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Collection methods and distribution modeling for Strepsiptera in the United States

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The twisted-wing parasite order (Strepsiptera Kirby, 1813) is difficult to study due to the complexity of strepsipteran life histories, small body sizes, and a lack of accessible distribution data for most species. Here, we present a review of the strepsipteran species known from New York State. We also demonstrate successful collection methods and a survey of species carried out in an old-growth deciduous forest dominated by native New York species (Black Rock Forest, Cornwall, NY) and a private site in the Catskill Mountains (Shandaken, NY). Additionally, we model suitable habitats for Strepsiptera in the United States with species distribution modeling. We base our models on host distribution and climatic variables to inform predictions of where these twisted-wing parasites are likely to be found. This work provides a useful reference for the future collection of Strepsiptera.

Key words: Strepsiptera, distribution modeling, *Stylops*, *Xenos*, Black Rock Forest

Introduction

Strepsiptera Kirby, 1813 (Insecta) have a cosmopolitan distribution, but they can be difficult to collect for many reasons. As the larval stages are obligate endoparasites of other insects, strepsipterans are necessarily restricted to the ranges of their hosts and may have patchy distributions among host populations (Kathirithamby 2002, 2018). The neotenic females dwell permanently within the abdomens of their insect hosts, with the exception of some members in the family Mengenillidae Hofeneder, 1910 (Kathirithamby 2002). Male strepsipterans can be collected independently of their hosts once they eclose and enter the free-flying adult stage. However, they are likely to still be found within their host ranges since they live for only a few hours and must mate within that time (Kathirithamby 2002, 2018). Females and males range from 0.5 to 5 mm and can be easily overlooked in host abdomens (females) or malaise traps (males; Kathirithamby 2018). There are no standard procedures for the collection of Strepsiptera, since they parasitize such a wide variety of insect hosts—they are documented to parasitize 7 orders comprising approximately 36 insect families, and these hosts inhabit many different environments (Pierce 1911, Kathirithamby 2009, 2018). Collection methods and timing for some groups have been published. Solulu et al. 1998 include methods for the capture and rearing of *Stichotrema* Hofeneder, 1910 (Strepsiptera: Myrmecolacidae Saunders, 1872) in bush cricket hosts of New Guinea. Hughes et al. (2004) and Hrabar et al. (2014) detail methods for capturing some species of the strepsipteran family Xenidae Saunders, 1872 in paper wasps in Italy and Canada. Nakase and Kato (2011) describe the collection of *Blissoxenos* Miyamoto and Kifune, 1984 (Strepsiptera: Corioxenidae Kinzelbach, 1970) from bug hosts in the family Blissidae Stål, 1862 living on bamboo in Japan. In the United States, James and Strong (2018) describe the use of light traps for capturing *Elenchus* Curtis, 1831 (Strepsiptera: Elenchidae Perkins, 1905) in Florida.

In the Nearctic, the extant families of this order presently documented are Corioxenidae, Halictophagidae Perkins, 1905, Elenchidae, Myrmecolacidae, Xenidae, and Stylopidae Kirby, 1813 (Kathirithamby 2002, Straka et al. 2015). Many genera of these families are present in the United States (Kathirithamby 2005). Of these, only a few species have been confirmed in New York through preserved specimen records or human observation to date: *Xenos peckii* Kirby, 1813 (Xenidae) in *Polistes fuscatus* Fabricius, 1793 and *P. metricus* Say, 1831 (Hymenoptera Linnaeus, 1758 Vespidae Latreille, 1802), *Eupathocera auripedis* Pierce, 1911 (Xenidae) in *Isodontia auripes* Fernald, 1906 and *I. mexicana* Saussure, 1867 (Hymenoptera: Sphecidae Latreille, 1802), *Pseudoxenos tigridis* Pierce, 1911 (Xenidae) in *Odynerus tigris* Saussure, 1857 (Hymenoptera: Vespidae), *Stylops advarians* Pierce, 1909 (Stylopidae) in *Andrena milwaukeensis* Graenicher, 1903 (Hymenoptera: Andrenidae Latreille, 1802), and *Elenchus koebelei*

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Pierce, 1908 (Elenchidae) in various Delphacidae Leach, 1815 (Hemiptera; Hughes et al. 2004, Kathirithamby 2005, Balzer et al. 2020, GBIF.org 2023). Here, we surveyed two locations in NY state for Strepsiptera, using multiple collection methods.

More data are necessary to gain a more accurate understanding of the cosmopolitan range of this order. These data may come most reliably in the form of increased collection efforts or in the digitization of specimen records whose collection localities currently lie inaccessible in museum archives. However, recent advances in ecological modeling—especially in software packaging and data availability—provide another option for investigating the whereabouts of Strepsiptera. Species distribution modeling (SDM) or ecological niche modeling, a quantification of the correlation between environmental variables and organismal distributions, has proven to be a valuable tool in ecology and biogeography (Miller 2010, Zurell et al. 2020). With SDM, we can use known occurrence data and environmental variables at each locality to estimate suitable habitat for a species. This is of particular value in conservation and climate change study, as dynamic SDM can predict change in species distributions over time (Miller 2010, Kass et al. 2018, Urbina-Cardona and Blair 2019). In recent years, SDM has experienced a boom in development and use—thousands of SDM software packages and applications have been published in the last decade, and more than 2,000 papers involving SDM have been published between 2023 and 2024 according to Google Scholar results (Merow et al. 2013, Urbina-Cardona and Blair 2019). Some of these studies have involved host–parasite systems, and feature joint models that can incorporate multitrophic interactions to predict parasite distributions or hypothesize distribution shifts in altered climate regimes (Waltari and Perkins 2010, Pickles et al. 2013, Carlson et al. 2017, Veitch et al. 2020, Mathieu-Bégné et al. 2021). We apply these methods to the twisted-wing parasites of the United States, thereby introducing a new tool to the study of Strepsiptera.

Materials and Methods

Specimen Collection

Our specimens were collected in Black Rock Forest (BRF), Cornwall, New York over the course of six trips in July and August of 2022 and 2023. BRF is an old-growth forest protected and maintained by a namesake scientific organization dedicated to its study—as such, this forest provides a uniquely mature and native environment in which to collect ecological data. We sampled six areas: flower patches by the BRF Science Center (41.41408°, −74.011919°), a patch of flowering vegetation in the parking lot (41.413249°, −74.011421°), the meadow of the Upper Reservoir (41.411015°, −74.007048°), Aleck Meadow (41.406405°, −74.014587°), meadows of Jim's Pond (41.387490°, −74.020348°), and brush near the Stone House (41.397177°, −74.021423°; Fig. 1). In addition to the BRF sites, we sampled one privately owned site in the Catskill Mountains, Shandaken, New York in June and July 2023 (42.129425°, −74.377613°). At all sites, we concentrated especially on areas where there were flowering patches of goldenrod (Asteraceae Bercht. and J.Presl) or Queen Anne's lace (Apiaceae Lindl.), since these are commonly visited by several hymenopteran hosts of Strepsiptera. To collect stylopized (parasitized by Strepsiptera) specimens, we prioritized the collection of known hosts of Strepsiptera through several methods.

