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Looking out for the little guy: species distribution modeling and conservation implications of the elfin skimmer *Nannothemis bella* (Odonata: Libellulidae)

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All relevant data are within the paper and its Supporting Information files.

Abstract. *Nannothemis bella* Uhler, 1857 (Odonata: Libellulidae), the smallest dragonfly in North America, inhabit bogs and sedge fens across their distribution, spanning from Quebec (Canada) south to Florida and west to Minnesota and Louisiana (USA). While common in the northern part of their range, *N. bella* is of conservation concern in the southern populations where they are disjunct and rare. Little work has been done on the ecology and geographic conservation of this species. To fill this knowledge gap, we constructed species distribution models (SDMs) to analyze the spatial distribution and climatic niche of *N. bella*, define factors in habitat suitability and estimate potential niche shifts under climate change and inform conservation efforts. Our present-day SDMs indicate the dominant environmental elements determining habitat suitability include the proportion of silt in soil, temperature seasonality, percentage of clay and coarse components in soil, and soil class. Our paleodistribution models show a southern distribution within the last glacial maximum, with a shift northward 8,326 to 4,200 years ago. Our projected SDMs for 2050 under RCP 2.6 and RCP 8.5 predict a significant decrease in habitat suitability throughout the entire range of *N. bella.* As such, *N. bella* is a species of conservation concern and conservation measures are imperative for its continued existence as a much-needed bioindicator for these freshwater ecosystems. Additionally, this ecological knowledge provides the foundation for identifying population sites from which to collect *N. bella* for future population genetic studies.

Keywords. Bioindicator, climate change, dragonfly, endangered, extinction, habitat suitability, paleodistribution, projected distribution, spatial distribution

Introduction

Among highly variable and diverse dragonflies, the family Libellulidae is the most species rich. Libellulidae inhabit lentic and lotic habitats (Letsch et al., 2016), and may be grouped as either fliers, perchers or intermediate style fliers (Corbet & May, 2008). Many dragonflies, despite being often ubiquitous at water bodies, still await a rigorous assessment of the drivers that influence their habitat suitability (Abbott et al., 2022; Kalkman et al., 2022).

Nannothemis bella Uhler, 1857 (Odonata: Libellulidae) is a monotypic species found in eastern North America (Tennessen, 2019). At approximately 1.8 cm long, it is the smallest dragonfly species in North America (Hilder, 1985) and is thought to be a poor disperser relative to other larger libellulids with greater distributions due to their small wing size. As such, it seems unlikely that the species can migrate in response to deteriorating habitat conditions. Previous research conducted on *N. bella* has focused on morphological description (Uhler, 1857; Tennessen, 2019), abundance observations at specific locations (Roble, 1994; Glotzhober, 2001), and male territorial behavior (Hilder, 1985; Lee, 1986). Nymphs of this species, thought to have a semivoltine (i.e., longer than a year) lifecycle, are small and compact with broad wing sheaths, have many long setae, and lack middorsal hooks. The number of instars is yet unknown (Tennessen, 2019). Male *N. bella* are territorial at breeding sites and are classified as perchers (Hilder, 1985). Females lay eggs within the territory of the male they copulate with (Lee, 1986). In addition, males who don't retain territory 'tend to die or emigrate sooner' than males who do (Hilder, 1985).

Much of the ecology and biogeography of *N. bella* is still unknown, which has hindered the process for extensively assessing conservation concern and constructing potential management plans. The distribution of the species spans from Quebec, south to Florida, and west to Minnesota and Louisiana. *Nannothemis* is common in the northern part of their range but in their disjunct southern ranges they are considered rare, and of conservation concern (NatureServe Explorer 2.0., 2023). *Nannothemis* is listed as critically imperiled in Mississippi, Virginia, Kentucky, Illinois, Indiana, Ohio, Pennsylvania, and Maryland (NatureServe Explorer 2.0., 2023). *Nannothemis bella* may be imperiled perhaps because of its affinity for very specific habitats: it inhabits bogs, fens, and the edges of small streams and lakes where *Sphagnum* is found (Hilder, 1985; Tennessen, 2019) and has also been recorded in acidic habitats (Bright, 1999). *Nannothemis* is often found in peatlands, which are vital for carbon sequestration and carbon storage (Nordström, 2022) but are being negatively impacted by anthropogenic activities; in Canada, for example, peatlands are drained for agriculture, mined for peat, or destroyed by urban development (Rochefort, 2000). Without these habitats, species that rely on peatland, such as habitat specialists like *N.bella*, are at risk of being lost. Further concern for *Nannothemis* concerns its ability to thermoregulate in response to a warming climate. Flight style influences the thermoregulation strategy of odonate species (May, 1976). Perches like *N. bella* thermoregulate behaviourally by controlling the external heat they receive (May, 1978). Voluntary avoidance of high temperatures becomes less effective as baseline temperatures rise, further imperiling the species.

