecticides, disease and competition from native and non-native species for floral resources. Recent declines in North American wild bees may in part be due to diseases, such as the fungal pathogen *Nosema bombi* and the *Varroa destructor* mite, carried by imported commercial bees (Graystock et al., 2016). Insecticides and other chemicals may be directly toxic or reduce the survival and reproduction of pollinators, whereas sub-lethal effects on pollinating insects include cognitive impairment leading to reduced foraging and homing success and also immune suppression leading to increased susceptibility to disease and parasites (Hladik et al., 2016). One of the few species with reduced potential future climate space was *Bombus pensylvanicus* (American bumblebee), previously abundant but with precipitous population declines linked to pesticide use, habitat loss, climate change and disease spread (U.S. Fish and Wildlife Service, 2024). Overall, species gains were predicted for most of Canada and Alaska, which have relatively abundant natural areas to support shifting species due to less of a human footprint currently than highly modified southern regions, albeit with concentrated land use in southern Canada (Beale et al., 2008; Coristine & Kerr, 2011). However, agriculture and urban areas are also likely to increase in warming locations, interfering with pollinator shifts (Coristine & Kerr, 2011).

Most species are expected to shift to remain within suitable climate space, and expansion of ranges may be a reasonable result for the majority of species, according to greater land area in northern North America (Chen et al., 2011). This modelling used occurrences from throughout North America, allowing models of continental distributions. However, warm climate tolerance of species may exceed modelled tolerances. Sampling likely was not complete throughout the extent, reducing observed climate space and predictions of potential distributions. Realized ranges generally have contracted with population decreases and do not display the full scope of climate tolerances. For example, the monarch model may suffer from extirpation from the full range of climate tolerance. Nonetheless, some species have expanded their climate space during recent decades. Models only cover a fraction of pollinator species, without accounting for species-specific responses related to physiology, behaviour, phenology, dispersal, pace of life, generalism, plasticity and genetic changes, and contrasting traits may facilitate or impede shifts (Beissinger & Riddell, 2021; Comte et al., 2024; Hällfors et al., 2024). Different modelling choices result in varying projections with associated uncertainties; for example, reduction in correlated climate variables by researchers may result in omission of relevant input variables and models that poorly fit the observations, as opposed to allowing the modelling algorithm to select important variables (Hanberry, 2024a). In this study, I selected six projections of future climate, statistically downscaled climate variables and typical climate variables, a standard non-linear ensemble classifier that is highly accurate, and recursive feature elimination to retain important variables (Fernández-Delgado et al., 2014; Hanberry, 2024a; Karger et al., 2017, 2018, 2020, 2021).

Unlike the results in this study of range expansions with northward shifts, a study of bee species distributions under climate change predicted future range contractions for nearly half of 31 bumblebee species in Canada and the United States (Sirois-Delisle & Kerr, 2018). Differences may arise due to specific modelled species (i.e. latitudes of current distributions) and modelling selections. For example, Sirois-Delisle and Kerr (2018) preselected four climate predictor variables of annual mean temperature, temperature seasonality, annual precipitation and precipitation seasonality. Conversely, in this study, 13 climate predictor variables were reduced through modelling to about six variables, on average, varying by species, and three temperature variables (annual temperature, temperatures of warmest and coldest quarters) were more important than any precipitation variables. It also is not clear how important seasonality is for species distributions, as opposed to tolerable ranges of temperature and precipitation.

Few continental studies of insect distributional changes are available due to limited survey data, while attribution to climate change is challenging, in part given the overwhelming influence of human activities on biodiversity (IBPES, 2019). Kerr et al. (2015) detected the failure of bumblebees to keep pace with warming at northern range limits during 1900–2010 compared with 1901–1974 in North America and Europe. Likely, a similar failure to migrate has occurred in many plants. In particular, warming has not occurred during recent

decades in the eastern United States, and no strong northern trend in tree species has been detected, albeit tree species have been expanding into the interior (and other) grasslands of North America following Euro-American settlement (Hanberry, 2022a; Taheri et al., 2021). Additionally, Kerr et al. (2015) identified southern range losses in bumblebees, but this may be due to intensive land use in warmer areas with greater human population densities (Beale et al., 2008). In Europe, 35 of 52 butterfly species shifted ranges to the north by 35–240 km during the 1900s (Parmesan et al., 1999). In subarctic Finnish Lapland, 90% of moth populations were stable (57%) or increased (33%) during 32 years (Hunter et al., 2014).