One method was indiscriminate sweep or aerial netting, a general collection method targeting any insect flying near or resting on the surrounding vegetation. To keep these specimens in optimal condition for genomic work, we deposited them in ethanol or attempted to keep them alive until they could be preserved by flash-freezing at a later date. With this method, postcollection identification and examination of all specimens was necessary to determine if they were stylopized. This was convenient for collection trips during which time was limited. However, collection without ethanol preservation could result in the early mortality of mass-collected specimens and any strepsipterans they house, rendering



Figure 1. A) A map of BRF featuring the collection sites of this study as labeled points; B) the Upper Reservoir Meadow site in BRF with R. J. A. M. and A. E. collecting, taken by Kathy LaPoint for the BRF Redden Grant Program; C) goldenrod patches at the BRF Science Center site, with R. J. A. M. and A. E. collecting, taken by Kathy LaPoint for the BRF Redden Grant Program; D) goldenrod at the Parking Lot site; E) the Aleck Meadow site with a view of the Aleck Meadows Reservoir; F) A. E. setting up the black light trap outside of the BRF Science Center; G) the private Catskills site with R. J. A. M. collecting.

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them largely inadequate for genomic work. Indiscriminate sweeping on tall grass or brush was a practical option for the daytime collection of hemipteran hosts, such as small leaf or planthoppers in Auchenorrhyncha.

Other methods were more discriminatory. We opportunistically sampled only known or potential host insects, then examined them for stylopization individually by collecting them via net or hand into clear polystyrene vials, such as those typically used to rear fruit flies, plugged with foam. The specimen could be immobilized in the vial if necessary by pushing the foam plug up to pin the insect against the bottom of the vial, thereby enabling easy examination of the abdomen. The advantage of this method was that any confirmed stylopized specimens could immediately be moved into separate enclosures and kept alive for later extraction or rearing of Strepsiptera. This method was especially effective for hymenopteran hosts that were foraging at flowers.

The last method we employed was black light trapping, which has been effective for the capture of males in previous work (James and Strong 2018). Our basic black light trap was composed of two 16.4 ft long battery-powered black light LED strips strung along a suspended white sheet near the BRF Science Center (41.414180°, −74.011848°). We kept the lights on and attended the trap at dusk into nightfall (19:00–22:00) and twilight into dawn (4:00–6:00), based on previously documented emergence and activity times of male Strepsiptera (Hughes et al. 2004, James and Strong 2018). If any males were present in the trap, we collected them into vials with an aspirator. We also collected any potential hosts that were attracted to the black light.

To keep any stylopized specimens alive following collection, we placed them into 3.97′L × 3.97′W × 2.57″H plastic rearing enclosures with a cotton ball substrate and insect jelly (water, sugar, fructose, fruit juice, seaweed extract, amino acid glycine, critic acid, and sodium citrate) for hydration and sustenance. If the hosts were stylopized by any male pupae, we examined the enclosure every day for signs of male emergence. Upon male eclosion, we separated the male from the host for imaging, then preserved the specimens in 95% ethanol or by flash-freezing for future molecular work. If the hosts were stylopized by females, we extracted the female by immobilizing the live host with wire and foam (Video S1), then pulling the female out with forceps. These were likewise preserved. In some cases, larvae were actively emerging from the female—these we counted individually, imaged or video recorded under a microscope, then preserved before pulling out the female. For some stylopized specimens, we kept the hosts alive in their rearing enclosures postextraction of the parasite to observe their survival rates and durations.

Species Distribution Modeling

To generate predictive models of host and Strepsiptera ranges, we gathered occurrence data for each host–parasite pair for which collection coordinates were available from the Global Biodiversity Information Facility (GBIF) and combined it with the locality data from our collection efforts. The full host and parasite species lists with corresponding reference data can be found as supplementary data at https://doi.org/10.5061/dryad.n5tb2rc34. Of the 78 strepsipteran species documented in the United States, only a subset had occurrence data. Of these, 51 species included specific coordinate data, and only 15 species had multiple unique coordinates. If hosts of these strepsipterans did not have occurrence data, we excluded these host species from the predictive analyses as well. Since our models require at least five occurrence data points to run, we ran models on genera instead of species to ensure that our predictions were robust. Our list was based on a checklist of strepsipteran species and their hosts in the United States from Kathirithamby 2005, plus a United States checklist (Zabinski and Cook 2023) and world checklist of the genus *Stylops* (Straka et al. 2015). Our GBIF search parameters specified human observation and preserved specimens as the basis of record, data with coordinates, and the United States as an administrative area to restrict the search. When necessary for lessening computational time, we reduced the data by specifying coordinate uncertainty between 0 and 1 m. The resulting occurrence datasets and their GBIF sources for each species can be found as supplementary data on the Dryad Digital Repository, and the raw occurrence data for Strepsiptera in the United States pulled from GBIF can be found as Table S2.

We took a SDM approach with the R package "wallace" and its modeling application Wallace v2.0 (Kass et al. 2018, 2023), using the algorithm MaxEnt (Maximum Entropy; Phillips et al. 2004) and incorporating Bioclim environmental data (Booth et al. 2014) as explanatory variables driving species presence. For each species of Strepsiptera, we incorporated its host presence–absence prediction (10 percentile training presence threshold visualization) as a categorical variable. We standardized our models by specifying their region of study to a shapefile of the 48 contiguous United States, which we generated in QGIS using publicly available data (United States Government 2023). We chose each model based on the average omission rate when applying a 10-percentile training presence threshold to withheld validation data (OR.10p), corrected Akaike information criterion (AICc), and area under the curve of a receiver operating characteristic plot (auc.val.avg; Peterson et al. 2011, Kass et al. 2021). Our R scripts for each model are openly available at https://doi.org/10.5281/zenodo.10573967. We visualized all data resulting from our models in QGIS v3.2.6 (Flenniken et al. 2020) and generated our host–parasite and species richness maps by using the QGIS Raster Calculator addition function.

