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Biogeography of Endemic Dragonflies of the Ozark-Ouachita Interior Highlands

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Biogeography of Endemic Dragonflies of the Ozark-Ouachita Interior Highlands

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of the requirements for the degree of
Master of Science in Biology

by

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ABSTRACT

A common pattern across many taxonomic groups is that relatively few species are widespread while the majority are restricted in their geographic ranges. Such species distributions are used to inform conservation status, which poses unique challenges for rare or cryptic species. Further, priority status is often designated within geopolitical boundaries, which may include only a portion of a species range. This, coupled with lack of distributional data, has resulted in species being designated as apparently rare throughout some portions of their range, which may not accurately reflect their overall conservation need. The Interior Highlands region of the central United States harbors a rich diversity of flora and fauna, many of which are regional endemics. Among these are four dragonfly species considered Species of Greatest Conservation Need: Ouachita spiketail (*Cordulegaster talaria*), Ozark Emerald (*Somatochlora ozarkensis*), Westfall's snaketail (*Ophiogomphus westfalli*), and Ozark clubtail (*Gomphurus ozarkensis*). I combined species distribution modeling with field surveys to better understand the current biogeography for the two species with ample presence data (*S. ozarkensis* and *G. ozarkensis*). Additionally, models were used to project species' distributions under two climate change scenarios of differing severity. To assess reliability of model predictions, I used two machine learning algorithms commonly used with limited, presence-only data. Current areas of suitability predicted by both algorithms largely overlapped for each species. An analysis of variable contribution showed congruence in important environmental predictors between models. Field validation of these models resulted in new detections for both species showing their utility in guiding future surveys. Future projections across two climate change scenarios showed the importance of maintaining current suitable areas as these will continue to be strongholds for these species under climate change.

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This section could easily be the longest as I’m incredibly grateful for many folks I’ve met during this endeavor. I’d like to thank my advisor, Dr. Adam Siepielski, for giving me this opportunity and offering crucial guidance, inspiration, and mentorship along the way. Thanks to Dr. Jason Bried for spearheading this project and providing expert Odonate knowledge. Our collaborators from the University of Oklahoma, Brenda Smith-Patten and Dr. Michael Patten, were beyond helpful by spending many hours in the field contributing surveys, sharing statistical expertise, and providing guidance throughout the entire project. I am very appreciative of Brenda’s kindness and encouragement in the field. Thanks to my committee members, Dr. Kusum Naithani and Dr. Daniel Magoulick for their expertise and guidance during this project. Additionally, thanks to Dr. Mona Papeş for her input on modeling techniques. I’d also like to thank Dr. Leslie Riley and Dr. Bob Verb who have offered continued confidence in me throughout my undergraduate and graduate careers.

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Boys, W.A., Siepielski, A.M., Smith-Patten, B., Patten, M.A., and Bried, J.T. Predicting the distribution of endemic dragonflies using a combined model approach. In preparation for *Journal of Insect Conservation*.

INTRODUCTION

The geographic range of a species is one of the most fundamental characteristics studied by biogeographers for centuries (Brown et al. 1996). How ranges vary across species and through time is a major topic of biogeographic research as a number of ecological and evolutionary processes shape where a species is found which in turn affects the ecological and evolutionary dynamics for species it interacts with. A persistent pattern seen across species is that relatively few are geographically widespread with the majority being restricted to smaller areas (Brown et al. 1996; Gaston 1996; Gaston and Fuller 2009). Further, widespread species tend to be more abundant than restricted species (Brown 1984; Gaston et al. 1997). These two patterns make up the framework for classifying organisms as rare or common, and thus have important implications in the conservation of biological diversity.

Range size alone is considered a strong predictor of extinction risk, and many species listed in the IUCN Red List were added solely based on range size metrics (Gaston and Fuller 2009). This poses unique challenges for rare or cryptic species, which are hard to detect and thus often lacking in distributional data. Moreover, conservation status is frequently designated within geopolitical boundaries and may not include the entire range of a species. This can result in a species being presumed rare within a given boundary, where conservation and management decisions are often made, when they may in fact be common elsewhere throughout their range (Rodrigues and Gaston 2002). Consequently, assessing conservation status of rare or cryptic species becomes difficult, though these species arguably warrant the most protection efforts.

One method to address this gap is by using Species Distribution Modeling (SDM) to predict the potential distributions of rare or cryptic species. In the literature, two terminologies are frequently used to refer to species-environment associations: SDMs and Environmental

Niche Modeling. These two terms are fundamentally different in what they aim to model, and we refer to SDMs in the present study since we acknowledge many dimensions of the ecological niche are not considered in these efforts (McInerny and Etienne 2013). SDMs are a correlative approach that associate species' occurrences with environmental data to predict areas of potential occurrence. Using SDMs to predict distributions of rare species can be of great benefit in assessing conservation need, but remains challenging due to the data demands of different algorithms (Papeş and Gaubert 2007).

Recent advances in modeling techniques have shown promise in the utility of modeling species with limited presence data, as is common for rare taxa. Two models in particular, MaxEnt and Random Forest, have consistently provided robust estimates for rare or cryptic species (Hernandez et al. 2006; Williams et al. 2009; Mi et al. 2017). MaxEnt is a machine learning algorithm that relies on occurrence data and background environmental predictors to associate known presences to a unique set of environmental conditions, and then predict the probability of presence onto other locations (Phillips et al. 2006, 2017; Elith et al. 2011). Random Forest is also a machine learning method built on the classification and regression tree framework, but fits many classification trees to a dataset and combines the predictions from all trees (Breiman 2001; Cutler et al. 2007). These methods are increasingly being applied to conservation assessments of rare or cryptic species by estimating potential habitat or helping guide field surveys (Guisan et al. 2006, 2013; Papeş and Gaubert 2007).