Geographic variation in the starting ecosystem and climate and the magnitude and direction of climate change, and land use likely will produce differential insect and plant responses (Deutsch et al., 2008; Freitas et al., 2009). Modelled species generally had distributions centred in the United States, with species losses, relative to the current predicted number of species, for these northerly species projected in Mexico, Central America, the Caribbean and most of the eastern half of the United States However, climate change probably will provide opportunities for species, particularly of warmer temperatures, to increase and expand. Warming may expand tropical zones and consequently favour the expansion of diverse tropical species (Freitas et al., 2009). Insects are relatively mobile, and examples of rapid expansion of both native species and non-native species exist. *Polistes exclamans* (Guinea paper wasp) has demonstrated the capacity to spread to previously unoccupied areas and maintain new populations in the United States (West, 1968). Monarch butterflies travel great distances across generations, and warmer temperatures will allow more movement (Thogmartin et al., 2020), although summer temperatures may exceed the optimal for monarchs in the future.

Pollinator species may be vulnerable to climate change due to altered phenology and consequent unbalanced biotic interactions, particularly in regions with seasonal temperature and light variation, north of tropical zones (Bartomeus et al., 2011). Differential phenologies may disrupt the synchronicity of plant–pollinator interactions in space or time if one partner relies more heavily on different cues, for example, temperature, day length or snow melt (Bartomeus et al., 2011). While the timing of plant flowering and insect emergence generally has remained synchronous as temperatures have increased in recent decades, pollinators are unlikely to benefit from more rapid life cycle rates or extended warm seasons, such as through shortened generation times or additional generations, unless host plants also are available for the life stages (Bartomeus et al., 2011). Of course, it may be favourable for insects if the insect-breeding bird interdependency is decoupled. Decoupling of temperature and photoperiod cues may be maladaptive for pollinators and plants that are pollinated, resulting in lessened growth, survival and reproduction and an overall competitive disadvantage for resources, leading to range shifts (Bale & Hayward, 2010).

Mortal thermal thresholds occur, but the response to temperature and precipitation gradients typically is unknown (Deutsch et al., 2008; Fründ et al., 2013). Generally, temperate and boreal species may be in climates that are currently cooler than their physiological optima, while tropical species may be close to thermal thresholds (Deutsch et al., 2008). Therefore, increased temperatures will be deleterious in locations that are already tropical ('hypertropical'; Hanberry, 2022c). Species, such as butterflies that originated and diversified in tropical climates and retain ancestral tolerances to warmer conditions, may have low warming-related extinction risks in most temperate environments, but bumblebees may experience greater limitations due to evolutionary origins under cooler conditions (Hines, 2008). In seasonally cold regions, frost-sensitive and non-diapausing species may experience increased survival during warm winters (Crozier, 2004). However, warming reduces the amount and duration of insulating snow cover, which may result in greater overwinter mortality for some species (Fründ et al., 2013; Williams et al., 2015). Species, such as honeybees that thermoregulate through the winter instead of entering dormancy, may have increased metabolic rates during warmer winters, which can deplete energy and water reserves (Fründ et al., 2013; Williams et al., 2015). For these continental models, mean annual temperature and mean temperature of the warmest quarter were most important for the majority of species, aside from moth species, for which precipitation of the driest month was slightly more important than mean annual temperature. Within regions, bees generally may use drier environments than flies, but species within a pollinator group may respond differently to moisture availability (Robson et al., 2018). Changes in both climate and phenology result in potential effects at multiple scales, including plant and insect dynamics important for species distributions and assemblages (Bale & Hayward, 2010).