Results and Discussion

Strepsiptera Species Survey

Of the strepsipteran species possibly present in New York, our collecting efforts confirmed the presence of *Xenos peckii* (Strepsiptera: Xenidae) in *Polistes fuscatus* (Hymenoptera: Vespidae), *Eupathocera auripedis* (Strepsiptera: Xenidae) in *Isodontia mexicana* (Hymenoptera: Sphecidae), *Stylops hartfordensis* (Strepsiptera: Stylopidae) in *Andrena nasonii* (Hymenoptera: Andrenidae), and *Pseudoxenos tigridis* (Strepsiptera: Xenidae) in *Ancistrocerus adiabatus* (Hymenoptera: Vespidae; Table 1). Our full collection

Table 1. Results of our survey for Strepsiptera in upstate New York

Strepsiptera species	Strepsiptera count	Strepsiptera sex	Host species	Host count	Localities
Xenos peckii	9	5 male 2 female 2 male pupae	*Polistes fuscatus*	5	BRF Science Center, BRF Aleck Meadow
Eupathocera auripedis	2	2 female	*Isodontia mexicana*	2	BRF Science Center
Stylops hartfordensis	1	1 female	*Andrena nasonii*	1	Catskill Site
Pseudoxenos tigridis	1	1 female	*Ancistrocerus adiabatus*	1	Catskill Site

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data can be found as supplementary data (Supplementary Table S1). For most potential hosts we did not collect any stylopized specimens. This is especially true for the potential hemipteran hosts—we collected more potential host Hemiptera than Hymenoptera but did not observe any stylopization in any of our hemipterans at all during specimen examination. This is unsurprising, since strepsipterans that infect Hemiptera have pocketed occurrences that are difficult to locate (Kathirithamby, pers. comm.). Although there is one record of *Elenchus koebelei* being collected in New York State, its source is the labeled coordinates of a single type specimen in the Smithsonian National Museum of Natural History that was collected in 1902 (Orrell et al. 2024). There is the possibility that strepsipterans were present within the hemipterans we collected, but that the parasites had not yet developed to the point of protrusion from the abdomen. This is based on life history data and collection methods from James and Strong (2018), which found that mature *Elenchus koebelei* in a Florida site were most abundant in mid-July through October. The publication warns that "early in a season hosts may be infected without external indication," and lack of data on the life history of any hemipteran-infecting Strepsiptera in temperate regions prevents us from being confident in predicting this timing.

Our most-collected genus was *Polistes* (umbrella paper wasps), of which there seemed from visual observation to be a relatively large population in Black Rock Forest. We observed the highest incidence of these paper wasps at the Upper Reservoir location in the grass of the meadow in July 2023, which contrasted previous observations in late August to early September 2022 where the highest observed incidence of the wasps was on goldenrod flowers. The wasps at the Upper Reservoir may have been foraging for prey or nest materials, as none of the wasps in this area observed or collected were on flowers. Additionally, none of those that we caught at this location were stylopized. Given the stylopization rate of the wasps we collected on flowers, especially in Aleck Meadow and near the BRF Science Center, we expected to collect multiple stylopized *Polistes* at the Upper Reservoir. This disparity may be due to the lack of appropriate host flowers at the Upper Reservoir—we did not see any goldenrod or Queen Anne's lace in or around the main meadow area. Additionally, the stylopized *Polistes* may have been exhibiting atypical behavior due to their parasites, i.e., aggregating at flowers instead of working for the colony. This has been observed in *Polistes dominula* Christ, 1791 stylopized by *Xenos vesparum* Rossi, 1793 in Tuscany, Italy (Hughes, Kathirithamby, Turillazzi, et al. 2004). There has also been evidence in other Hymenoptera that stylopization will cause unusual behavior in flowers (Nakase and Kato 2021).

Two of the specimens were stylopized by gravid females with planidia (larvae) that began to emerge less than a day after collection. The planidia of the *Pseudoxenos tigridis* female never fully emerged before the host died, but they were present at the opening of her brood canal and viewable through a microscope (Fig. 2). In contrast, the planidia of the female *Eupathocera auripedis* began emerging while her live host was being immobilized with wire and foam for parasite extraction. We counted 164 triungulin as a cohort before a lull in emergence. More planidia emerged during the extraction, and many more could be seen through the female's cuticle. Roughly half of the female's body was taken up by planidia whose cuticle had already fully sclerotized to a darker color, while the other half was undeveloped planidia whose stemmata were the only darkened part of the body visible through the female cuticle (Video S2). The number of offspring per female documented in Strepsiptera lies in the multiple thousands, with some species of Myrmecolacidae producing up to 750,000 larvae (O'Connor 1959, Borror et al. 1989, Osswald et al. 2010).



Figure 2. Gravid female *Pseudoxenos tigridis* cephalothorax between the sclerites of her host (*Ancistrocerus adiabatus*), with triungulin larvae visible in the opening of the brood canal.

For two of our host specimens whose strepsipterans emerged or were extracted, we documented their survivorship postseparation. These were one *Polistes fuscatus* with one *Xenos peckii* male that eclosed 3 d after collection, and one gravid *Eupathocera auripedis* female that was extracted from its host 1 day after collection. The *P. fuscatus* was collected on 29 July 2023, and the male *X. peckii* eclosed on 1 August 2023. The host *Polistes* expired roughly one week later on 9 August 2023. We collected the *I. mexicana* with female *Eupathocera mexicana* on 28 July 2023, and extracted the gravid *E. auripedis* from its host wasp on 30 July 2023. The host *Isodontia* expired on 31 August 2023, making its postseparation survivorship approximately 1 mo.

Species Distribution Modeling

We present one species range prediction for *Xenos peckii*, and genus range predictions for *Elenchus*, *Halictophagus*, *Paraxenos*, *Pseudoxenos*, *Xenos*, and *Stylops* (Table 2). For each of these, we have included maps of the United States plotting the predicted strepsipteran ranges in yellow within the magenta-colored predicted ranges of their hosts in the United States. We also present a map with all available Strepsiptera occurrence predictions layered as a rough estimation of species richness for this order in the United States (Fig. 8).

The accuracy of SDM, as with all models, can be influenced by a variety of factors. These species distribution models of Strepsiptera, in particular, are shaped by locality data that are almost certainly incomplete and may be biased by factors such as the discernment of the observer or collector, human population density in the areas of observation, and identification accuracy. Dataset size for each species has also heavily influenced each model's results (Merow et al. 2013, Zurell et al. 2020). As such, these predicted distributions should be considered hypotheses as they must be tested and validated with additional sampling data or modeling in the future.