In the U.S., states are currently required to develop comprehensive wildlife action plans aimed at preventing vulnerable species from declining to levels beyond recovery (Lerner et al. 2006). Of the many taxa listed in the initial wildlife action plans, nearly two thirds of all Odonate species were included as Species of Greatest Conservation Need (SGCN) (Bried and Mazzacano

2010). Distributional data for this group was based on county level records at the time, however a new citizen science database for Odonate occurrences has since been constructed (Donnelly 2004a, b, c; Abbott 2006). Citizens can upload occurrences of odonate species which are then vetted by regional experts. It has been suggested that as these plans continue to be updated, SDMs should be used to better inform distributions of SGCN (Bried and Mazzacano 2010).

There are four dragonfly SGCN listed in the Arkansas state wildlife action plan, all regional endemics of the Interior Highlands that spans across parts of Arkansas, Oklahoma, Kansas and Missouri. The Interior Highlands consists of various physiographic regions, namely an elevated plateau formation dominating the Ozark mountains located in northern Arkansas and southern Missouri and east to west folded ridge terrain forming the Ouachita mountains in southern Arkansas and Oklahoma (Foti and Bukenhofer 1998). This region is rich with endemic species, including insects (Allen 1990; Robison and McAllister 2015). It has been recognized that the conservation concern for the endemic dragonflies of this region is due to limited knowledge and presumably restricted ranges of these species (Patten and Smith-Patten 2013).

The Ozark Clubtail (*Gomphurus ozarkensis*) was initially collected in 1952 and thought to be the Plains Clubtail (*Gomphus fraternus*) or the Cocoa Clubtail (*Gomphus hybridus*) but was later described in 1975 as its own species (Westfall 1975). This species is found in highland lotic habitats and is classified as a spring species because of its short, synchronized emergence period in early May (Susanke 1991) and is currently listed as an S1, or critically imperiled species in the state of Arkansas. The Ozark Emerald (*Somatochlora ozarkensis*) is another endemic species that frequents Interior Highland streams and was first described in 1933 from Latimer Co., Oklahoma (Bird 1933). Its flight season lasts from May-September and it is currently listed as an S1 species. The Westfalls Snaketail was first described from southern Arkansas in the Ouachita

Mountains in 1985, though much of the known occurrences are in southern Missouri (Cook and Daigle 1985; Harp and Trial 2001). It is known to frequent medium sized rocky rivers with shallow rapids, and flies from May-July. Its rank is listed as S1S2, or currently unknown within the state of Arkansas. The most recently described species is the Ouachita Spiketail (*Cordulegaster talaria*), which is only known from small seeps in the Ouachita mountains (Tennessen 2004). It flies early in the season from April-May and is listed as S1in the state.

The limited knowledge of important habitat characteristics and distributions of these species merits further research to better inform conservation status. Two of the four species, *O. westfalli* and *C. talaria*, are especially rare and known only from a handful of sites. Even with recent advances in SDM techniques, a minimum overall species prevalence across the study region needs to be met to produce reliable predictions (Proosdij et al. 2016). This study was implemented to provide extensive field surveys and distribution modeling for the two more prevalent species, *S. ozarkensis* and *G. ozarkensis,* in order to better inform conservation status throughout the Interior Highlands region. To address this, we employed the use of two machine learning SDMs combined with targeted field surveys guided by the predicted distributions. We also projected these distributions into the future under various climate change scenarios to assess where conservation efforts should continue to be focused.

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Predicting the distribution of endemic dragonflies using a combined model approach

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ABSTRACT

Aquatic macroinvertebrates are declining at an alarming rate, particularly regional endemics. Knowledge of species distributions is a critical component for assessing conservation need but is often lacking for cryptic or rare taxa, especially invertebrates. One approach to better inform this gap is by using species distribution modeling (SDM) to predict suitable habitat and guide field surveys. This remains challenging, however, due to high input data demands of different algorithms. Here we employ two machine learning algorithms known to provide robust predictions for rare species by modeling the current and future distributions of two endemic dragonflies of the Ozark-Ouachita Interior Highlands region that are considered Species of Greatest Conservation Need. Current suitable areas predicted by both algorithms largely overlapped for each species, but different environmental variables were most important for predicting their distributions. Field validation of these models resulted in new detections for both species showing their utility in guiding subsequent field surveys. Future projections largely showed the importance of maintaining current suitable areas as these are predicted to be strongholds for these species under two climate change scenarios. Our results suggest that SDMs are a useful tool for better informing the distributions of rare species.

Keywords: Anisoptera, endemicity, species distribution modeling, aquatic insects, Interior Highlands

INTRODUCTION

Invertebrates are disproportionately understudied, though they make up the majority of animal diversity (Stork 1988). Climate change is predicted to have large effects on this group; indeed insect biomass has already declined in various regions throughout the world having cascading impacts throughout multiple trophic levels (Thomas 2004; Hallmann et al. 2017; Lister and Garcia 2018). Declines are even greater for aquatic insect taxa, with orders Ephemeroptera, Plecoptera, Trichoptera, and Odonata already having lost a large proportion of species (Sánchez-Bayo and Wyckhuys 2019). Of these species, habitat specialists or regional endemics may be the most vulnerable as predictions frequently show large reductions in suitable habitat under various climate change scenarios (Domisch et al. 2013a; Markovic et al. 2014; Li et al. 2014).

