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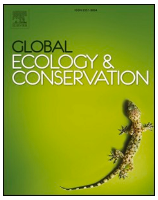

Climate-driven range shifts of a rare specialist bee, *Macropis nuda* (Melittidae), and its host plant, *Lysimachia ciliata* (Primulaceae)

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ABSTRACT

Earth's climate is on track to surpass the proposed mean global temperature change limit of 1.5°C above pre-industrial levels, threatening to disrupt ecosystems globally. Yet, studies on temperate bee response to climate change are limited, with most studies of non-*Apis* bees focusing on the eusocial genus *Bombus*. Here, we assess the response of a rare habitat and host plant specialist bee, *Macropis nuda*, to projected climate change scenarios. We use species distribution models of *M. nuda* and its host plant, *Lysimachia ciliata*, trained on publicly available occurrence records, to evaluate bee distribution and habitat suitability changes under four climate change scenarios. We find that the bee and host plant distributions respond synchronously to increased greenhouse gas emissions, which result in range-wide habitat suitability loss and a northward range shift. These results provide an important example of a temperate solitary bee's response to climate change and help inform conservation efforts to preserve pollinator biodiversity and pollinator-host plant relationships.

1. Introduction

Wild, unmanaged bees provide essential pollination services in agricultural and natural ecosystems (Klein et al., 2007; Ollerton et al., 2011). Yet, with increasing land-use intensity and climate change, insects (Stork, 2018), including pollinators (Goulson et al., 2015), are in decline. There is no single cause of pollinator decline; instead, a combination of threats act in tandem to reduce population sizes, fragment populations, and restrict the distribution of vulnerable bee species. Drivers of bee decline include direct mortality via pesticides and disease and reductions in habitat and floral resource availability from environmental and climate change, herbicides, and invasive species (Vanbergen et al., 2013; Goulson et al., 2015).

In response to climate change, a portion of species may thrive, becoming "winners" as they capitalize on the shifting ecological dynamics, while the remainder, the "losers," face extinction, redistribution, and range contraction (McKinney and Lockwood, 1999). The capacity of a species to respond to climate change depends on its life history, physiology, habitat specialization (e.g., xeric vs. temperate), and niche breadth (McKinney and Lockwood, 1999; Pörtner and Farrell, 2008; Öckinger et al., 2010; Somero, 2010). Smaller body sizes, for example, may indicate lower dispersal capacity (Öckinger et al., 2010), which can prohibit a species from successfully migrating within its climate niche, particularly across fragmented habitats (McKinney and Lockwood, 1999; Öckinger et al., 2010). Likewise, a narrow feeding niche (e.g., limited diet breadth) increases susceptibility to habitat loss and climate change (Öckinger et al., 2010) and is an attribute of specialist bees, which are already thought to be in decline (Biesmeijer et al., 2006;

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Bommarco et al., 2010; Bartomeus et al., 2013; Burkle et al., 2013; Wood et al., 2016; Bogusch et al., 2020).

Many studies have linked climate change to species declines globally (e.g., McCarty, 2001; Møller et al., 2008; Chen et al., 2011; Meyer-Gutbrod et al., 2021); however, the implications for bee decline and conservation are not fully understood (Goulson et al., 2015; Dicks et al., 2021). To date, only a few empirical studies have assessed the impacts of climate change on non-*Apis* bee populations (Kerr et al., 2015; Soroye et al., 2020). This knowledge gap is particularly notable in solitary bees, where no long-term historical studies have directly evaluated the effects of climate change on population decline or range shifts. However, Species Distribution Models (SDMs) are increasingly being used to make predictions about how bee distributions may change under future climate conditions and have reported contrasting results, particularly between xeric and temperate species (Roberts et al., 2011; Kuhlmann et al., 2012; Martins et al., 2015; Silva et al., 2015, 2018; Biella et al., 2017; Dew et al., 2019; Gonzalez et al., 2021; Martínez-López et al., 2021). Despite their limitations related to sampling bias, imperfect detection, and abundance estimation (Guillera-Arroita et al., 2015), model-based methods provide an opportunity to work around the constraints imposed by our incomplete knowledge of species distributions, termed the Wallacean Shortfall (Lomolino, 2004; Whittaker et al., 2005; Martins et al., 2015).

The "oil bees" are among the numerous species of solitary bees for which we have limited distribution data. The group consists of 440 species in the Apidae and Melittidae that rely on floral oil-producing plants for brood cell construction and provisioning (Danforth et al., 2019). Primarily found in tropical and subtropical habitats, all oil bees use specialized, highly variable morphology to collect oils from their host plants, which they use for larval food and nest construction (Danforth et al., 2019). The genus *Macropis* (Melittidae) is the only oil bee genus endemic to the Holarctic (Michez and Patiny, 2005). All 16 extant *Macropis* species are pollen specialists on *Lysimachia* (Primulaceae) but collect nectar from several other plant species. *Macropis* species nectar from members of the genus *Apocynum*, with *A. androsaemifolium* thought to be a major nectar source for the species considered in this study. (Michez and Patiny, 2005). There are four described species of *Macropis* in North America, and all are considered rare. Compared to their European relatives, the distributions and ecology of North American *Macropis* species are poorly understood (Michez and Patiny, 2005; Danforth et al., 2019).