The Strepsiptera species richness distribution model (Fig. 10) shows areas of high richness along the eastern coast, East North Central region, and West South Central region, and low species richness in the Rocky Mountain region. However, plotting the points of GBIF reference data for each identified taxon in the United States indicates that this low species richness could be due to insufficient surveying or observation data in that area (Fig. 11). According to GBIF and museum collection data, specimens of Strepsiptera have been collected in states in the Rocky Mountain region that have the lowest species richness of Strepsiptera predicted by the model (Colorado, Montana, and Wyoming). Various species of

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Table 2. Strepsiptera and host data included in each species distribution model

Strepsiptera	Species included	Strep. unique Coord.	Host taxa	Host unique Coord.	Map	Model scripts
Xenos peckii	*Xenos peckii*	88	*Polistes fuscatus*, *Polistes metricus*	29,599	Figure 3	S8, S9
Elenchus	*E. koebelei*, *Elenchus sp.*	12	*Liburnia sp.*, *Prokelisia sp.*, *Sogatella sp.*	20	Figure 4	S10, S11
Halictophagus	*H. acutus*, *H. americanus*, *H. bidentatus*, *H. callosus*, *H. insularum*, *H. omani*, *H. oncometopiae*, *H. philaroniae*, *H. serratus*, *Halictophagus sp.*	11	*Cicadellidae sp.*	1,030	Figure 5	S12, S13
Eupathocera	*E. auripedis*, *E. erynnidis*, *E. luctuosae*, *E. lugubris*, *E. westwoodii*	21	*Ammophila sp.*, *Isodontia sp.*, *Pachodynerus sp.*, *Podalonia sp.*, *Sphex sp.*,	4,309	Figure 6	S14, S15
Pseudoxenos	*P. arvensidis*, *P. bishoppi*, *P. foraminati* *P. fundati*, *P. hookeri*, *P. jonesi*, *P. louisianae*, *P. neomexicanus*, *P. robertsoni*, *P. tigridis*	8	*Ancistrocerus sp.* *Odynerus sp.* *Monobia sp.*, *Rhynchium sp.*, *Stenodynerus sp.*	7,901	Figure 7	S16, S17
Xenos (excluding *X. peckii*)	*X. hunteri*, *X. pallidus*, *X. rubiginosi*	10	*Polistes sp.*	1,158	Figure 8	S18, S19
Stylops	*S. advarians*, *S. aino*, *S. bipunctatae*, *S. bruneri*, *S. championi*, *S. claytoniae*, *S. cornii*, *S. crawfordi*, *S. cressoni*, *S. erigeniae*, *S. hartfordensis*, *S. hippotes*, *S. medionitans*, *S. multiplicatae*, *S. nudae*, *S. pacificus*, *S. sparsipilosae*, *S. swenki*	20	*Andrena sp.*	21,968	Figure 9	S20, S21

For a full list of host species, see Kathirithamby (2005) and Supplementary Data Files.

Halictophagus, Stylops, Eupathocera, and *Caenocholax* have been recorded in Colorado; Halictophagidae, *Stylops*, and other unidentified Strepsiptera have been recorded in Montana; and *Eurystylops tetonensis* Bohart has been collected in Wyoming (GBIF.org 2023). The models of suitable area generated based on our reference data do not fit the climatic parameters of these areas, but this is almost certainly due to incomplete data in these regions. We did not include any strepsipterans from the GBIF dataset that were unidentified to genus level, which also broadens the gap between our models and true strepsipteran distributions. It is likely that increased survey efforts in the Rocky Mountain region and western United States will reveal that the true species richness and diversity of Strepsiptera in the United States are much higher than what is projected by these SDMs.

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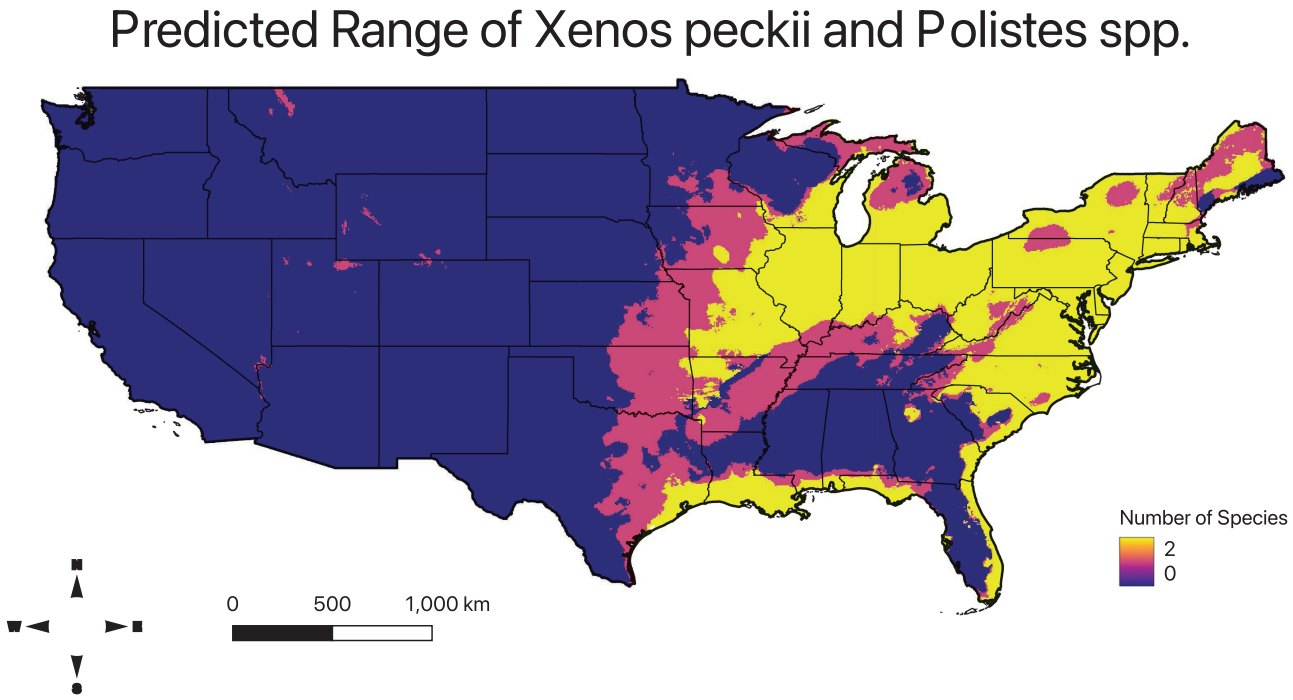

Figure 3. The predicted distribution of Xenos peckii (Xenidae) within the combined range of its hosts Polistes fuscatus and P. metricus, based on GBIF occurrence data.