Although insects are increasingly being targeted for conservation, general knowledge of distributions and habitat requirements are often scarce due to lack of study and issues in detectability. Odonates are of particular concern as they are important predators in aquatic and terrestrial habitats and serve as useful indicators of environmental health (Corbett 1999). A global assessment of extinction risk for odonates found 10% of this group is threatened with extinction, though there are considerable data gaps for 35% of odonate species (Clausnitzer et al. 2009). Further, species found in lotic habitats may be more at risk than lentic species (Korkeamäki and Suhonen 2002; Clausnitzer et al. 2009; Simaika and Samways 2015; Collins and McIntyre 2017). A species range size is considered a strong predictor of extinction risk, thus it is important to understand the factors that shape a species current distribution, as well as how its distribution will shift in response to climate change (Gaston and Fuller 2009).

Under current legislation, each state within the U.S. has developed a comprehensive wildlife action plan aimed at preventing wildlife from declining to levels beyond recovery (Lerner et al. 2006). Nearly two thirds of Odonate species were included as Species of Greatest Conservation Need (SGCN) in the original wildlife action plans of each state. However, at the time, distribution data for this group was based on the North American Odonata Dot Map Project which was restricted to county level records only (Donnelly 2004a, b, c). Therefore, the scale of presence localities did not allow for associations with fine-scale environmental data shaping their habitat requirements. Furthermore, conservation status was assigned within state boundaries, though many species ranges span multiple states. Assigning status within geopolitical boundaries can result in a species being presumed rare when they may in fact be common elsewhere throughout their range (Rodrigues and Gaston 2002). As these plans continue to be updated, one method to better inform conservation status is by using species distribution modeling (SDM) to predict potential areas of occurrence (Bried and Mazzacano 2010). SDMs have been extensively used for vertebrate taxa, but are increasingly being applied to invertebrates including Odonates (Bried and Samways 2015; Collins and McIntyre 2015).

Using SDMs to predict distributions of rare or cryptic species can be of great benefit, but remains challenging due to the data demands of different algorithms (Papeş and Gaubert 2007). Despite these limitations, two models in particular, maximum entropy (MaxEnt) and Random Forest, have consistently provided robust estimates for species with limited presence data (Hernandez et al. 2006; Williams et al. 2009; Mi et al. 2017). MaxEnt models use species presence data and background environmental variables to associate known presences to a unique set of environmental conditions, and then predict the probability of presence onto other locations (Phillips et al. 2006; Elith et al. 2011). Random Forest models are built on the Classification and

Regression Tree (CART) framework, but fit many classification trees to a dataset and combine the predictions from all trees (Breiman 2001; Cutler et al. 2007). Both of these models have been used to estimate odonate distributions, though MaxEnt has been implemented more frequently (Collins and McIntyre 2015).

The use of SDMs in conservation assessments has become more prevalent and can help inform data gaps by estimating suitable habitat, helping guide field surveys for rare or cryptic species, and predicting changes in distributions through climate change (Guisan et al. 2006, 2013; Papeş and Gaubert 2007). Four species of dragonflies are listed as Species of Greatest Conservation Need (SGCN) in the state of Arkansas: Ouachita Spiketail (*Cordulegaster talaria*), Westfalls Snaketail (*Ophiogomphus westfalli*), Ozark Emerald (*Somatochlora ozarkensis*) and the Ozark Clubtail (*Gomphurus ozarkensis*). These species are endemic to the Interior Highlands region spanning parts of Arkansas, Oklahoma, Missouri, and Kansas. They are all understudied and of conservation concern due to limited knowledge of their distributions and habitat requirements (Patten and Smith-Patten 2013). Two of these species, the Ouachita Spiketail and the Westfalls Snaketail, are especially rare and known from only a few localities. Even with recent advances in modeling techniques, a minimum overall species prevalence across the study region needs to be met to produce reliable predictions (Proosdij et al. 2016).

This study was implemented to provide extensive field surveys and distribution modeling for the two more prevalent species, the Ozark Emerald (*Somatochlora ozarkensis*) and the Ozark Clubtail (*Gomphurus ozarkensis*), to better inform conservation status throughout the Interior Highlands region. Currently, both species are ranked as S1, or critically imperiled in the state of Arkansas (Fowler and Anderson 2015). To address this, we employed the use of two machine learning SDMs shown to perform well with limited presence data and combined their predictions to help guide targeted field surveys. We also projected these distributions into the future under various climate change scenarios to assess where conservation efforts should be focused.

METHODS

Current distribution modeling

Presence data

Presence data were obtained from the online database OdonataCentral (Abbott 2006) and complemented with unpublished data from collaborators at the University of Oklahoma (Smith-Patten). OdonataCentral is a citizen science database and allows users to upload occurrences of adult odonates throughout the Western hemisphere which are then vetted by regional experts. To date, there are over 175,000 records of odonates submitted to the database. In addition, records from museum specimens and previous literature are included in the database, however we removed records with only county centroid coordinates unless specific location notes were included. We used these notes to georeference records in Google Earth (Google Inc. 2019) to obtain more precise geographic coordinates. In total, we identified 55 presences for the Ozark Clubtail and 50 presences for the Ozark Emerald (Figure 1). Spatial autocorrelation of presences used in distribution modeling can result in inflated measures of prediction accuracy (Veloz 2009; Kramer-Schadt et al. 2013). However, previous studies have shown that when modeling rare species, each presence location matters and can largely influence prediction outcomes (Almeida et al. 2010; Silva et al. 2013, 2016). Therefore, we did not explicitly control for spatial autocorrelation among presence localities. However, we did remove Ozark Emerald localities that fell outside of the Ozark-Ouachita Interior Highlands region (Figure 1) for ease of generating pseudo-absences from the same area for both species.