This investigation aims to define the species distribution of *N. bella* to determine what climatic factors influence habitat suitability and how that habitat may change to further inform conservation efforts. As addressed above, due to *N. bella* frequently inhabiting acidic environments we expect that pH will be a significant factor in predicting habitat suitability. Furthermore, suitable habitat may be considered for future sampling guided by genetic sampling results. In order to determine a baseline distribution of *N. bella*, we utilize past, present and future species distribution modeling (SDMs). SDMs are a technique used to estimate the distribution of a species by combining occurrence data with 'spatially explicit environmental data' to generate an envelope of suitability (Goodman et al., 2022). Occurrence data can be obtained from a litany of sources including natural history collections, citizen-science observations, and abundance surveys by public and private institutions. Environmental data is predominantly derived from field stations or remote sensing satellites and interpolated into climatic variables of temperature and precipitation. ENMs of odonates have gained significant popularity within the past few years, which have been used to assess species diversity across latitudes, diversity of habitat (lentic/lotic, forest/non-forest), conservation status, endemism, response to climate change, fires and anthropogenic disruption, and paleo-distributions (Bush et al., 2014; Collins, 2014; Collins & Mcintyre, 2015; Dorji et al., 2020; Nidup et al., 2020; Abbott et al., 2022; Cancellario et al., 2022; Goodman et al., 2022; Kalkman et al., 2022). Overall patterns of future odonate distributions indicate substantial habitat loss and extinction for endemic low-dispersing riverine species, while high-dispersing large-bodied species will shift northward (Hassall & Thompson, 2008; Flenner et al., 2010; Jaeschke et al., 2013; Bush et al. 2014; Simaika & Samways, 2015; Kietzka et al., 2018; Boys et al., 2021). Although Abbott et al. (2022) mapped the distribution of all Nearctic species (including *N. bella*), the distribution was only for the present. The biogeographical patterns seen across populations of *Nannothemis bella* and what the drivers of its habitat preferences are, and if they change in the future have yet to be comprehensively studied.

Methodology

Occurrence records

We created species distribution models using occurrence data from The Global Biodiversity Information Facility (GBIF, 28 July 2023). We selected occurrences that were museum samples or iNaturalist research grade observations, which possessed verified latitude and longitude coordinates, a photograph of the sighting, observation date, and at least ⅔ agreement on species identification by the community. We filtered data to include coordinates with an uncertainty range of 100 m, removed occurrences from erroneous localities (i.e., middle of the ocean, natural history museum/collection), and included occurrences across their range. In total, we downloaded 356 occurrences as a tab-delimited CSV file to be used in further analysis.

Environmental data

We conducted all analyses using the statistical programming language *R v. 4.1.2* (R Core Team, 2021), and all layers were in a latitude/longitude coordinate system with a WGS84 datum. We acquired environmental rasters at 2.5 arc-second resolution (~ 5 km at the equator) from the Worldclim database, which consists of 19 bioclimatic variables, extrapolated from monthly minimum and maximum temperature, humidity, mean, and coefficient of variation of annual solar radiation, and averaged from the years 1970–2000 (Fick & Hijmans, 2017). Furthermore, because we suspected that *Nannothemis bella* were influenced by the acidity of water and the presence of peat, we acquired soil data from the Global Soil Information Facilities (GSIF) (Hengl et al., 2021) at 250 m resolution at a depth of 0–5 cm (Hengl et al., 2017). The soil factors used were soil pH in H_20, proportion of sand (> 0.05 mm), silt (≥ 0.002 mm and ≤ 0.05 mm), and clay (< 0.002 mm) particles in the fine earth fraction (g/100 g), volumetric fraction of coarse fragments (> 2.0 mm; $cm^3/100\ cm^3$ (vol%)), and a global categorical raster of the United States Department of Agriculture (USDA) Soil Taxonomy Suborders of 67 soil classes (Hengl et al., 2021; Goodman, 2022). We rescaled our soil variables to match the resolution of our WorldClim variables. Soil data was used rather than wetland mapping as a proxy for bog habitat due to differing habitat definitions across international resource management boundaries.