The current study focuses on the ground nesting oil bee, *Macropis nuda,* which is only known to gather floral oils and pollen from one host plant species, *Lysimachia ciliata*, with which it shares an unequal dependency (Simpson and Neff, 1983). That is, *M. nuda* relies on floral resources gathered from *L. ciliata* for brood cell construction and provisioning, but *L. ciliata* does not rely exclusively on *M. nuda* for pollination (Simpson and Neff, 1983). We see this unequal dependency represented in the described distributions of these two species. *Macropis nuda* is believed to occupy an extensive and possibly disjunct distribution encompassing much of the northern

Fig. 1. An *M. nuda* female nectars from *Apocynum cannabinum* (A) adjacent to a known nest site on a lakeshore near Rensselaerville, NY, US (B). *M. nuda* collect pollen (C) exclusively from *L. ciliata* (D) which they mix with floral oils gathered from elaiophores at the base of the corolla (E).

United States (US) and southern Canada, with most observations in the northeastern US. However, to our knowledge, *M. nuda* only occupies a subset of its host plant's range, which extends into the southern US (Mitchell, 1960; Cane et al., 1983; Michez and Patiny, 2005; Sheffield and Heron, 2018). Both species share similar habitat specialization and occupy wetlands and damp forest habitats (Fig. 1; Lichvar et al., 2012; Wood et al., 2019).

Despite its expansive range, *M. nuda* is generally considered a rare and declining bee species (Bartomeus et al., 2013) and may be facing localized extirpations, such as in southern Idaho (James Cane, *personal communication*). However, the status of *M. nuda* remains unclear, particularly in light of its recent rediscovery in Michigan after more than 50 years as part of a targeted collection effort performed by Wood et al. (2019). Due to this rare and uncertain status, the threat of climate change-related habitat loss is concerning for this specialist. As a temperate solitary specialist bee, *M. nuda* represents a group of understudied species concerning climate change. Here, we evaluate how the distributions of *M. nuda* and its host plant, *L. ciliata*, may change under various climate change scenarios and how potential range shifts may alter the conservation status of *M. nuda*. We hypothesize that *M. nuda*, as a temperate specialist bee, will experience a reduction in suitable habitat as its climate niche shifts northward and up in elevation.

2. Materials and methods

2.1. Occurrence data

We obtained *M. nuda* occurrence records from the Global Biodiversity Information Facility (GBIF; gbif.org, 2021a), American Museum of Natural History Arthropod Easy Capture (AMNH; AMNH, 2003), Symbiota Collections of Arthropods Network (SCAN; scan-bugs.org, 2021), and USGS Biodiversity Information Serving Our Nation (Macropis nuda Occurrences published by BISON, 2021). We acquired additional occurrence records through publications and personal communications (36 records; Wood et al., 2019, Hardy et al., 2021, Brianne Du Clos, Gail MacInnis, Michael Roswell, and Michael Veit, *personal communications*) and research-grade iNaturalist observations (12 records), not reported elsewhere. For *L. ciliata* and *A. androsaemifolium,* we obtained occurrence data exclusively from GBIF (*L. ciliata:* gbif.org, 2021b, *A. androsaemifolium:* gbif.org, 2021c). We filtered the occurrence records to exclude duplicates, observations with mismatched geolocation and metadata descriptions, or which were georeferenced to institutions (see supplemental methods). We thinned the resulting dataset to 10 km with the R package spThin to reduce the effects of sampling bias (Radosavljevic and Anderson, 2014; Aiello-Lammens et al., 2015; Sillero and Barbosa, 2021). Unless otherwise stated, we performed all analyses in R (ver. 4.0.2; R Core Team, 2021).

2.2. Regional model and targeted collection

We performed two independent modeling workflows with MaxEnt (ver. 3.4.1; Phillips et al., 2017) through ENMeval2.0 (Kass et al., 2021). First, we trained a regional model on 25 *M. nuda* occurrences between 1970 and 2020 located in a ten by six-degree study area with 0.5 arc-minute resolution centered around New York State and southern New England (Fig. S2). The purpose of this model was to aid in site selection for targeted collection and facilitate additional observations in the northeastern US. Second, we generated a range-wide model to assess the potential for *M. nuda* redistribution under future climate conditions; this model is covered in detail below (see Section 2.3).

Given the essential role of *L. ciliata* in the life cycle of *M. nuda* (Cane et al., 1983), we included the corresponding *L. ciliata* habitat suitability predictions, modeled with an SDM, as a biotic covariate. The utility of including biotic covariates in an SDM is not fully resolved, but some studies have supported their use (de Araújo et al., 2014; Atauchi et al., 2018). However, this contrasts with the expectations of the Eltonian Noise Hypothesis, which posits that biotic variables do not improve model performance when modeling distributions at large geographic scales (Soberón and Nakamura, 2009).