4.2 | Ecological solutions to support pollinator shifts due to climate change

Although interactions among land use and climate change may make the identification of reasons for pollinator declines complicated, the most effective management to support pollinators and their predicted shifts to new locations may be the provision of flowering and nesting resources, as well as limited chemical application and mowing (Hanberry et al., 2021). Floral resource availability may be the primary direct factor limiting the abundance of bees and likely limits other pollinators that rely on floral nectar and pollen for energy (Roulston & Goodell, 2011). Flower management can be practised by anyone, from public land managers to private citizens. Indeed, public involvement may be the most widespread approach to supply flowering plants because gardening and wildlife-watching are rewarding to a range of stakeholders. The provision of floral resources may be effective at multiple scales, from potted plants and flower beds to large management units and settings, such as residential and urban land uses, agricultural field borders and rights of way. Bees, in particular, may be successful in human-disturbed ecosystems with moderate habitat loss (Winfree, 2010).

Flowering plants need to be available from the last spring frost to the first fall frost, during the full active period of pollinators,

with overlapping bloom times (Hanberry et al., 2021). A diversity of plants will generate continuous blooms and match pollinator shapes, sizes and colour preferences, as opposed to mass-flowering by a single dominant plant. Regional or state and province plant lists of native plants attractive to pollinators and suited for small-scale plantings have been developed by different organizations (Xerces Society, 2017). Inventorying existing conditions and identifying reference conditions can help guide the development of management plans to improve pollinator habitat. For example, many locations in the United States that historically contained herbaceous layers are now dominated by trees; management options are available to control tree densities and allow coexistence with forbs (e.g. Bragg et al., 2020).

Herbicide application to remove 'weedy' native species from agricultural crops, lawns, rangelands, pastures and right-of-ways is antithetical to the provision of floral resources (Hopwood et al., 2016). For example, common milkweed (*Asclepias syriaca*) remains a noxious weed in some locations (Monarch Joint Venture, 2024) and is commonly treated with herbicides, despite dependence on milkweeds by the monarch butterfly. Even non-native flowering plants may support pollinators, particularly generalist species, provided that pollinators have the morphology to access pollen or nectar rewards (Stout & Morales, 2009). Nonetheless, non-native plants can reduce native plant and pollinator abundance, and invasive plant removal generally benefits native plants and pollinators if native flowering plants become available in replacement of non-native plants (Larson et al., 2006).

Planting of native flowers helps to prevent the spread of non-native plants (i.e. integrated vegetation management) and also can support predator insects and parasitoids, the natural enemies of damaging insects (i.e. integrated pest management; Harvey & Fortuna, 2012). Diverse native plants with a variety of root systems typically are well-adapted to a range of environmental conditions, including those elicited by drought and other weather extremes, producing better water infiltration and erosion control (Hopwood et al., 2016). Establishment time and initial costs may be greater than those of non-native grasses, but the upkeep of native plants may be cost-effective in the long term due to fewer requirements for mowing, herbicides and other repeated weed control measures (Hopwood et al., 2016). In addition to reduced and more targeted pesticide applications, best management practices for pollinator survival include reduced and targeted mowing (Hopwood et al., 2016).