We processed occurrences using a spatial thinning distance set to 5 km to match the resolution of our climate data and to prevent spatial autocorrelation and pseudoreplication using the 'spthin' package in R (Aiello-Lammens et al., 2015). We generated 50,000 random background points over our study extent, defined as a bounding box with a study regional-buffer distance of 3-degrees. We chose this buffering distance to encapsulate the hypothesized dispersal limitations of *N. bella* and to capture potentially undersampled populations (Peterson & Soberón, 2012). We partitioned occurrences using the spatial partition block method (k = 4), as this method is most preferred for large sample sizes, and whose range of the species is large (Radosavljevic & Anderson, 2014). Finally, we removed highly correlated environmental variables using the 'vifcor' package (Naimi, 2017). Highly correlated environmental variables were defined as variables with correlations of over 0.7 (Pearson Coefficient). In ENM analyses, the balance of correlation threshold against the number of environmental variables retained for analysis is an area of active study with coefficients ranging from 0.5–0.9 (Dormann et al., 2012; Howard et al., 2014; Mesgaran et al., 2014; Yan et al., 2020). Since fewer variables create underfitting models, we chose a moderate correlation threshold (0.7), which acted as a natural break in which higher thresholds significantly reduced the number of environmental variables retained. The final model used nine WorldClim predictor variables and five soil predictor variables.

Model building

The machine learning algorithm MaxEnt (Phillips et al., 2017) was used to estimate the species' response to the environment, using the ENMeval v3.4.4 package (Kass et al., 2021). This algorithm allows for increases and decreases in model complexity based on two settings—feature classes and regularization multipliers. Feature classes determine the fit of the model, whereas regularization multipliers determine how much complexity is penalized. This may result in some environmental variables being removed from the model. The models created used the feature classes linear (L), hinge (H), a combination of linear quadratic (LQ), or a combination of the three (LQH) and regularization multipliers 1 to 4, of which 4 penalizes complexity the most. This resulted in 16 possible models.

Optimal models were chosen with 10-percentile omission rate, average omission rate when applying a 10-percentile training presence threshold to the data, values closest to 0.1. This threshold omitted the lowest 10% suitability locations from the data (Radosavljevic & Anderson, 2014; Kass et al., 2021). If 10-percentile omission rate values for models were tied, the model with the highest average AUC value (area under the curve) was chosen. AUC is a scale-invariant value that measures how well a model is able to distinguish between true positives and false negatives and is used as a relative comparison between models (Lobo et al., 2008; Radosavljevic & Anderson, 2014).

To investigate model behavior, we examined predictor variable importance values and marginal response to suitability. Permutation importance is calculated by randomly permuting the values of all variables but one, building a new model, then calculating the difference between each model's training AUC and that of the global model (Phillips, 2021). Marginal response curves show the modeled relationship of each variable individually with the occurrence data when all other variables are held constant and are affected by the complexity of the model settings (Phillips et al., 2017).

We made habitat suitability predictions for *N. bella* using both thresholdless and thresholded metrics. We transformed raw maxent predictions to a scale of 0–1 to approximate probability of occurrence using the 'cloglog' transformation (thresholdless) (Phillips et al., 2017). We also generated a threshold prediction, calculated from the 10-percentile omission rate from our model evaluation. We generated future predictions of the distribution of *N. bella* by projecting our models to the Worldclim bioclimatic datasets for the years 2050 and 2070. We utilized the global circulation model CCSM4 using the Representative Concentration Pathways (RCP) 2.6 (high effort to curb carbon emissions) and 8.5 (low effort) to compare distributional changes of *N. bella* under different climate scenarios. Although studies have estimated increases in soil turnover and respiration rate within the next 100 years, no comprehensive global soil map subclass data has been gener-

Table 1. Permutation importance and response behavior of most significant environmental variables.

Environmental variable	Percent contribution	Permutation importance	Response behavior
Percent silt (%)	21.95	29.60	Negative linear hinge
Temperature seasonality (°C)	31.70	28.49	Quadratic
Percent clay (%)	14.32	21.26	Negative linear hinge
Percent coarse (%)	21.92	18.53	Quadratic
Soil class	9.82	1.14	Positive correlation with haplic podzols (marginal), negative correlation with haplic alisols (marginal)
Precipitation of wettest month (mm)	0.09	0.40	Negative linear
Precipitation seasonality (%)	0.20	0.38	Negative linear hinge
Annual mean diurnal range (°C)	0.01	0.14	Constant linear

ated for future climate scenarios (Bond-Lamberty et al., 2010; Shojaeezadeh et al., 2024). As such, we included our present soil rasters in each future climate scenario with the assumption soil topography being unchanged significantly for within the next 100 years. Furthermore, we estimated the predictions of *N. bella* since the last glacial maximum (LGM: 20 ka) using the PaleoClim database (Brown et al., 2018). Maps were projected into the past for five time periods: 21 ka, 17.0–14.7 ka, 14.6–12.9 ka, 12.9–11.7 ka, 11.7–8.325 ka, and 8.326–4.2 ka. Due to incompatibility with WorldClim and PaleoClim variables, projections were built off a modern map utilizing CHELSA Anthropocene bioclimatic variable raster set (Karger et al., 2023).