Environmental predictors

For current distribution models at the catchment level, landscape metrics summarized for individual stream segments were downloaded from the EPA’s national StreamCat database (Hill et al. 2016). This database includes over 517 habitat metrics, including both natural and anthropogenic landscape data, summarized for 2.6 million streams within the conterminous U.S. (Hill et al. 2016). StreamCat environmental variables were chosen based on knowledge of odonate biology and relevant literature (Domisch et al. 2011, 2013b; Hassall 2012; Kuemmerlen et al. 2014; Collins and McIntyre 2015, 2017). To reduce overfitting, StreamCat environmental predictors were removed if highly correlated (r>0.7) (Dormann et al. 2013). These data are based on the National Hydrography Dataset Plus V2 geospatial framework and allow for modeling of individual stream segments, which were clipped to the Ozark-Ouachita Interior Highlands region based on Leasure et al. (2016). Presence locations were uploaded into QGIS (QGIS Development Team 2018) and snapped to the nearest stream segment by using the Snap Geometries to Layer tool. Each point location was inspected to ensure proper stream associations and reassigned when necessary.

Modeling techniques

Two machine learning methods, MaxEnt and Random Forest, were used to model the distributions of the Ozark Clubtail and the Ozark Emerald. MaxEnt models were executed in the open source software interface (Phillips et al. 2017). Model parameters were kept at default settings, except models were run with a 10-fold cross validation since we lacked enough presence data to create a testing set. Predictions were made onto the background StreamCat data across the entire region in the format of logistic probabilities.

Random Forest models were executed using the Caret (Kuhn 2018) package in the statistical program R (R Core Team 2018). Random Forest models require absence data, which were not available. Therefore random, pseudo-absences were generated using the *spsample* function in the R package *sp* (Pebesma & Bivand 2005), constrained by the Ozark-Ouachita Interior Highlands region boundary. An equal number of pseudo-absences to presences were generated for both modeled species (Barbet-Massin et al. 2012). A total of 500 trees were created and models were run with a 10-fold cross-validation. Binary predictions (present/absent) were projected onto background StreamCat data. An analysis of variable contribution was performed to assess which environmental predictors had the most influence on distribution predictions.

To combine model outputs, MaxEnt predictions were transformed into binary format by applying the minimum training presence threshold. Streams predicted as suitable by both models were then extracted. Since MaxEnt predicted a larger area for both species, we ultimately clipped the MaxEnt predictions to the Random Forest predictions, which allowed us to convert back into the logistic format. The resulting maps were then used to guide field surveys for both species.

To assess SDM accuracy, we used the area under the curve (AUC) which is a metric that represents the probability that a random presence or absence are correctly assigned by the model (Phillips et al. 2006). An AUC score of 0.5 means the model is no better than random chance in correctly assigning presence or absence of species. We also used the out-of-sample (OOS) error rate to assess random forest models, which is a measure of prediction error generated by the cross-validation technique.

Field Surveys

Baseline surveys to obtain more presence localities and check on existing populations were conducted during summer 2017. Following these, combined stream predictions from MaxEnt and Random Forest models were used to guide field surveys during summer 2018. Due to variability in stream accessibility, a range of sites were chosen across the spectrum of probabilities of presence (0-1). Additionally, some opportunistic sites not predicted by both models were sampled. Each species was targeted during its peak flight season, May – July for the Ozark Clubtail and June-September for the Ozark Emerald. Surveys were conducted by two observers; however, these observations were not independent and combined upon completion of each survey. Upon arrival at a site, a safe access location to the stream was identified and observers walked 50m upstream from any road or bridge crossing. A handheld Garmin GPSMAP® 64 device was used to mark the stream access point.

Adult surveys

Adult surveys were only conducted in 15.5ºC and above conditions. No surveys were conducted in heavy or steady rainfall, however, the presence of light or intermittent rain was no deterrent and noted if present. Surveys were conducted over a 50m transect that was measured upstream from the access point. Start time of the survey was recorded and both observers walked the transect, one on each bank when accessible. Observers searched for odonates in flight and perching on nearby vegetation or substrate. All adults were captured with aerial nets and identified in hand to species when possible. Observations of sex, mating pairs, tenerals, general behavior, and oviposition behavior were recorded, as they can help identify breeding sites. Specimens not able to be identified in the field were collected and taken to the laboratory for further identification. A voucher specimen of each species from every site was collected and deposited at the University of Arkansas. However, since the focal species are considered SGCN, photos of these individuals were taken in the field and served as vouchers in some instances. Focused adult surveys were conducted over an hour time span; however, some adults were detected during subsequent larval and habitat surveys. Additionally, observers were opportunistic while driving to and from each site and stopped to capture any suspected focal species as the Ozark Emerald is known to fly in feeding swarms in open areas at dawn and dusk.

Exuviae surveys

Exuviae, or the exoskeleton of the final instar left behind after adults emerge, were searched for during the adult survey time allotment. However, observers also opportunistically collected exuviae found later during larval surveys. All exposed substrate, including rocks, emergent vegetation, and sticks were searched for the presence of exuviae. If found, all Anisoptera exuviae were collected for identification in the laboratory and the substrate they were attached to was noted.