For the plant SDMs, we used 19 bioclimatic variables from CHELSA (ver. 2.1), derived from the 1981–2010 climate normals (Karger et al., 2017). Additionally, we included elevation (Fick and Hijmans, 2017), soil sand content (Hengl, 2018a), soil water content (Hengl and Gupta, 2019), and proximity to water layers. We calculated proximity to water as the Euclidean distance to surface water using the proximity tool in QGIS (ver. 3.16) and the European Commission Joint Research Centre's global surface water occurrence dataset (Pekel et al., 2016). We utilized the same variables for the *M. nuda* models, with the addition of the plant SDMs as predictors. We retained all environmental variables without explicitly addressing collinearity in the regional model. Evaluations by de Marco and Nóbrega (2018) and Feng et al. (2019) suggest that MaxEnt model performance is robust to collinearity – unless extrapolated across time and space – due to the internal variable selection process.

We used ENMeval to test a range of model complexities by training models with combinations of linear, quadratic, and hinge feature classes and regularization multipliers between 1 and 5, similar to Guevara et al. (2018), to balance model complexity and reduce overfitting (Shcheglovitova and Anderson, 2013; Radosavljevic and Anderson, 2014). We use geographically structured cross-validation to assess the performance of the 20 models generated in ENMeval for each species (see supplemental methods). We considered models with a delta Akaike Information Criterion corrected for small sample sizes (ΔAICc) < 2 highly supported (Warren and Seifert, 2011). We chose a single "optimal" model based on the maximum area under the receiver operating characteristic curve (AUC) of the highly supported models.

In July 2021, we performed targeted surveys for *M. nuda* in the northeastern US. To inform site selection, we used the habitat suitability maps generated with the regional SDMs. We visited 46 sites predicted to have moderate to high habitat suitability ($>$0.5). We performed an opportunistic survey at each location where we first attempted to locate the host plant or a nectar plant and, if successful, watched for bee visitation. We added positively identified *M. nuda* observations to the final occurrence dataset for range-wide modeling.

2.3. Range-wide model

To assess how *M. nuda* and its host plant may respond to future climate change scenarios, we defined an extensive study area (Fig. S2) that covers the known range extent of both *M. nuda* and *L. ciliata*. Due to the large spatial extent and computational limitations, we used five arc-minute resolution (approximately 10 km at the equator) for the range-wide analyses. Considering these changes and new field observations, we repeated variable selection before generating the range-wide models. We added three additional variables for consideration: (i) solar radiation during meteorological summer (calculated as the mean solar radiation during June, July, and August; Karger et al., 2017), which corresponds to the bloom period of *L. ciliata* and the period of adult bee activity and may have implications for foraging behavior and reproductive success (Burrill and Dietz, 1981; Vicens and Bosch, 2000), (ii) Soil clay content (Hengl, 2018b), and (iii) soil pH (Hengl, 2018c), both of which may alter the suitability of soils for nesting (Antoine and Forrest, 2020). In contrast to the regional model, we chose to exclude the distribution of *A. androsaemifolium* due to observed variability in nectar plant use (e.g., *Apocynum cannabinum*), which suggests that the distribution of *A. androsaemifolium* may not accurately represent nectar availability, or limitation, across the landscape. We excluded proximity to water due to the coarse grain of the range-wide models limiting the utility of this layer for identifying shoreline and wetland habitats. Finally, we excluded soil moisture, which may fluctuate with climate change (Allen et al., 2011) and for which we do not have forecasted datasets.

For future projections, we used bioclimatic variables representing two periods, 2041 – 2060 (2050) and 2081 – 2100 (2090), and four Shared Socioeconomic Pathways (SSPs); SSP 126, SSP 245, SSP 370, and SSP 585. SSPs are similar to Representative Concentration Pathways from the Intergovernmental Panel on Climate Change's (IPCC) fifth assessment in that they represent different atmospheric concentrations of greenhouse gases (IPCC, 2013). However, SSPs incorporate socioeconomic narratives into each emissions scenario, such as the influence of demographics, economic development, geopolitics, and land-use change (Riahi et al., 2017). We obtained bioclimatic variable projections for each period and SSP from eight General Circulation Models (GCMs) developed for the World Climate Research Programme's Coupled Model Intercomparison Project Phase 6 (see supplementary methods) through worldClim (ver. 2.1; Fick and Hijmans, 2017). To generate final model predictions, we calculated the average suitability for each combination of period and SSP over all eight GCMs.

Additionally, to determine if the inclusion of biotic interactions improved model performance, we modeled *M. nuda* with (biotic + abiotic) and without (abiotic-only) the modeled distribution of *L. ciliata*. We quantified the similarity of the biotic + abiotic and the abiotic only model predictions with Pearson's Correlation Coefficient and Warren *I* (Warren et al., 2008), a similarity statistic that quantifies the degree of overlap between two predicted distributions. We evaluated the difference in model fit between the biotic + abiotic and abiotic-only models and selected the best performing model using AIC and AUC. We used the abiotic + biotic range-wide model for all following analyses.

We calculated the extent of the collinearity shift between the baseline (present-day) covariates and those used for the future projections under each GCM. When training MaxEnt models for transfer across space or time, a collinearity shift may reduce the predictive accuracy and should be quantified and mitigated (Elith et al., 2011; Feng et al., 2019). To address multicollinearity in the model covariates, we used Pearson's correlation coefficient to subset the variables based on a threshold of $r > |0.7|$ (Feng et al., 2015). We selected 10 of the 23 possible variables for use in the model (Table 1). Of the chosen variables, two pairs, Bio12 and Bio18, and Bio5 and soil pH, exceeded the correlation coefficient thresholds in several combinations of GCM, period, and SSP. However, we found no absolute changes of r greater than 0.1. We chose to retain these variable pairs since minor shifts in collinearity between the baseline and future projections are unlikely to impact model performance or transferability (Feng et al., 2015).