Results

We constructed 16 models with WorldClim and soil rasters. Of the present models with both WorldClim and soil rasters, model L4 was the most optimal (Figures 1A, 1B). It possessed a 10-percentile omission rate 0.13, an average AUC value of 0.83, and 21 non-zero lambda values (model coefficients). The optimal CHELSA map used for the past projections was LQH3 with a 10-percentile omission rate of 0.14 and an average AUC value of 0.77.

Modern-day predictions of *N. bella* derived from our optimal model (Figure 2) suggests that the range of *Nannothemis* is largely restricted to the coast of Canada and the United States, stretching as far north as Nova Scotia, to far south as the Chesapeake. Suitability is also high within the great lakes region, tapering off near eastern Minnesota. Furthermore, southern along the Appalachian Mountains, possessing intermediate to high suitability, breaking at eastern Louisiana. Our 10-percentile omission rate maps also reflect this pattern.

We observed near-identical patterns of suitability for *N. bella* for our future climate variables of 2050 and 2070 and across RCP scenarios. Within our cloglog-scaled predictions, we observe substantial drops in suitable habitat across the entire range of *N. bella*, with a faint low/intermediate amounts of suitable habitat still present within the great lakes region. Interestingly, we do observe patterns of suitable habitat in our 10-percentile omission maps within the years 2050 and 2070 which are the same as our modern-day predictions, with suitable habitat expanding northward into Southern Canada, and southward along the Appalachian Mountains.

Finally, our paleo-distributions for *N. bella* indicate a southern distribution within the LGM, with suitability being highest along the coasts of the Chesapeake, extending eastern across the great plains of Southern United States. Within our maps projected 8,326 to 4,200 years ago, we observe a shift northward, reflecting more modern-day distributions for *N. bella*, with areas of highest suitability being located within the great plains (at this time, the great lakes did not exist), as well as coastal Northern United States and Southern Canada.

Response curves were obtained for model L4 from the present models with both WorldClim and soil rasters (Supplemental Figure 4). The response curves showed that percentage of silt and temperature seasonality are the most significant environmental variables, with permutation importance of 29.60% and 28.49%, respectively (Table 1). These are followed by permutation importances of 21.26% for percentage of clay and 18.53% for percentage of coarse soil (Table 1). Soil class (1.14%) , precipitation of the wettest month (0.40%), precipitation seasonality (0.38%), and annual mean diurnal range (0.14%) are additional factors (Table 1).

Of the 19 WorldClim variables and 5 soil variables, only 9 were deemed significant for habitat suitability preferences in *N. bella*. Four factors were found to be particularly important—silt, temperature seasonality, clay, and coarse soil. *N. bella* prefers soil up to ~ 40% silty with no clay or coarse components (Supplemental Figure 4). It should be noted that the quadratic curve for coarse soil is sharp, likely because the occurrences occur across a large range and the software has more difficulty extrapolating overall patterns (Supplemental Figure 4I). A visual inspection of the soil response curves and soil rasters match well. *N. bella* appears to be in areas of low coarse soil (Supplemental Figure 5D). Occurrences are in pockets of low clay soil and ~ 40% silty soil areas except for an outlier point in Ohio (Supplemental Figure 5A, 5B). GBIF inspection notes that said occurrences are *N. bella* and have verifiable photographs and is not taxonomic misidentification. As a result, this is likely one of the southernmost ranges of the species and may have a particular microhabitat.