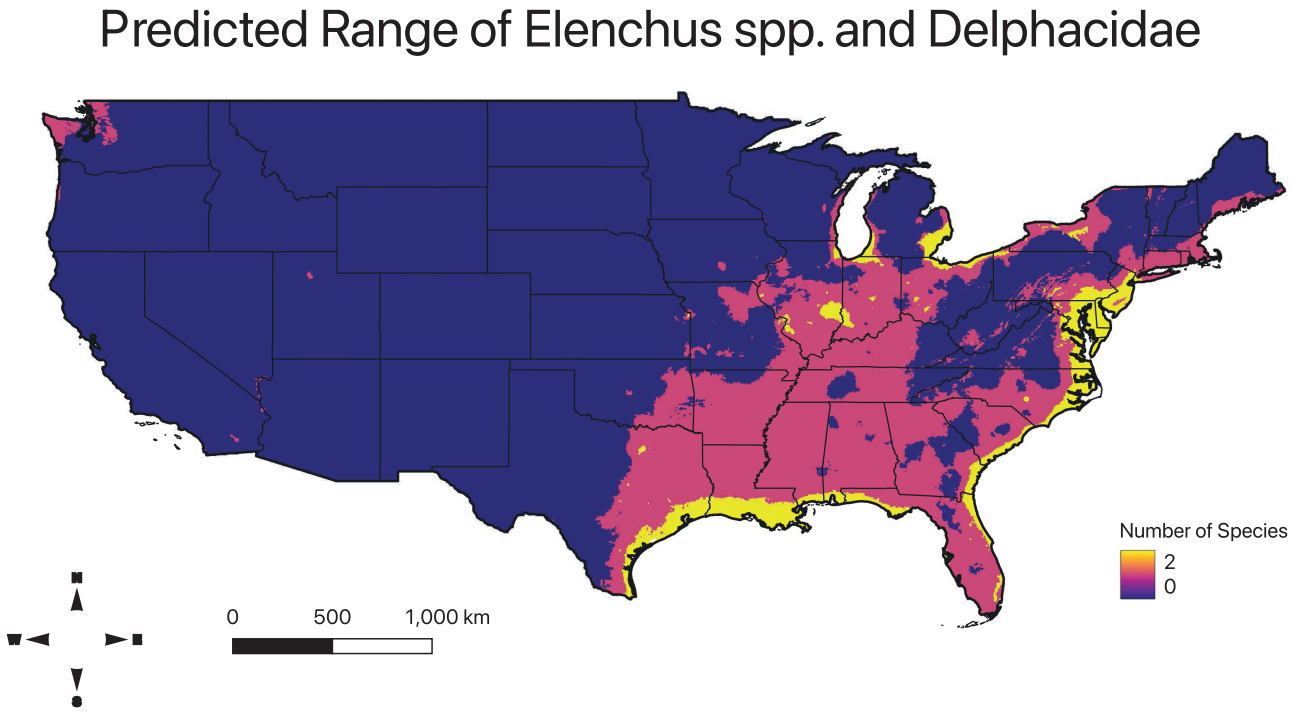

Figure 4. The predicted distribution of *Elenchus* spp. (Elenchidae) within the combined range of its hosts in the hemipteran family Delphacidae, based on GBIF occurrence data.

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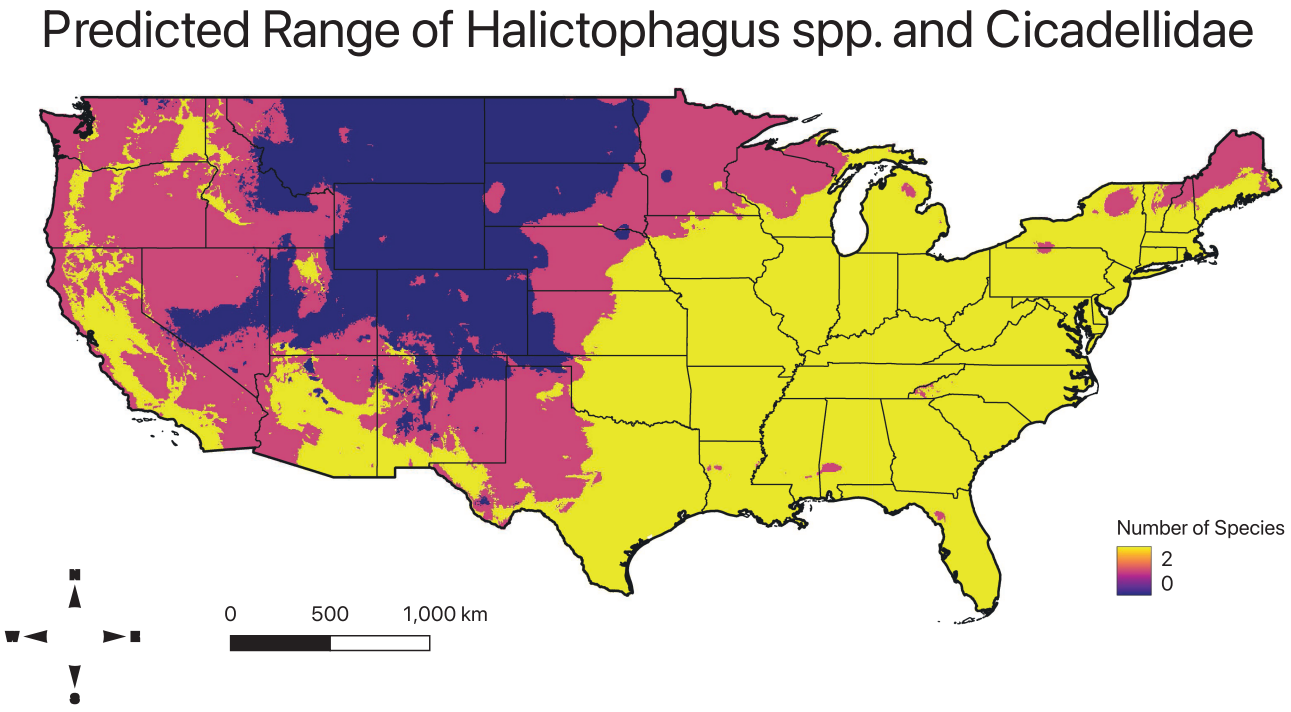

Figure 5. The predicted distribution of *Halictophagus* spp. (Halictophagidae) within the combined range of its hosts in the hemipteran family Cicadellidae, based on GBIF occurrence data.