We quantified the niche overlap of the bee and its host plant at each period and SSP using Warren *I*. To calculate the extent of the northward shift, we used weighted centroids, where higher suitability cells, closer to one, were assigned higher weights than low suitability cells. Using weighted centroids allowed us to estimate range shift without thresholding, which reduces the information included in the model predictions by converting a continuous suitability scale to a binary metric (Guillera-Arroita et al., 2015). We then evaluated the change in mean suitability from baseline using paired t-tests ($\alpha = 0.05$) of the $\log_{10}$ transformed data. Similarly, we assessed the change in the suitability of North American conservation areas included in the World Database on Protected Areas (UNEP-WCMC, 2021).

Table 1
The bioclimatic and environmental variables included in the range-wide model after addressing collinearity.

Bio4	Temperature seasonality
Bio5	Maximum temperature of warmest month
Bio8	Mean temperature of wettest quarter
Bio12	Annual precipitation
Bio15	Precipitation seasonality (coefficient of variation)
Bio18	Precipitation of warmest quarter
Clay content	% soil clay content at 0 cm depth
Sand content	% soil sand content at 0 cm depth
pH	Soil pH at 0 cm depth
DEM	Elevation

3. Results

3.1. Regional model

For the regional *L. ciliata* and *A. androsaemifolium* SDMs, the best-performing models used a combination of linear and quadratic feature classes and a regularization multiplier of one. No other pairs of model hyperparameters met the first selection criteria in either species (Table S1, S2). Two *M. nuda* models were highly supported. We selected the model with linear and quadratic feature classes and a regularization multiplier of two based on its higher AUC (0.84; Table S3).

During targeted collection in July 2021, we recorded 53 distinct patches of *L. ciliata* and six new *Macropis* localities across 46 sites. In addition to *M. nuda* (three sites), we collected individuals of the two other *Macropis* species endemic to the study area, *M. ciliata* (one site) and *M. patellata* (two sites; Fig. 2), indicating that our model may also predict suitable habitat for related *Macropis* species. Based on the regional models, the median predicted suitability of both the new *M. nuda* and *L. ciliata* occurrence localities was 0.89.

3.2. Range-wide model

After spatial thinning, we retained 1867 *L. ciliata* occurrences in the range-wide study area (Fig. S1). Two hyperparameter combinations, which varied only in the feature class (hinge vs. linear, quadratic, and hinge), were highly supported (Table S4); however,