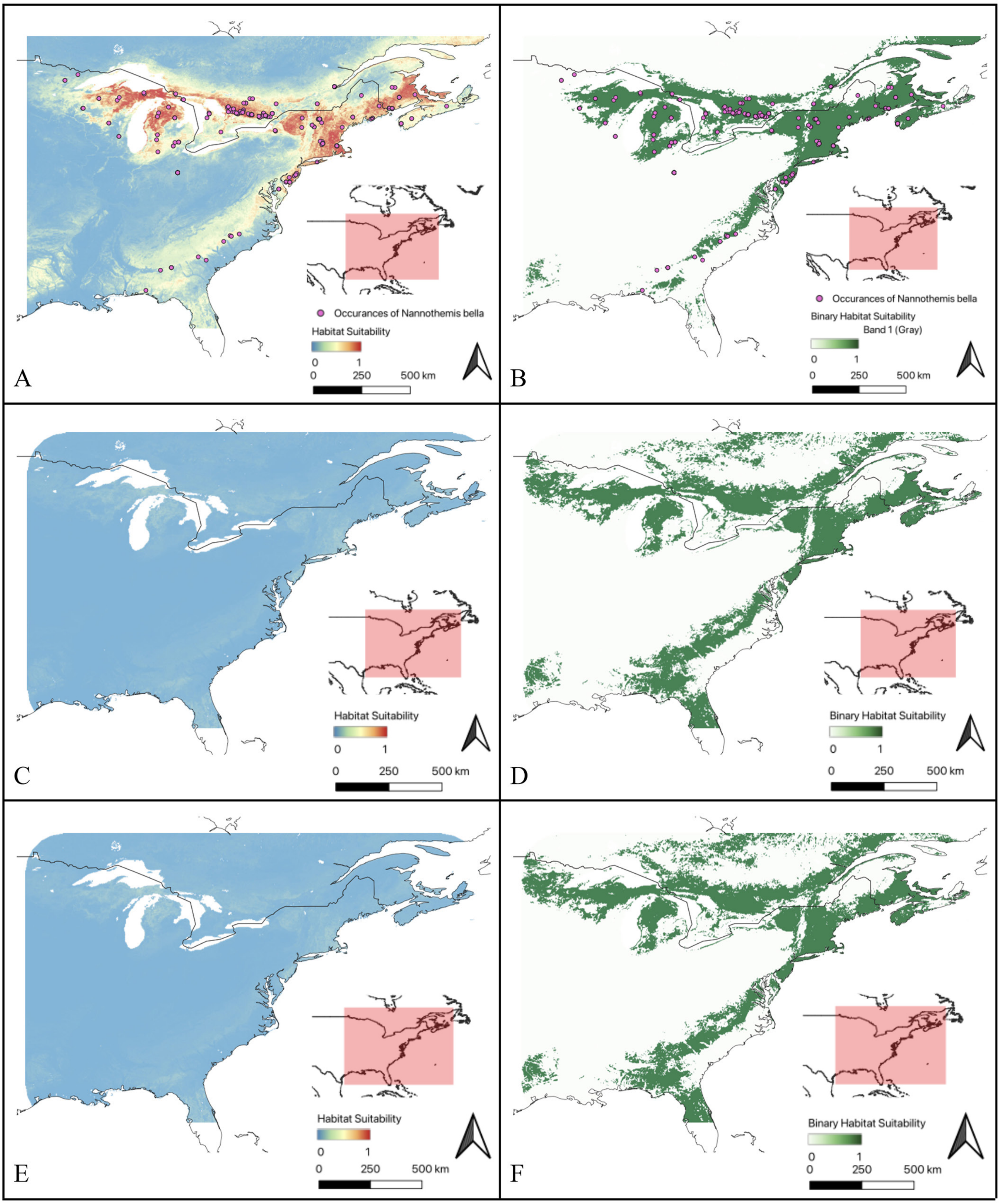

Figure 1. SDMs of *N. bella* with WorldClim and Soil rasters. Used precipitation, temperature, soil and occurrence data to predict suitable habitat for *N. bella.* Cloglog on left, 10-percentile training presence on right. (A+B) Present-day range; (C+D) projected 2050 range under RCP 2.6.; (E+F) projected 2050 range under RCP 8.5.