Larval surveys

In-stream habitat and larval sampling technique within the 50m transect were characterized according to Barbour et al. 2009. Suspected habitat for the focal species was targeted for sampling. To target the Ozark Emerald larvae, large instream rocks were overturned, and the exposed benthos was sampled, as well as root banks along the transect. Mud, gravel, and detritus such as leaf litter were sampled for the Ozark Clubtail. An aquatic D-frame dip net with mesh size of 0.5µm was used to collect samples. All odonates were sorted out in the field and preserved in 70% ethanol for further identification in the lab.

Future distribution modeling

Environmental predictors

StreamCat environmental predictors are not available for future time periods, thus current and future (2070) climatic conditions were characterized based on the bioclimatic dataset including 19 temperature and precipitation variables available through the WorldClim database (Hijmans et al. 2005). Future climatic environments were generated from global climate models that are based on different representative concentration pathways (RCPs). These pathways represent various levels of future greenhouse gas emissions, and thus differing levels of severity of climate warming. RCP 8.5 accounts for continuous rising in carbon dioxide emissions into the twenty-first century, while RCP 6.0 accounts for a peak in emissions around 2080 followed by slight decline. We characterized future environments within the study region by including bioclim variables representing these two emission scenarios generated by the Community Climate System Model 4. Current and future bioclim variables were downloaded at a spatial resolution of 2.5 minutes, and variables were removed if highly correlated ($r>0.7$) (Dormann et al. 2013).

MaxEnt and Random Forest algorithms were used to model the future distributions of the Ozark Clubtail and the Ozark Emerald for both RCP scenarios. New occurrence data collected following field surveys were incorporated into these models resulting in 63 presences for the Ozark Clubtail and 58 for the Ozark Emerald. MaxEnt models were executed as above; however when using raster predictors, MaxEnt removes duplicate presence records as to retain only one location per pixel. The bioclim predictors used had a spatial resolution of ~5km, and the numbers of presences ultimately used for MaxEnt training were 53 for the Ozark Clubtail and 47 for the

Ozark Emerald. To obtain the average prediction from the cross-validation models, logistic probabilities were averaged across each fold for every projected scenario.

Random Forest models were executed as above, however; to remain consistent with MaxEnt models, presence data were thinned based on a distance of 5km (R package *spThin*; Aiello-Lammens et al. 2015). An equal number of random pseudo-absence points were generated (R package *sp*; Pebesma et al. 2018) within the Ozark-Ouachita Interior Highlands region.

To combine model outputs, we used the Raster Calculator tool in QGIS (QGIS development team 2018) to multiply binary prediction rasters produced by Random Forest models with the logistic raster predictions generated by MaxEnt. The resulting maps show areas predicted as suitable by both models.

RESULTS

Baseline field survey results

A total of 36 sites were surveyed throughout Arkansas and Oklahoma during summer 2017, including a mix of known localities and opportunistic sites. We detected the Ozark Clubtail twice, once at a known locality and once at an opportunistic site. The Ozark Emerald was detected once at a known locality, however we captured a female with eggs and thus added evidence of a new breeding location.

Current distribution models

MaxEnt models fit well with area under the curve (AUC) scores of 0.876 for the Ozark Clubtail, and 0.868 for the Ozark Emerald (Table 1). The Random Forest model for the Ozark Clubtail had a good model fit with AUC of 0.84 and out-of-bag error rate (OOB) of 14.68%. For the Ozark Emerald, Random Forest had a fair model fit of 0.73 and OOB of 29% (Table 1). An analysis of variable contribution showed similarity between species (Table 2). Variable importance for the Random Forest models showed congruence with MaxEnt variable contributions for the Ozark Emerald, but slightly different variables for the Ozark Clubtail (Table 2). Percent coniferous forest, human population density and stream base flow were the top three important variables for the Ozark Emerald for both models. This largely coincides with what know from its observed distribution, which are typically streams found in steep, mixed-forest habitats. These three variables were also the top three important predictors for the MaxEnt model of the Ozark Clubtail, however stream base flow, mean annual precipitation, and mean annual temperature were the top three variables for the Random Forest model. From what we know about the observed distribution of the Ozark Clubtail, it prefers medium sized streams with open canopy and cobble riffles.

Overall, MaxEnt predicted more streams as suitable compared to Random Forest (Fig. 2A, 2D). Random Forest models largely overlapped with the highest probability streams from the MaxEnt models (Fig. 2B, 2E) yet had lower AUC scores. After combining model predictions, the Ozark Emerald is predicted to occur mostly in the Ozark mountains in Missouri and Arkansas, as well as the Ouachita mountains in southern Arkansas and Oklahoma. The Ozark Clubtail is predicted to occur mainly in the Ouachita mountains of Arkansas and Oklahoma (Fig. 2C, 2F).

Field survey results from model predictions

Combined model predictions were used to guide field surveys during summer 2018. A total of 77 sites were surveyed throughout Arkansas, Oklahoma, and Missouri. We detected 8 new presence locations for the Ozark Emerald, including one new breeding site. Seven of these detections were predicted by both models and occurred across a wide range of probabilities (0.2-1.0). One site was only predicted by MaxEnt. We also detected 8 new presence locations for the Ozark Clubtail. Two of these were predicted by both models, while the remaining were located at low probability (0 – 0.2) streams predicted by MaxEnt. Overall, these predictions increased detections for both species compared to previous survey years.