On farmlands, the most common crops are wind-pollinated grasses, which replace floral resources in productive grasslands (Garibaldi et al., 2011). Nonetheless, canola and other *Brassica* species, flax (*Linum usitatissimum*), sunflower (*Helianthus annuus*) and cotton (*Gossypium*) are crops that benefit from pollination. Pollination services provided by wild bees may exceed those of managed honeybees, albeit wild bees are considered as an aggregate group, but reliance on a single species for pollination also carries risks (Garibaldi et al., 2011). Stakeholders are becoming interested in protecting and enhancing populations of native bees to increase pollinator portfolios because pollinator diversification provides redundancy and reliability to serve the pollination needs of agricultural settings across a range of production scenarios (Calderone, 2012). Research on maintaining diverse wild insects for crop pollination is not well developed, but increasing abundance, diversity and continuity of floral resources in field borders or patches will supply foraging and nesting resources and protection from pesticide application (Garibaldi et al., 2011; Kennedy et al., 2013). Organic farms, semi-natural areas and restored or uncultivated patches become increasingly important to pollinators as the percentage of the landscape in cropland increases (Winfree, 2010). Bee abundance and richness were greater in diversified and organic fields compared with intensive monoculture agriculture in a variety of agroecosystems (Kennedy et al., 2013). The frequency of crop flower visits by pollinators and crop yield increases with the proportion of natural or semi-natural (i.e. semi-degraded) areas in agricultural systems (Kennedy et al., 2013; Wratten et al., 2012). Enhancement of pollinator nutrition by floral resources will help buffer populations against combined effects of pathogen infection and pesticide exposure (Garibaldi et al., 2011). Natural areas also will reduce soil erosion, improve biological pest control, nutrient cycling, water-use efficiency, wildlife conservation, and aesthetic and recreational value (Garibaldi et al., 2011; Wratten et al., 2012).

Right-of-ways (easements for transportation purposes), roadsides and other areas degraded by land use disturbance supply opportunities for the restoration of native flowering plants and the provision of pollinator migration corridors and way stations (Hopwood et al., 2016). For example, Iowa, United States, legislated an Integrated Roadside Vegetation Management Program during 1989 to promote an ecologically integrated approach to roadside management; since then, about 40,000 ha of 240,000 ha of state and county roadsides have been planted in native vegetation (Hopwood et al., 2016). However, roads cause animal mortality, and plantings should be placed some distance from roadsides, depending on factors, such as traffic and ecological context, and not be located in the median to avoid attracting pollinators and other animals to roads (Keilsohn et al., 2018). If immediate ground cover is required, sterile wheat grass or nurse crops may provide erosion control and weed suppression during native plant establishment (Hopwood et al., 2016). In addition to forb enhancement, best management practices include limited mowing and herbicide use that is targeted to specific problem areas. Guidelines include reducing mowing to no more than twice during the growing season, reducing the area mowed to the minimum zone required for safety, using flushing bars and mowing slowly, mowing during the day when pollinators are active and better able to avoid mowers, and varying mowing times annually to allow diverse species to reproduce, preferably mowing very early and late in the growing season (Hopwood et al., 2016).

In residential and urban areas, lawns are the dominant herbaceous vegetation (Milesi et al., 2005). Indeed, lawns are the largest 'crop' in the United States, covering 128,000 km^2, about three times the area of corn (Milesi et al., 2005). In addition to not being beneficial to pollinators, lawns require homeowner time and investment (USD$35 billion) in lawn care (Larson et al., 2014). Water, fertilizers,

herbicides and fossil fuels are applied to lawns in amounts equivalent to agriculture and human fatalities occur to maintain a 'lawn ideal of a highly manicured and intensively managed turfgrass yard with limited or no vegetation attributes' (Burr et al., 2018; Enabling the Future, 2017; NWGC, 2007). Mowing is a widespread activity that directly reduces pollinator populations (Hopwood et al., 2016). Because turfgrass lawns are perceived to be the standard agreed upon by society, outreach efforts are central for transition to pollinator-friendly lawns (Burr et al., 2018).

Private citizens can act as land managers of their own property to add conservation value (Hanberry et al., 2021). Revised landscaping with the addition of flowering plants and reduced mowing schedules can increase pollinator habitat (Hopwood et al., 2016). Although the replacement of lawns by short-statured native plant cover would be ideal, clovers are one example of low-maintenance, user-friendly plants that are more beneficial to pollinators than turfgrass lawns (Larson et al., 2014). Some states provide exemptions to homeowner association rules if alternative lawns save water or are certified native (e.g. Colorado General Assembly, 2024). Regional planting guides from conservation organizations, gardening clubs, native plant chapters, outdoor education centres and organizations, such as county conservation districts and cooperative extension offices, provide guidance on lawn alternatives that benefit pollinators (e.g. Xerces Society, 2017).