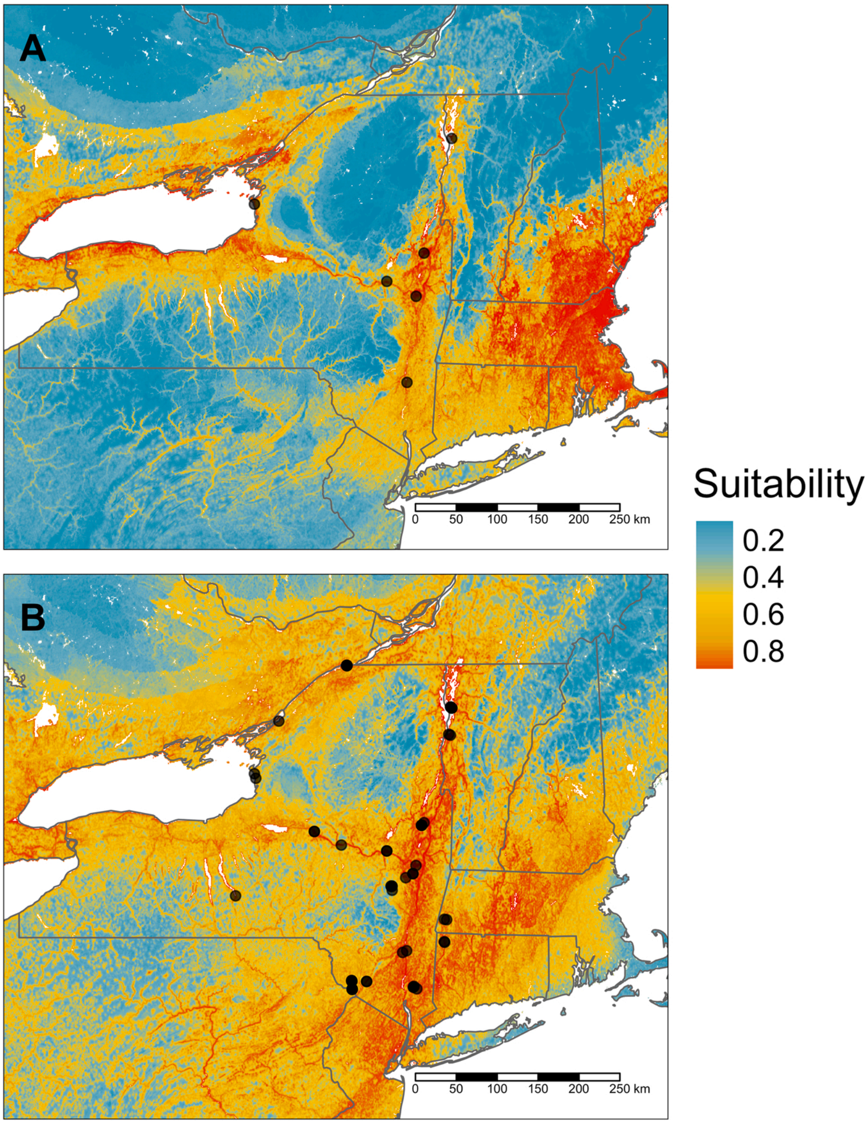

Fig. 2. Regional habitat suitability predictions for *M. nuda* (A) and *L. ciliata* (B) were used to facilitate targeted collection in July 2021. Dots represent new observations of all three *Macropis* species and patches of *L. ciliata* observed during the targeted survey.

we selected the former because it had an incrementally higher AUC (0.89). The weighted centroid of the suitability map for *L. ciliata* under projected climate change shows a northward shift between 485 km under SSP 126 to 1031 km under SSP 585 by 2090 (Fig. 3). By 2090, we project a decrease in the mean suitability of the study area from 0.14 to between 0.11 (SSP 126) and 0.09 (SSP 585; $p < 2.2e-16$). However, in the Canadian Rocky Mountains, suitability increased by 0.10 – 0.13 in 2050 before decreasing in 2090 under the high emissions scenario (Fig. 4).

After spatial thinning, the *M. nuda* dataset consisted of 60 occurrences across the species' known range (Fig. S1). When using complex combinations of hyperparameters, the number of parameters exceeded the number of observations in six of the 20 models specified by ENMeval and were excluded from consideration. We selected a single optimal biotic + abiotic only model with linear, quadratic, and hinge feature classes and a regularization multiplier of four (Table S5). The optimal abiotic-only model used linear and quadratic feature classes and a regularization multiplier of one (Table S6). Compared to the abiotic-only model, performance was improved when the biotic interaction with *L. ciliata* was included (AICc: 1218/1250, AUC: 0.89/0.87). However, the resulting predictions were generally consistent. We found that the predicted outputs in each period were highly correlated ($0.86 < r < 0.90$) and showed a high degree of overlap when compared using Warren *I*.

We observed no reduction in niche overlap between *L. ciliata* and *M. nuda* in any combination of period and SSP, with Warren *I* equal to approximately 0.93 in all scenarios. We projected a similar northern shift in the weighted centroids of *M. nuda* as observed in its host plant, between 356 km and 762 km by 2090 (Fig. 3). Bivariate mapping of host plant and bee habitat suitability shows that under all SSPs, areas of high *M. nuda* suitability are generally constrained to regions of high *L. ciliata* suitability (Fig. 5). However, the expanse of high suitability in the west appears to be bisected by the Canadian Rockies. The southwestern section is predicted to have higher suitability for *M. nuda* and the northeast for *L. ciliata*. For *M. nuda,* the projected range shift corresponds with a small but significant increase in the suitability of conservation areas (paired t-test; $p < 2.2e-16$). However, across the extent of the study area, we predict a 21–25% decrease in mean *M. nuda* habitat suitability from the baseline by 2090.

4. Discussion

Our models suggest that climate change will impact the availability of suitable *M. nuda* habitat and result in a substantial northward shift in the species' range. The magnitude of the change is sensitive to the level of greenhouse gas emissions and socioeconomic scenarios represented by the four SSPs considered here. Higher emissions necessitate greater range shifts to track the climate niche of *M. nuda* and result in greater reductions in suitability across the region. However, even low emissions scenarios are likely to demand substantial range shifts for *M. nuda* and its host plant, *L. ciliata*. Our results suggest that the climate niche width of *M. nuda* populations may not be sufficient to avoid the loss of highly suitable habitat, even under the most optimistic scenarios (IPCC, 2021).

While no long-term, retrospective studies have explored the response of *M. nuda* to climate change. Studies on how close relatives have responded to past climate changes may lend some insight. Triponez et al. (2015) evaluated how two European *Macropis* species, *M. fulvipes* and *M. europaea,* and their host plant, *Lysimachia vulgaris,* responded to the changing climate following the last glacial