Future distribution models

MaxEnt models fit well with AUC scores of 0.979 for the Ozark Clubtail, and 0.982 for the Ozark Emerald (Table 1). The Random Forest model for the Ozark Clubtail had a fair model fit with AUC of 0.766 and OOB of 25%. For the Ozark Emerald, Random Forest had a good model fit with AUC of 0.80 and OOB of 21.25% (Table 1). An analysis of variable contribution showed similarity in important habitat characteristics between species (Table 3). The top three important variables for both species were precipitation of the coldest quarter, precipitation of the wettest quarter, and mean temperature of the driest quarter. The only exception to this was for the Random Forest model of the Ozark Emerald where precipitation of the warmest quarter was more important than precipitation of the driest quarter (Table 3).

Overall, MaxEnt predicted more area as suitable under all climate change scenarios compared to Random Forest (Fig. 3, Fig. 4). MaxEnt predictions remained similar across all scenarios for both species however, Random Forest models predicted smaller suitable areas under the RCP 6.0 scenario (Fig. 3, Fig. 4). Predicted suitability then increased slightly under the RCP 8.5 scenario (Fig. 3, Fig. 4). Both MaxEnt and Random Forest models show distributions are predicted to shift slightly west further into Oklahoma and north further into the Ozark mountains for both species. Random Forest predictions, although smaller than MaxEnt predictions, showed large overlap with the highest probability areas predicted by MaxEnt models as shown by combining model predictions (Fig. 3, Fig. 4).

DISCUSSION

Conservation efforts are increasingly being applied to insects, but assigning status is challenging due to limited distribution data. SDMs are becoming more common for modeling insects, such as odonates, however fewer than 25% of odonate species have been modeled (Collins and McIntyre 2015). The aquatic to terrestrial life cycle of these insects allows for modeling approaches that focus on water bodies, terrestrial landscapes, or both. Small scale catchment level modeling can provide more accurate predictions for stream species than coarse scale landscape models, and may also better inform management practices as local catchments are often the unit for conservation efforts (Kuemmerlen et al. 2014). We have demonstrated the value of catchment level predictions for increasing detections of cryptic dragonflies that can aid in guiding conservation efforts.

There is no shortage of modeling techniques available, including ensemble approaches that combine predictions from multiple models (Thuiller et al. 2009). However, machine learning methods have been shown to generally outperform other models such as those built on regression techniques (Elith* et al. 2006). We therefore chose to combine predictions from two machine learning algorithms that have consistently provided robust predictions for species with limited presence only data as in this study. Our results suggest there is some utility in this approach as we increased detections for both modeled species compared to baseline field surveys the previous year. Any additional detections for rare or cryptic taxa, such as our focal species, are especially valuable to the understanding of their distributions and habitat requirements.

Climate change is predicted to alter the distributions of freshwater taxa, and odonates in Britain have largely shifted northward during a period of climate warming (Hickling et al. 2005). Endemic species and habitat specialists are expected to be particularly vulnerable to these changes (Domisch et al. 2013a). Indeed, Odonate assemblages in the Western U.S. and in the UK have homogenized as a result of widespread expansion of habitat generalists (Ball-Damerow et al. 2014; Powney et al. 2015). This has led to a pervasive loss of spatial variation in odonate assemblage composition. However, not all endemic species seem to be more affected. A damselfly endemic to the Pampa region in South America was projected to persist, though undergo range contractions, through multiple climate change scenarios (Pires et al. 2018). Future projections of our focal taxa also suggest persistence, though slight range contractions and biogeographic shifts to the west and north, in light of global climate change. This suggests that making generalizations about the effects of climate change based on endemism may not be particularly useful, and instead each study should assess these impacts in their own context.

Further, lentic odonate species were found to have a greater affinity to shift distributions and track climate changes compared to lotic species (Hof Christian et al. 2012). While most odonate species that declined in abundance in a historical assessment in California were habitat specialists, certain types such as lotic specialists did not change significantly (Ball-Damerow et al. 2014). This is in congruence with a study in Japan where lotic breeding dragonflies in mountain streams were less prone to extinction compared to lentic species (Kadoya et al. 2009). Determining whether lentic or lotic species are more at risk of declining is largely context dependent, as our study suggests potential resilience of endemic, lotic breeding dragonflies in a changing climate.

Using SDMs to better inform conservation and management efforts can be especially helpful. In this study, future projections suggest conservation efforts should continue to be implemented within the study region given the limited predicted shifts in these species' distributions. By contrast, other studies have shown potential range shifts of odonates in response to climate change, particularly lentic species (Hof Christian et al. 2012). Regardless of whether projections show shifts in a species distribution or not, we caution against these efforts being used to forego current or future conservation plans. That is, if a species is predicted to show a shift in its distribution outside of its current management jurisdiction, that agency should not abandon current efforts. Instead, we suggest these techniques can be used to implement cross-boundary collaborations between adjacent political units as a means to create more accurate conservation assessments (Rodrigues and Gaston 2002). Such cross-boundary, joint management collaborations will likely become increasingly common as species distributions shift in response to global change. While this may pose challenges for allocating conservation and management responsibility efforts, we suspect they will ultimately become necessary.