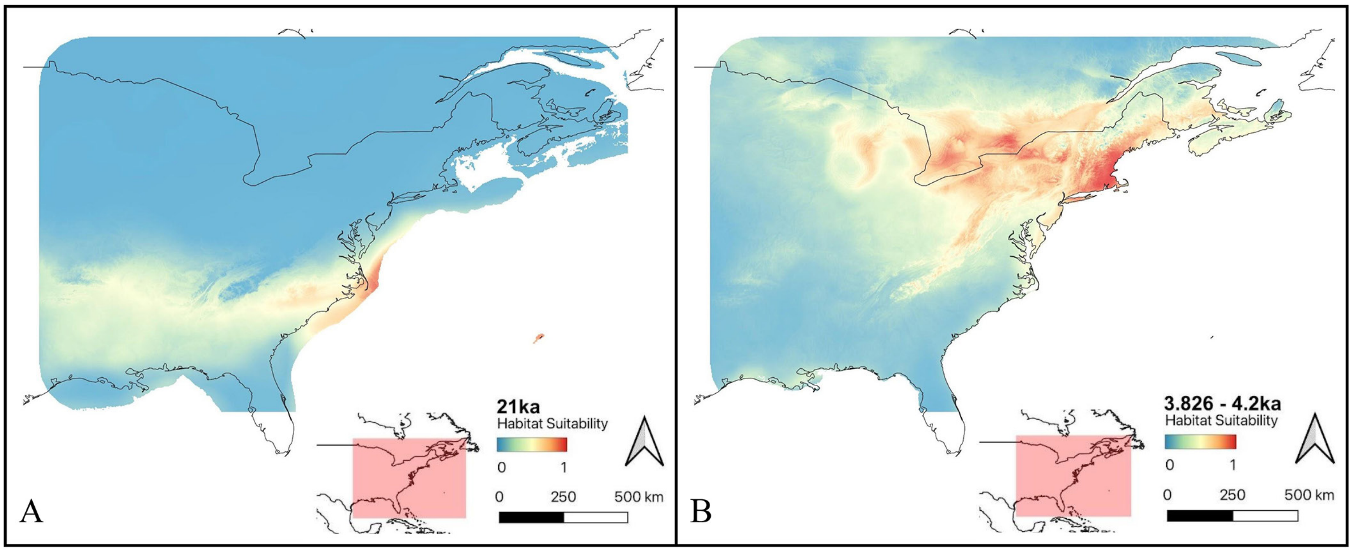

Figure 2. Projected cloglog SDMs of *N. bella* with PaleoClim rasters. (A) Projected range for 21,000 years ago; (B) projected 8,326 to 4,200 years ago.

Discussion

Life history traits and habitat suitability

The response curve for temperature seasonality implies *N. bella* has low tolerance for temperature variation greater than or less than 10˚C yearly (Supplemental Figure 4B). This appears to match sightings in bogs, which tend to be more insulating than other fen types (Vitt et al., 1995). We hypothesize that this temperature sensitivity may be due to the possible semivoltine nature of the *N. bella* nymph, with silt at the bottom of bodies of water such as bogs potentially providing insulation for organisms during winter. For example, Gomphidae nymphs tend to bury themselves in substrate in lentic or lotic waters. Specifically, *Dromogomphus* nymphs are found in silty, lentic water and are a semivoltine species (Tennessen, 2019). Similarly, *Gomphus vulgatissimus* prefers a sandy or silty bottom habitat and is semivoltine or partivoltine (Richter, 2008; Buczyński et al., 2016). Silt particles are relatively spherical and allow for air and water circulation (Lintern, 2018). As such, we hypothesize that silty soil is a significant factor in habitat suitability due to the overwintering of the nymph stage. Several genera of nymphs noted as semivoltine species are found in silty habitat. *Nannothemis bella* appears to prefer podzol soil (0.72), found in boreal forests that occur commonly in its northern habitat (Table 1). A large amount of soil factors possessed high cloglog values compared to others (> 0.61). Alisols, an acidic, easily eroded soil that occurs in subtropical and temperate regions appear to be unsuitable (0.43) for *Nannothemis*. The species seems to occur in soil between a pH of 3 and 8 without a clear preference within this range (Table 1). It also seems like pH is less of an important factor because levels do not change much across the distribution (Supplemental Figure 5C).

The most suitable habitat is on coastlines or near large lakes, the high heat capacities of which moderate temperature throughout the year (Scott & Huff, 1996). More suitable habitat for *N. bella* is seen in the Northern United States and Canada than in more southern states, despite there being occurrences further south. It should be noted there is limited suitable habitat in areas where *N. bella* is listed as a species of conservation concern. Of note, there is a large gap in suitability in the Appalachian Mountains region. *Nannothemis bella* may have preferences for altitude, making the Appalachians a large barrier to dispersal. In this case, gene flow between populations across the Appalachian Mountain range should be studied. Present day cloglog and 10-percentile training presence SDMs show some differences in suitable habitat. In this, it is important to acknowledge that the 10-percentile training presence SDMs are less refined and omit only the lowest 10% suitability habitat. *N. bella* has a large range in suitable precipitation of the wettest month, possibly due to its large current geographic range (Table 1). Habitats with temperature ranges of ~ 10°C over the year are most suitable (Table 1). Even though *N. bella* is found in areas with large temperature ranges, it is most often found near large bodies of water where land temperatures are buffered. Ideal precipitation seasonality is low, meaning low variation in monthly precipitation totals over the course of the year is preferred (Table 1). In short, *N. bella* likes a consistent amount of rain. Finally, there is a large range of suitable annual mean diurnal range (Table 1). Due to inhabiting high latitude temperate zones, *N. bella* appears to have an affinity for large daily temperature fluctuations.