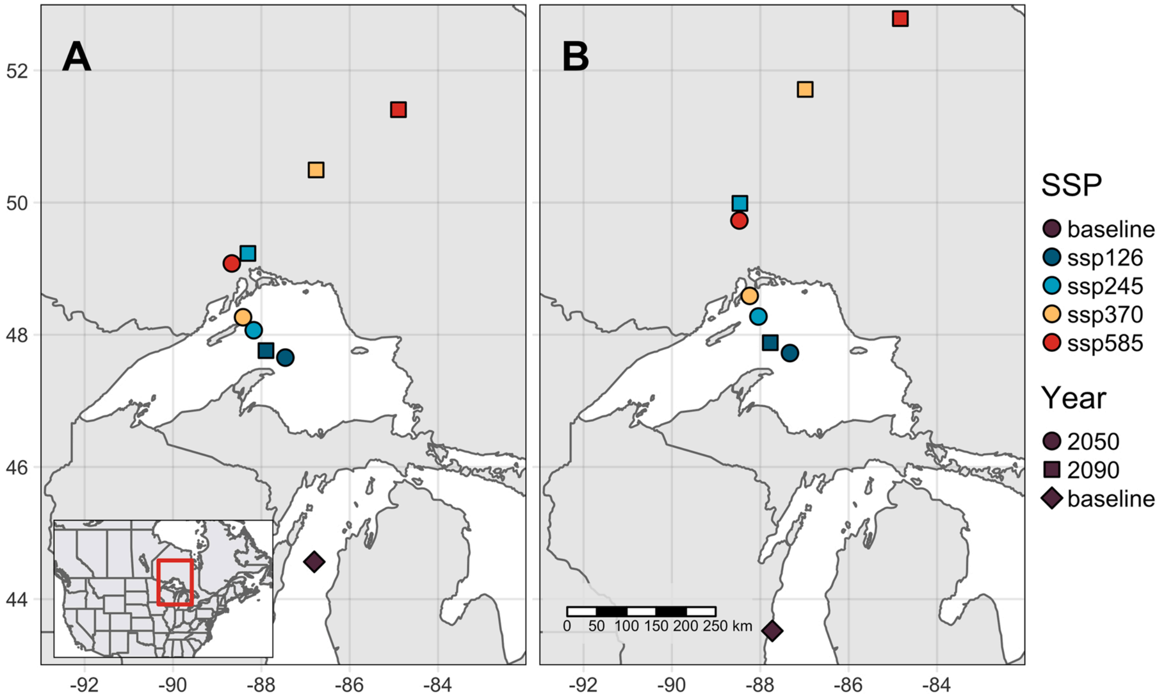

Fig. 3. Weighted centroids of the range-wide models of *M. nuda* (A) and *L. ciliata* (B) habitat suitability showing northward shifts.

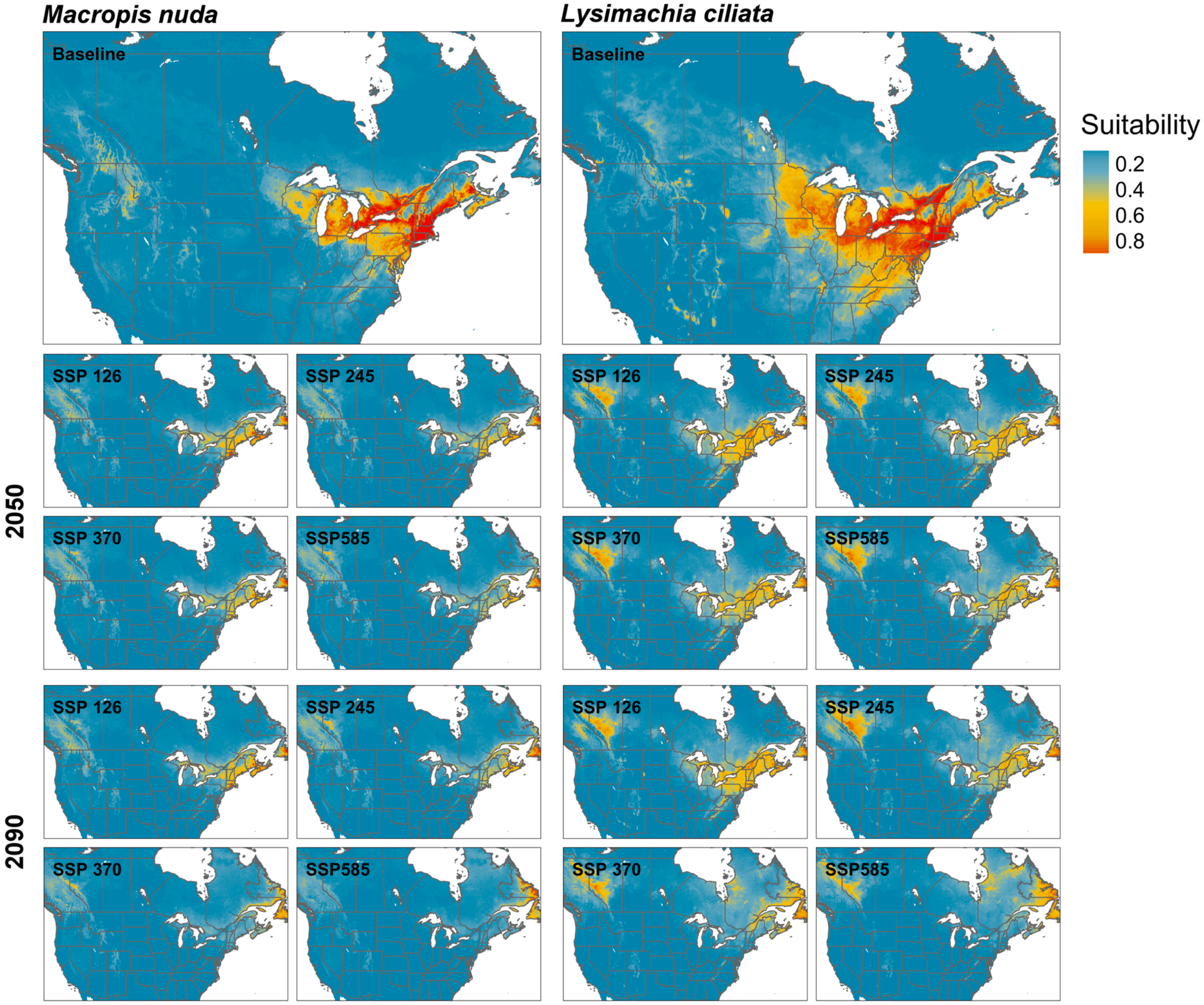

Fig. 4. Habitat suitability predictions for *M. nuda* and its host plant *L. ciliata* under baseline (2000) climate conditions and in 2050 and 2090 under four different climate change scenarios.