Modifying anthropogenic areas to serve both human and pollinator needs may be particularly relevant in suburban and urban areas through citizen engagement in conservation practices (Hall et al., 2017). Pollinators function on smaller temporal and spatial scales than many other species, and their needs can be met by individual and community actions (Hall et al., 2017). Urban areas may support more pollinators than croplands; for example, bumblebees may have greater reproductive output, food stores and lower brood parasitism in urbanized areas compared with medium-intensity agriculture containing a mixture of grassland and crop fields (Samuelson et al., 2018). Common green spaces that include flowers provide ecosystem services, supporting both pollinators and human health and well-being (Kuo, 2015). At community scales, as cities and towns expand on the landscape and fragment pollinator habitat, maintaining connectivity by establishing a series of high-quality greenspaces and converting manicured lawns to diverse native plant community gardens may be critical for countering pollinator declines and maintaining native pollinator populations in the face of climate change.

5 | CONCLUSIONS

Pollinator species have declined globally during the last several decades, and climate change adds pressure to existing stressors of habitat loss and degradation, chemicals and diseases. I modelled pollinator species, centred in northern North America, to predict potential climate space of summer distributions over time. Centres of distributions showed shifts of around 500–650 km latitudinally in response to end-of-century warming, which is equivalent to the distance shifted since deglaciation, with turnover in Mexico, Central America, the Caribbean and most of the eastern half of the United States. However, according to predictions with associated uncertainties, most pollinator species, including culturally important monarchs (*Danaus plexippus*), may gain potential climate space in the future due to greater land area in northern North America. Meaningful and beneficial ecological solutions are available for citizens, communities and organization, to provide resources and reduce stressors that may help support declining pollinators shift to new locations.

AUTHOR CONTRIBUTIONS

Brice Hanberry performed all authorship tasks.

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CONFLICT OF INTEREST STATEMENT

The author declares no conflicts of interest.

DATA AVAILABILITY STATEMENT

Species distribution models are available from the Forest Service Research Data Archive at https://doi.org/10.2737/RDS-2024-0014 (Hanberry, 2024b).

RELEVANT GREY LITERATURE

You can find related grey literature on the topics below on Applied Ecology Resources: Butterflies, Climate change, Insects, Moths.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Removal of records (A, C) resulted in generalized predictions, including apparent commission error, relative to precise predictions from models of all records (B, D).

Table S1: Taxa, species, predicted areas (km^2; future mean is mean area predicted for six climates of 2071–2100), ratios in area between future mean area and area for 1981–2010 climate, species synonyms and authorities, and number of records.

Table S2: Important variables and value (out of 100) for final models by species.

Table S3: Predicted areas (km^2) for 20 ka, 10 ka, 6 ka, 1981–2010, and six end-of-century climates. Future climates were the SSP3-7.0 (ssp370) scenario general circulation models GFDL-ESM4 (GFDL; Geophysical Fluid Dynamics Laboratory, USA), IPSL-CM6A-LR (IPSL; Institut Pierre Simon Laplace, France) and UKESM1-0-LL (UKESM1; Met Office Hadley Centre, UK) and the SSP5-8.5 (SSP585) scenario general circulation models GFDL-ESM4 (Geophysical Fluid Dynamics Laboratory), MPI-ESM1-2-HR (MPI; Max Planck Institute for Meteorology) and MRI-ESM2-0 (MRI; Meteorological Research Institute) and the SSP5-8.5 (ssp585) scenario general circulation models GFDL-ESM4 (Geophysical Fluid Dynamics Laboratory), MPI-ESM1-2-HR (MPI; Max Planck Institute for Meteorology) and MRI-ESM2-0 (MRI; Meteorological Research Institute).

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