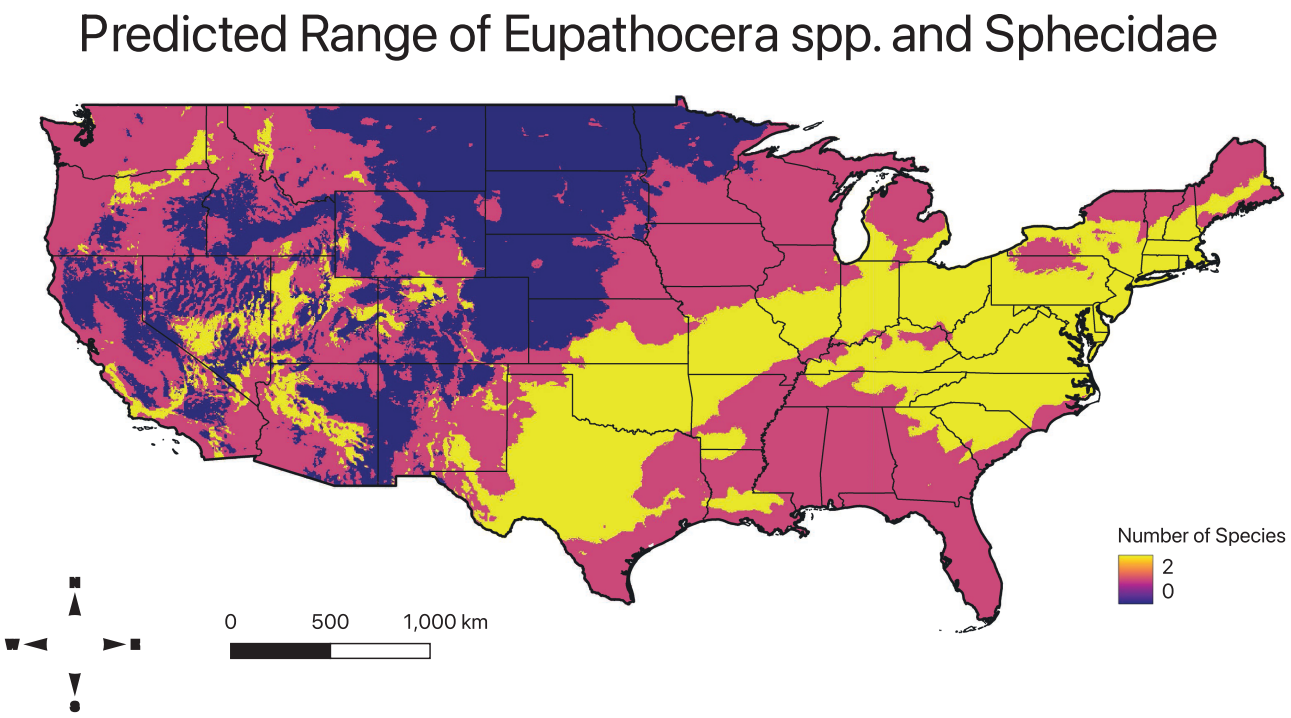

Figure 6. The predicted distribution of *Eupathocera* spp. (Xenidae) within the combined range of its hosts in the hymenopteran family Sphecidae, based on GBIF occurrence data.

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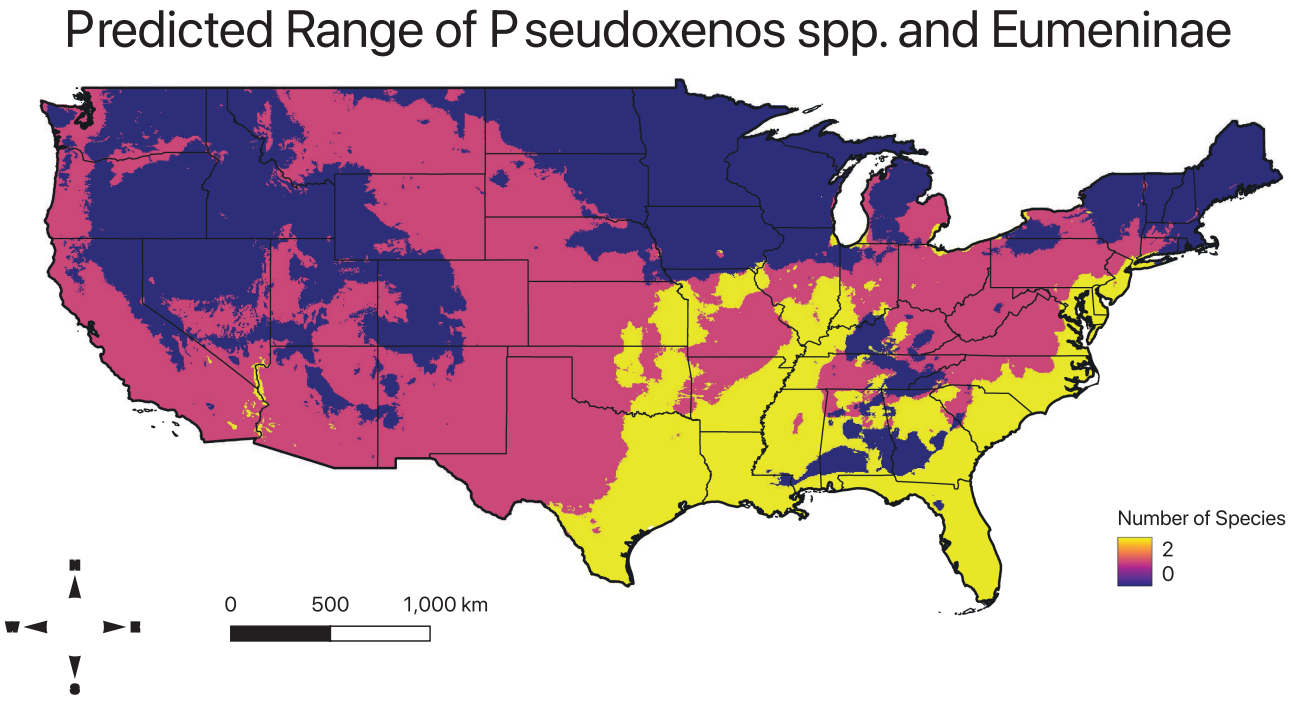

Figure 7. The predicted distribution of *Pseudoxenos* spp. (Xenidae) within the combined range of its hosts in the hymenopteran subfamily Eumeninae, based on GBIF occurrence data.