Projected distributions

Projected SDMs for *N. bella* anticipate a dire future for the species. Projections for 2050 and 2070 under both RCP2.6 and RCP8.5 do not show significant differences, with the best-case scenario projection map, 2050 RCP2.6 (Figures 1C, 1D), being almost identical to the worst-case scenario projection map, 2070 RCP8.5 (Supplemental Figure 1D). In the best-case scenario, the cloglog-scaled map (Figure 1C) shows almost no suitable habitat left. While the corresponding binary map (Figure 1D) shows more suitable habitat options than the present-day map (i.e., habitat extends further north, as well as more into Florida and further south), it should be noted that this habitat is suboptimal. Cloglog predictions display suitability on a continuum and emphasize the highest suitable areas within our study extent, yet thresholded maps (10-percentile training presence) flatten predictions based on omission, correcting for uncertainty, which may explain the differences between our two map predictions. Overall, these projections indicate that there may not be much, if any, suitable habitat left in less than 30 years' time. As such, *N. bella* is a species of conservation concern and conservation measures are imperative for its continued existence.

Conservation status

Threatened and endangered (T & E) status for *N. bella* does seem to overlap well with suitability predictions for the species across its range (NatureServe Explorer 2.0., 2023). Overall, *N. bella* possesses a global status of G4 (Apparently Secure), however this can be accredited to the rarity of the species in some parts of its range and its overabundance in others (particularly within New Jersey, New York, Maine, Ontario, Quebec, New Brunswick, Nova Scotia). Areas of high suitable habitat for *N. bella* do possess lower T&E rankings for the species, corresponding to their high abundance within these regions. States and Provinces which list *N. bella* as S4 (Apparently Secure) include Ontario, Nova Scotia, and Maine, while States and provinces which do not give *N. bella* a status include Minnesota, Michigan, New Hampshire, Massachusetts, and New Jersey. States which list *N. bella* as S1 (Critically Endangered), possess few occurrences for the species, and subsequent low suitability within our models, these states include Illinois, Indiana, Kentucky, Ohio, Virginia, Pennsylvania, Maryland, and Delaware. A combination of high ranking and low-ranking states for *N. bella* do belong to the MidWest Landscape Initiative's (MLI) Regional Species of Greatest Conservation Need (RSGCN) list, suggesting populations of high and low abundance are being equally assessed and conserved at the regional level within each of the listed states. Interestingly, Alabama, Louisiana, South Carolina, and West Virginia do not give a status rank to *N. bella*, yet our models do suggest intermediate to high suitability along the Appalachian Mountains despite the low number of occurrences we recovered within this region; the Appalachian Mountains traverses all four of these states. As such, we recommend the elevation of *N. bella* within Alabama, New Orleans, North Carolina, and West Virginia to a higher T & E rank in order to preserve the species in these more rare populations, as well as including these states as a part of the MLI to create a cohesive multistate assessment and regional conservation plan for the species.

Nannothemis, like other dragonflies, can be used as a bioindicator of freshwater health. As such, its species decline may be an indicator of ecosystem health. In these systems, like other odonates, *Nannothemis* are important food sources for other members of the freshwater food web like fishes, frogs and birds, while also acting as top invertebrate predators consuming midges, mosquitoes, and other pest fly species along with other aquatic invertebrates. Dragonflies are predators that constrain mosquito populations (Chovanec & Raab, 1997; Mandal et al., 2008). They are noted to be indicators for the ecological integrity of the ecosystem structure, specifically the connection of aquatic ecosystems to other systems via the land-water-interface (Chovanec & Raab, 1997). Their use as bioindicators can be attributed to a large body of knowledge for many dragonfly species, correlation between structural parts of habitat and the presence of species, and their dependence on habitats with aquatic and terrestrial microhabitats. For example, researchers used *Gomphus flavipes* nymphs to assess the contamination level of aquatic systems in the Hungarian Upper Tisza Region. They found the accumulations in the larva in different rivers reflected the pollution levels (Simon et al., 2017). Further studies describe morphological and physiological markers correlated with decline in river quality (Manjula et al., 2024). Furthermore, dragonfly species are identifiable, and they can be determined to oviposit at the body of water and have relatively long developmental phases (Chovanec & Raab, 1997). Experimental studies across Asia, Africa, and South and North America have determined that dragonfly/damselfly nymphs have the potential to control mosquitoes (Singh, 2003; Mandal et al., 2008). Further investigations have utilized dragonfly diversity and assemblage variations as ecological indicators for restoration success in central European degraded raised bogs and to justify conservation potential (Krieger et al., 2019; Sushko, 2020). Information about the distribution and abundance of *Nannothemis* can contribute to similar datasets in North America.