maximum. The authors found that although *L. vulgaris* could disperse northward better than either of the bee species, all three successfully tracked their climate niche (Triponez et al., 2015). Our models suggest that a similar response is possible in the North American species, where we project that *L. ciliata* may shift further north than *M. nuda* by the same period in high emissions scenarios. Furthermore, *M. nuda* and *L. ciliata* share similar ecology with their European counterparts, including (i) an unequal dependency (Cane et al., 1983; Triponez et al., 2015), (ii) similar animal-mediated host plant dispersal (Oh et al., 2008), and (iii) potential dispersal limitations arising from specialization on a patchy habitat. Coupling these similarities with our projections of a largely synchronous range shift and the expansive climate niche of *L. ciliata*, we suspect that floral resources will be available throughout the future climate niche of *M. nuda*.

However, our models do not account for variation in response based on biotic factors other than host plant distribution (e.g., changes to competition, host shifts, phenological mismatch, or disease) and their relationship with climate velocity (HilleRisLambers et al., 2013). Furthermore, static SDMs cannot address barriers to dispersal or accurately account for dispersal capacity (Franklin, 2010). In this case, while there are no studies of *M. nuda* dispersal, the modeled habitat suitability is patchy. Consequently, dispersal limitations, barriers, and ecological sinks may prohibit *M. nuda* from following its climatic niche. We addressed this limitation in part by including the biotic relationships with *L. ciliata* as a predictor, which limits the suitability of areas that may be unsuitable for its host plant. However, we cannot fully address these limitations without further study of bee dispersal.

Despite these limitations, SDMs remain a valuable resource for informing conservation decision-making regarding climate change (Wiens et al., 2009). As we have demonstrated, SDM is a promising, less resource-intensive method for facilitating targeted bee collection and increasing our understanding of bee distributions, habitat preferences, and conservation status. For *M. nuda*, we anticipate that existing conservation areas will increase in suitability marginally with climate change. However, this occurs predominantly in the expansive protected areas of western North America, a region with relatively low suitability overall. Therefore, we