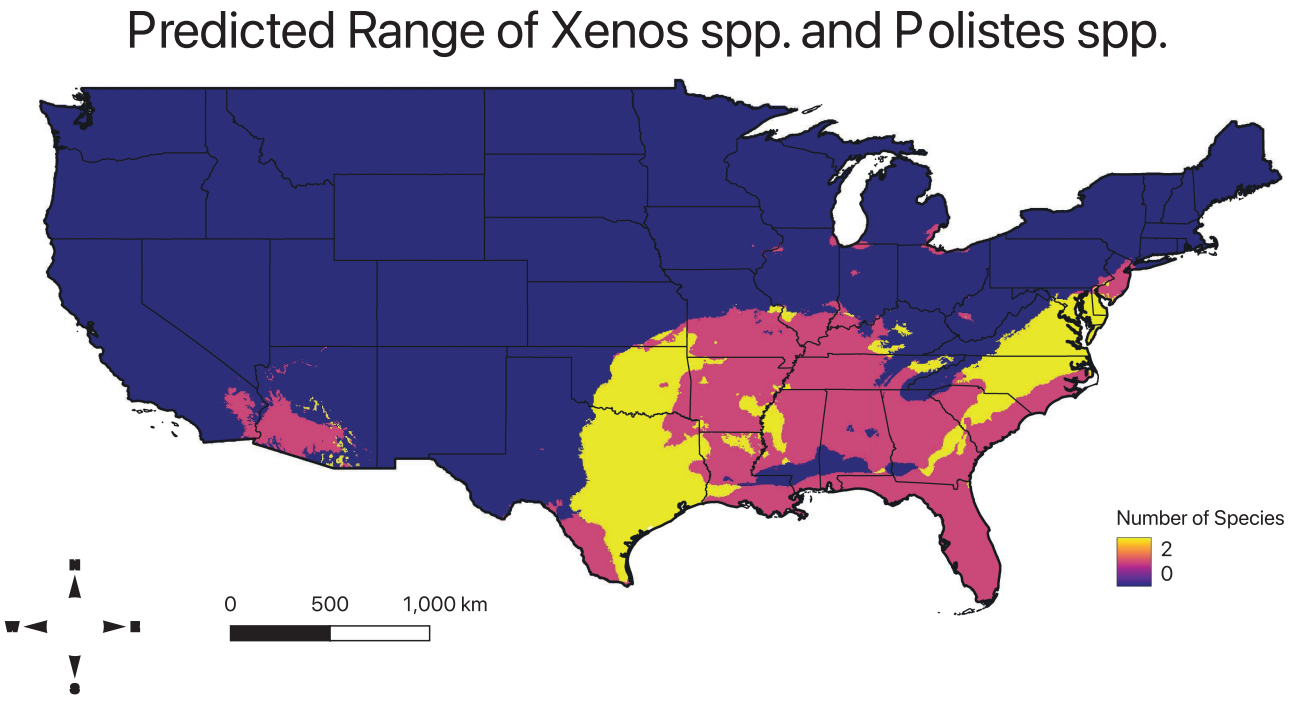

Figure 8. The predicted distribution of *Xenos* spp. (Xenidae) excluding *Xenos peckii*, within the combined range of its hosts in the genus *Polistes*, based on GBIF occurrence data.

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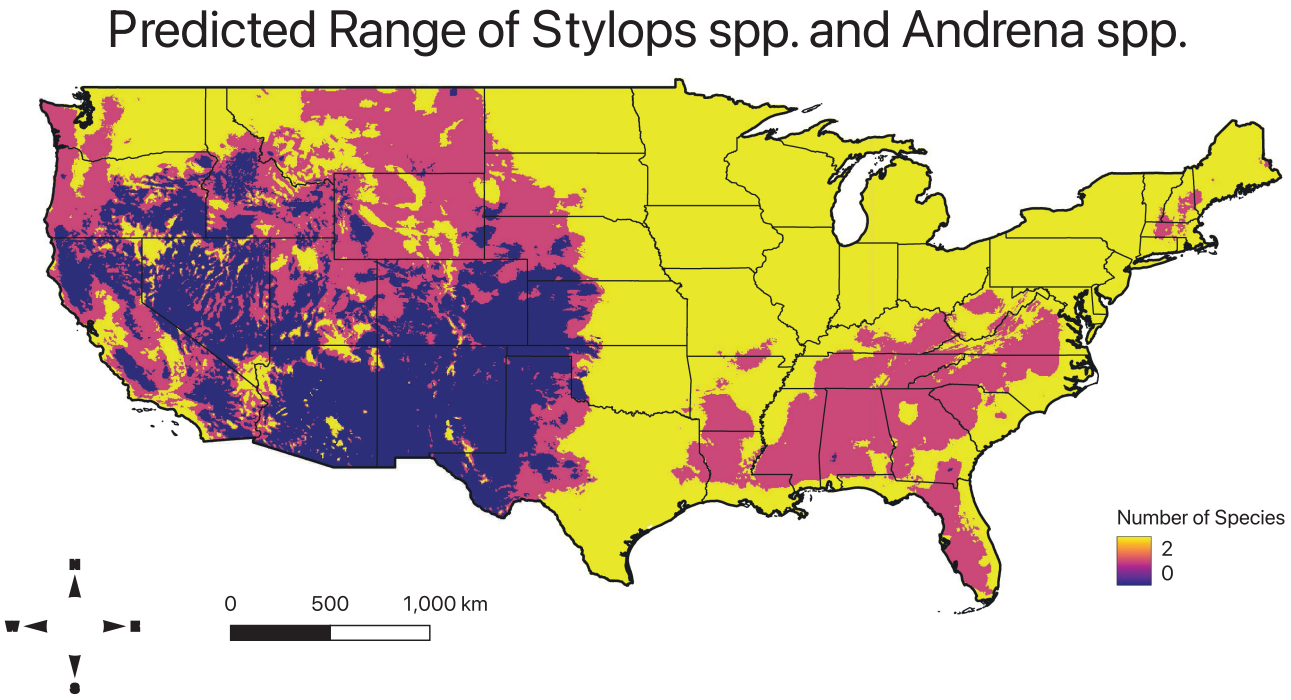

Figure 9. The predicted distribution of *Stylops* spp. (Stylopidae) within the combined range of its hosts in the genus *Andrena* (Hymenoptera: Andrenidae), based on GBIF occurrence data.