Limitations

Two terminologies are often used in the literature when modeling species-environment relationships: SDM and Environmental Niche Modeling. These two terms are fundamentally different in what they aim to model. SDMs are a correlative approach that associate species presences to environmental data and one limitation to this method is that biotic interactions are not considered, thus many aspects that constitute a species niche are not addressed (Elith and Leathwick 2009). As such, we refer to SDMs in the present study since we acknowledge the underlying processes resulting in observed occurrence patterns are not modeled (McInerny and Etienne 2013). That is, the results are entirely phenomenological and not mechanistic. The predicted distributions of these species were modeled using climatic variables, and though these are appropriate given the life history traits of odonates (Corbett 1999), they do not account for dispersal ability or species interactions which are also important in determining species distributions. The presence of a species in an area does not necessarily mean that area is suitable. Species distributions likely include sink populations where the presence of a species may be a result of ongoing dispersal and not of long-term positive population growth rate resulting from a suitable environment (Pulliam 1988).

Further limitations of this approach include using adult records as presences, since odonates have a complex life cycle and thus different habitat requirements as nymphs and adults. Using only adult records as input for distribution models can produce misleading predictions of habitat suitability (Patten et al. 2015). However, our focal taxa were already data deficient and lacked information about nymph, exuviae or breeding behavior at known presence localities. Thus, we acknowledge that using only adult records as input for these models may not accurately represent the distribution or habitat suitability for nymphs, which is often the critical life stage influencing population regulation (McPeek and Peckarsky 1998). Nonetheless, these models resulted in higher detections of adults, including one new breeding location for the Ozark Emerald, and are therefore useful as a means to guide future field surveys that may target the aquatic stage or capture evidence of breeding.

CONCLUSIONS

This study provided extensive field surveys and distribution modeling for two understudied dragonflies of conservation concern throughout the Interior Highlands region. We demonstrated the utility of SDMs in guiding field surveys and increasing detections of cryptic or rare species. These surveys can lead to better informed conservation assessments for species of concern. Further, these models can be projected into the future and serve as a resource to develop conservation plans in light of different climate change scenarios. Projections of our focal taxa suggest that not all regional endemics are particularly vulnerable to changes in future climate as there still remain areas of high predicted suitability. Given the current method of assessing conservation need at the state level, we recommend using SDM techniques to facilitate cross-boundary collaborations since species ranges often do not coincide with geopolitical boundaries. Finally, we caution against using these methods to forego conservation planning as there are limitations to these models and other factors such as dispersal and biotic interactions will certainly affect species distributions in the future.

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TABLES AND FIGURES

Table 1. Accuracy metrics for current and future distribution models.

	Species	Presences	MaxEnt AUC	Random Forest AUC	OOS Error Rate
Current Models	Ozark Emerald	50	0.868	0.730	29
	Ozark Clubtail	55	0.876	0.840	14.680
Future Models					
	Ozark Emerald	58	0.982	0.800	21.250
	Ozark Clubtail	63	0.979	0.766	25

Table 2. Variable importance or percent contribution for current distribution models at the catchment scale.

Species	Variable	%Contribution or Importance
Ozark Emerald		
MaxEnt	% Coniferous forest	27.700
	Stream base flow	23.600
	Population density	13
Random Forest		
	Stream base flow	100
	Population density	95.330
	% Coniferous forest	90.360
Ozark Clubtail		
MaxEnt	Population density	32.900
	Stream base flow	21.900
	% Coniferous forest	14.300
Random Forest	Stream base flow	100
	Mean Annual Precipitation	64.060
	Mean Annual Temperature	62.650

Table 3. Variable importance or percent contribution for future distribution models.

Species	Variable	%Contribution or Importance
Ozark Emerald		
MaxEnt	Precip. of coldest quarter	55.300
	Precip. of wettest quarter	22.700
	Mean temp. of driest quarter	11.400
Random Forest		
	Precip. of wettest quarter	100
	Mean temp. of driest quarter	37.990
	Precip. of warmest quarter	18.400
Ozark Clubtail		
MaxEnt	Precip. of coldest quarter	44.500
	Mean temp. of driest quarter	28.400
	Precip. of wettest quarter	19.800
Random Forest		
	Precip. of wettest quarter	100
	Mean temp. of driest quarter	40.715
	Precip. of coldest quarter	20.321