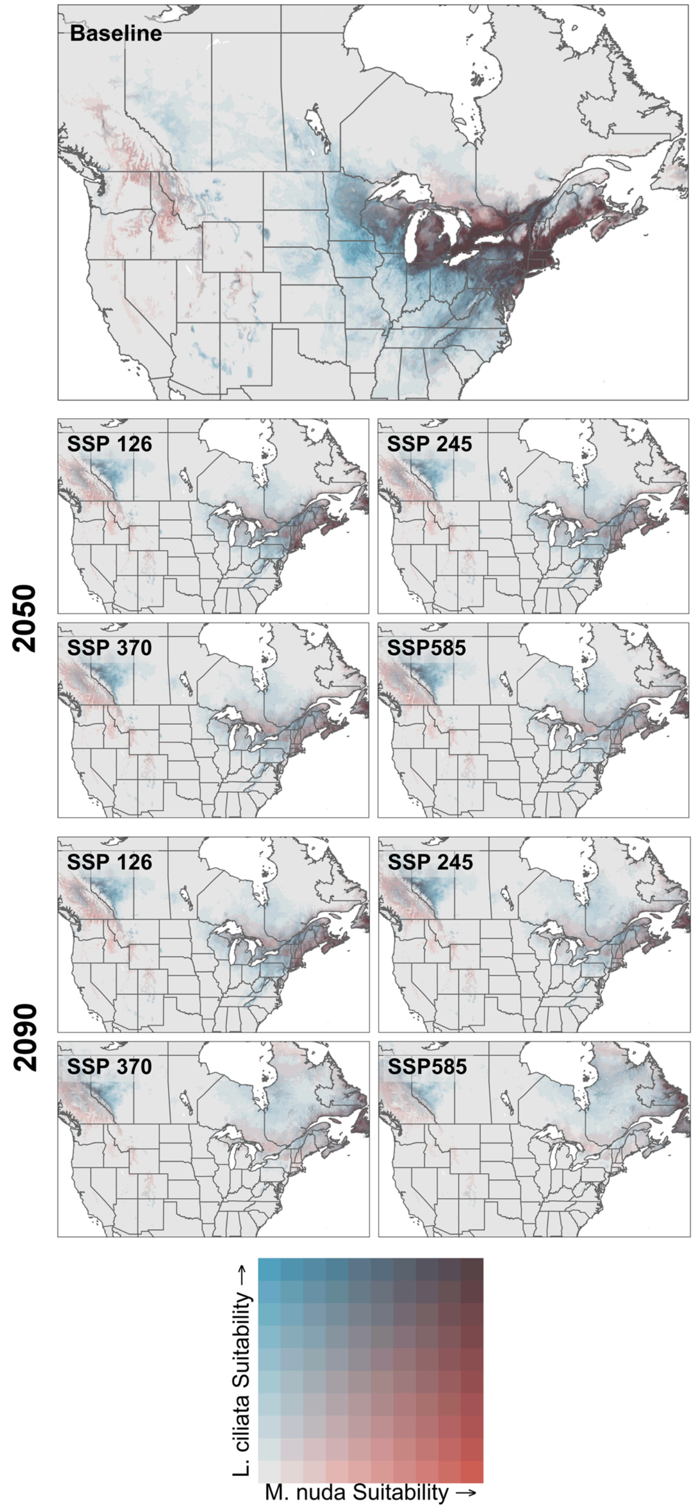

Fig. 5. Bivariate maps of *M. nuda* and *L. ciliata* suitability at the baseline (2000) and 2050 and 2090 under SSP 126 (B), SSP 245 (C), SSP 370 (D), and SSP 585 (E) show a generally synchronous range shift.

suggest these protected areas are of limited value for *M. nuda* conservation.

Although our results principally inform the conservation and management of *M. nuda*, management decisions based on the results we report here are likely to have broader applicability, particularly for other temperate wetland bees in the northeastern US, such as

M. ciliata and *M. patellata*. Accordingly, supporting *M. nuda* as its climate niche shifts northward, especially in eastern North America, is crucial for conserving this species and others with a similar climate niche. By protecting suitable habitats within the current range of *M. nuda* and northward into its projected range, we can ensure connectivity between current and future habitats, limit barriers to dispersal, and create essential transitional habitats to support climate-driven range shifts. Conservationists should prioritize landscapes based on projected suitability and measures of landscape-level climate resilience, including topographic roughness and maximal elevation difference (Lawrence et al., 2021). In New York, some landscapes that meet these criteria are already conserved, principally in the Adirondack Park preserve. This area retains moderate suitability in low carbon emissions scenarios but may function as an ecological trap with higher emissions, stranding *M. nuda* at elevation as its climate niche shifts northward (Bonebrake et al., 2018).

While we expect climate change to be a significant driver in the redistribution of *M. nuda*, it is only one of several threats from anthropogenic environmental change (Sage, 2020). The success of any conservation actions will require practitioners to account for the multiple interacting determinants of habitat suitability not considered here. In existing and proposed protected areas, land managers should consider the impacts of land-use practices, which may reduce nesting habitat and floral resource availability. While far from an exhaustive list, we recommend the protection of shorelines and banks from erosion and compaction from heavy recreational use, the installation of shoreline retaining walls, or other development which is likely to reduce or remove riparian habitat. Additionally, we emphasize the importance of preventing the introduction and establishment of invasive species, such as purple loosestrife, *Lythrum salicaria*, which can deteriorate wetland habitats and outcompete native flora (Blossey et al., 2001), potentially reducing floral resource availability.

Our results add to the growing body of evidence showing a disparity between xeric and temperate bee species' responses to climate change. Only a few studies – focused on species in the genus *Bombus* (Apidae) – have used historical data to investigate how temperate, cold-adapted bee species respond to climate change (Kerr et al., 2015; Rasmont et al., 2015). Kerr et al. (2015) examined historical range shifts in North American and European *Bombus* species. They provided evidence of range constrictions where the tailing southern margin crept northward, compressing the extent of available habitat against relatively stationary northern margins. However, several studies, which used SDMs to evaluate the impacts of climate change on temperate bee distributions, show evidence of an elevational and poleward shift (Martins et al., 2015; Biella et al., 2017; Martínez-López et al., 2021). The results we present here are generally consistent with other studies of temperate bee responses to climate change and inconsistent with xeric, arid-adapted bee species, which are predicted to experience range expansions (Silva et al., 2018; Dew et al., 2019). Among bees, these xeric species may prove to be climate "winners," capitalizing on the expansion of arid desert habitats. For temperate bees, however, the prognosis appears less optimistic.

5. Conclusion

Our models predict that climate change will result in *M. nuda* losing suitable habitat in a large part of its range throughout the northeastern US, even in the most optimistic scenarios. High future greenhouse gas emissions correspond to a larger range shift and a reduction in mean suitability across their range. Our model projections generally correspond with responses documented in other temperate bee species, a shift towards the poles and up in elevation (Martins et al., 2015; Biella et al., 2017; Martínez-López et al., 2021). We project that these changes to its distribution will generally occur in synchrony with its host plant, *L. ciliata*.

It is improbable that, without a sweeping and rapid response to limit emissions and mitigate the continued warming of Earth, *M. nuda* will remain within its present-day distribution. Conservationists interested in protecting regional bee biodiversity should consider preserving intermediate habitats between the current range of this species and the future projected range. Continued development and marginalization of wetland and riparian habitats will likely reduce habitat connectivity, compounding existing dispersal constraints (Öckinger et al., 2010; de Araújo et al., 2014). Unfortunately, like many rare habitat specialist bees that resemble *M. nuda*, we lack foundational knowledge of their ecology. The use of SDMs to inform targeted collections, gather further ecological observations, and generate predictions about future distributions is likely to prove valuable for informing bee conservation and, in turn, the conservation of essential ecosystem services and functions.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The model code is archived at https://doi.org/10.5281/zenodo.6491145.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02180.

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