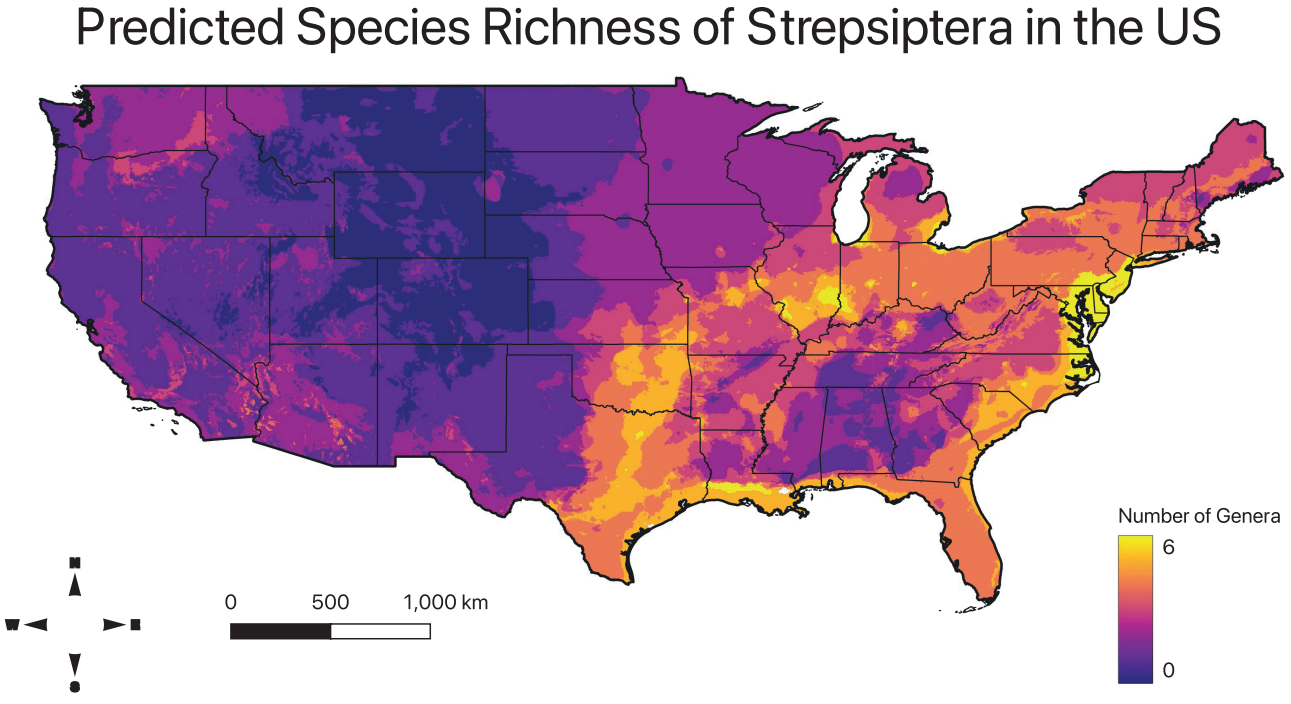

Figure 10. A heat map depicting species richness for Strepsiptera in the US, based on all predicted distributions of strepsipteran genera generated for this study.

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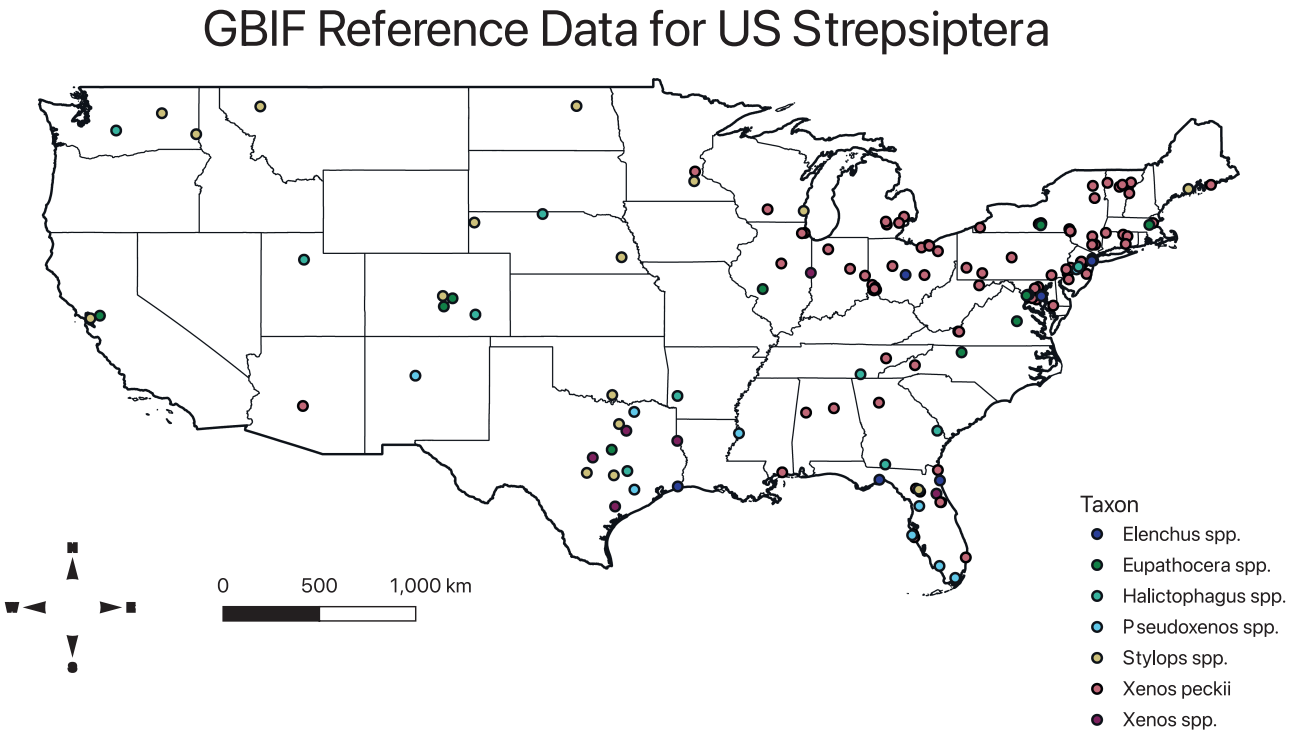

Figure 11. A plot of all GBIF reference data for the strepsipteran taxa included in these distribution models.

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Author Contributions

Rebecca Jean Millena (Conceptualization [Equal], Data curation [Equal], Formal analysis [Equal], Funding acquisition [Equal], Investigation [Equal], Methodology [Equal], Visualization [Equal], Writing—original draft [Equal]), Anna Eichert (Data curation [Equal], Investigation [Equal], Methodology [Equal], Validation [Equal], Visualization [Equal], Writing—review & editing [Equal]), and Jessica Ware (Funding acquisition [Equal], Project administration [Equal], Resources [Equal], Supervision [Equal], Writing—review & editing [Equal])

Data Availability

The data that support the findings of this study are available in the Dryad Digital Repository at https://doi.org/10.5061/dryad.n5tb2rc34.

Supplementary Material

Supplementary material is available at *Environmental Entomology* online.

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