Linking anthropogenic factors to current distribution

Suitable habitat for *Nannothemis* is rapidly declining, possibly as a result of anthropogenic factors (e.g., global warming, urban development, agriculture). This is particularly evident for *Sphagnum* peatland species richness between 40°N and 50°N, due to elevated temperature and a lower water table that favor vascular plants over *Sphagnum,* which could alter soil pH conditions

*(*Ma et al., 2022*).* Peatlands are used for forestry and agriculture, which both require drainage (Page & Baird, 2016). This could lead to increases in toxic silt in runoff resulting from chemical fertilizers and pesticides, industrial chemicals or the deposition of excess sediment (Bashir et al., 2020). As silt is the most significant factor in habitat suitability (Table 1), it follows that changes in the conditions of silt would have pronounced impacts on populations. A secondary hypothesis is that habitat loss due to changes in temperature seasonality due to climate change. Migratory dragonfly species have larger and smoother wings, a larger anal lobe, and longer and denser thoracic pilosity (Suárez-Tovar & Sarmiento, 2016). *Nannothemis bella* are behavioral thermoregulators and have small wings that make them unlikely to be able to migrate far in response to temperature changes. As the yearly temperature range shifts and/or broadens, *N. bella* may be unable to withstand new temperatures and unable to find new habitat, further endangering the species. Habitat-based restoration approaches, as suggested by White et al. (2015) are recommended. This may include restoring water infrastructures and increasing and managing aquatic and riparian vegetation (Monzó & Verdú, 2022).

Past distributions and current genetic diversity

In analyzing the projected maps into the past, it should be noted that the CHELSA modern map is less optimal than the WorldClim/Soil raster map and does not match the occurrences as well. The projected map to the last glacial maximum ~ 21,000 years ago implies that *N. bella* inhabited what is now the southern United States around the coastline (Figure 2A). Due to its similarities with dragonflies of the *Nannophya* genus found in Asia and Australia, estimates of its origin were much older than this (Kohli et al., 2021). For both hypotheses to hold, it is possible that earlier variants originated elsewhere, but the modern day *Nannothemis* originated around 21,000 years ago. In this case, the past projections we see are migration patterns of the species within recent evolutionary history. As the glaciers retreated, we see suitable habitat for *N. bella* move further north and shift further west, curving around the Appalachian Mountains (Supplemental Figure 2). As the Great Lakes were forming, around 14,000 years ago, *N. bella* appears to have expanded its range northward (Supplemental Figure 2; Hough, 1963). These projection maps have implications for population genetics hypotheses. Due to the species originating in what is now the southern United States, more genetic diversity would be expected in the Appalachians. However, this may be influenced by the relative sizes of different populations. In contrast, more genetic isolation would be expected into the Great Lakes regions due to the species' dispersal patterns. In projecting the origination points with maps of Pangea, it seems like they would have touched Africa. However, it is possible that a stem species of *Nannothemis* and *Nannophya* existed across the whole range of Pangea.

Study limitations and further investigations

We strove to conduct an objective assessment of the species distribution of *N. bella*. There were limitations in data availability, such as potential sampling bias in citizen science datasets leading to more occurrences in areas with higher human density and a lack of observational data in areas that are undersampled. However, this was countered as best as possible in the model parameters, which were thinned and based on biology of species with a 3-degree buffer based on our estimated maximum dispersal capability of *N. bella*. While our models may not capture the entire idealized range, they are robust for where we know the species has previously been recorded. Further studies may use other datasets based on country-specific wetland classification schemes to better map *N. bella*'s distribution through peat or bog habitat, providing finer resolution for local conservation plans. As such, given the lack of data and current research on *N. bella*, we believe that this provides valuable insight into the species and a foundation for further research.

Conclusion

This project has helped us glean information that was previously unknown about the natural history of *N. bella* and fills in some of the ecological knowledge gaps. Specifically, soil type has been shown to be a limiting factor in habitat suitability, along with temperature seasonality for this species. We have modeled the distribution of *N. bella* over the past 20,000 years, in the present day, and projected to 2070. Through this, we conclude that the distribution of the species is diminishing as a result of climate change and anthropogenic interaction such as destruction of peatland habitats and pollution and sedimentation. The SDMs created in this study identify sites for future population genetics studies. Finally, the rapid decrease in suitable *N. bella* habitat are indicators that conservation management plans for the species must be established to prevent extinction. This is imperative, as our projected best-case scenario shows almost no suitable habitat left by 2050.

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Supplementary Material

Figures 1–5.