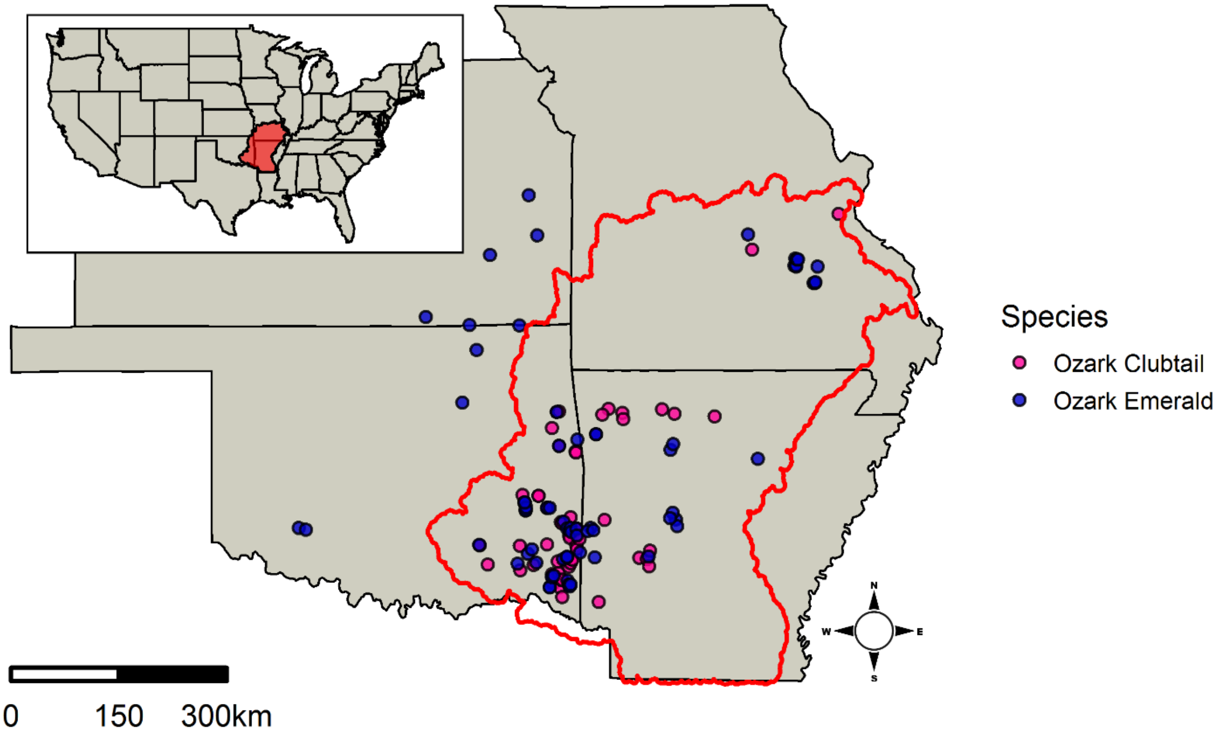

Figure 1. Presence localities used in current distribution models. Ozark-Ouachita Interior Highlands region outlined in red.

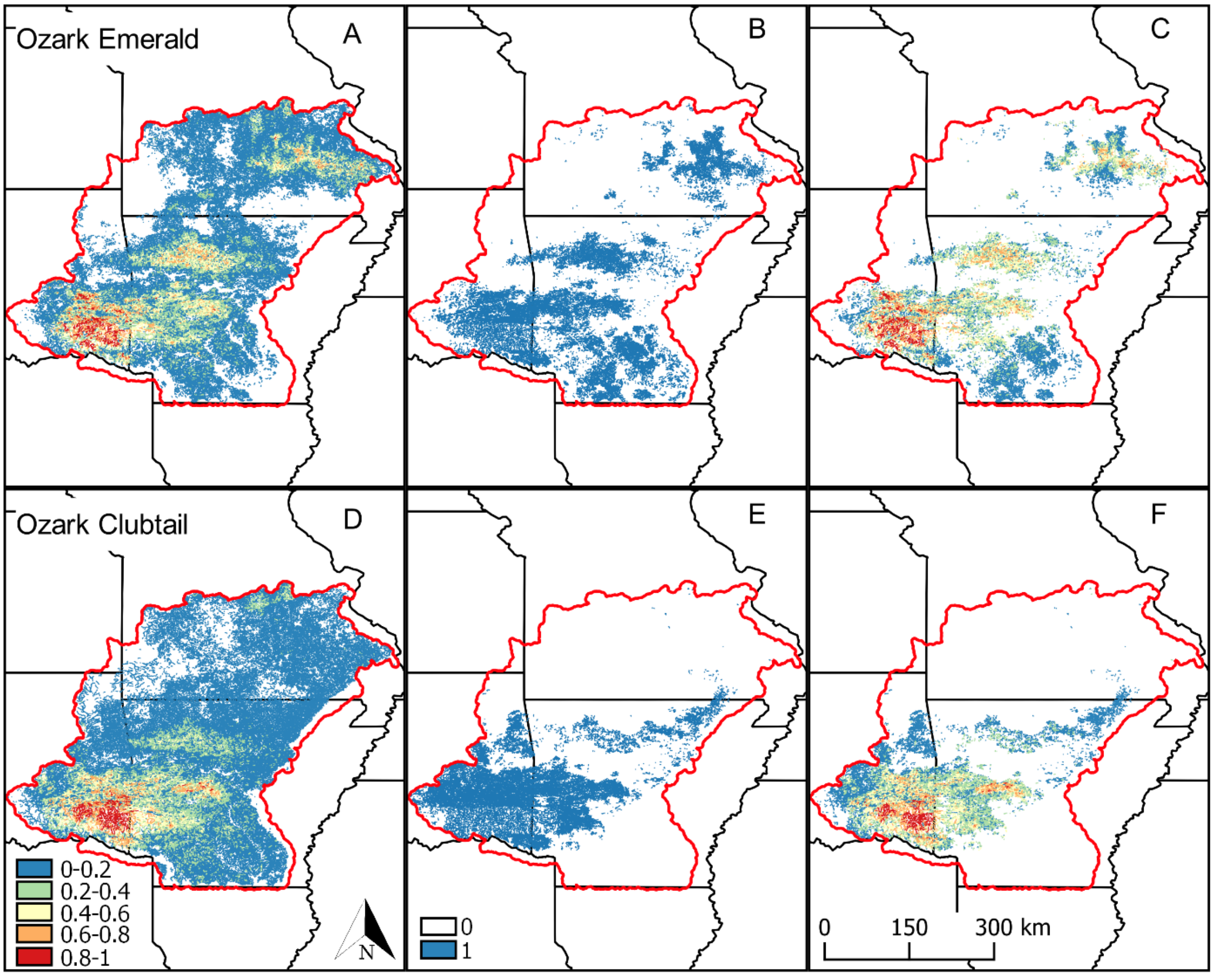

Figure 2. Stream level predictions of both focal species. MaxEnt-only predictions shown in A and D. Random forest predictions in B and E. Combined model predictions in C and F. Ozark-Ouachita Interior Highlands region outlined in red.

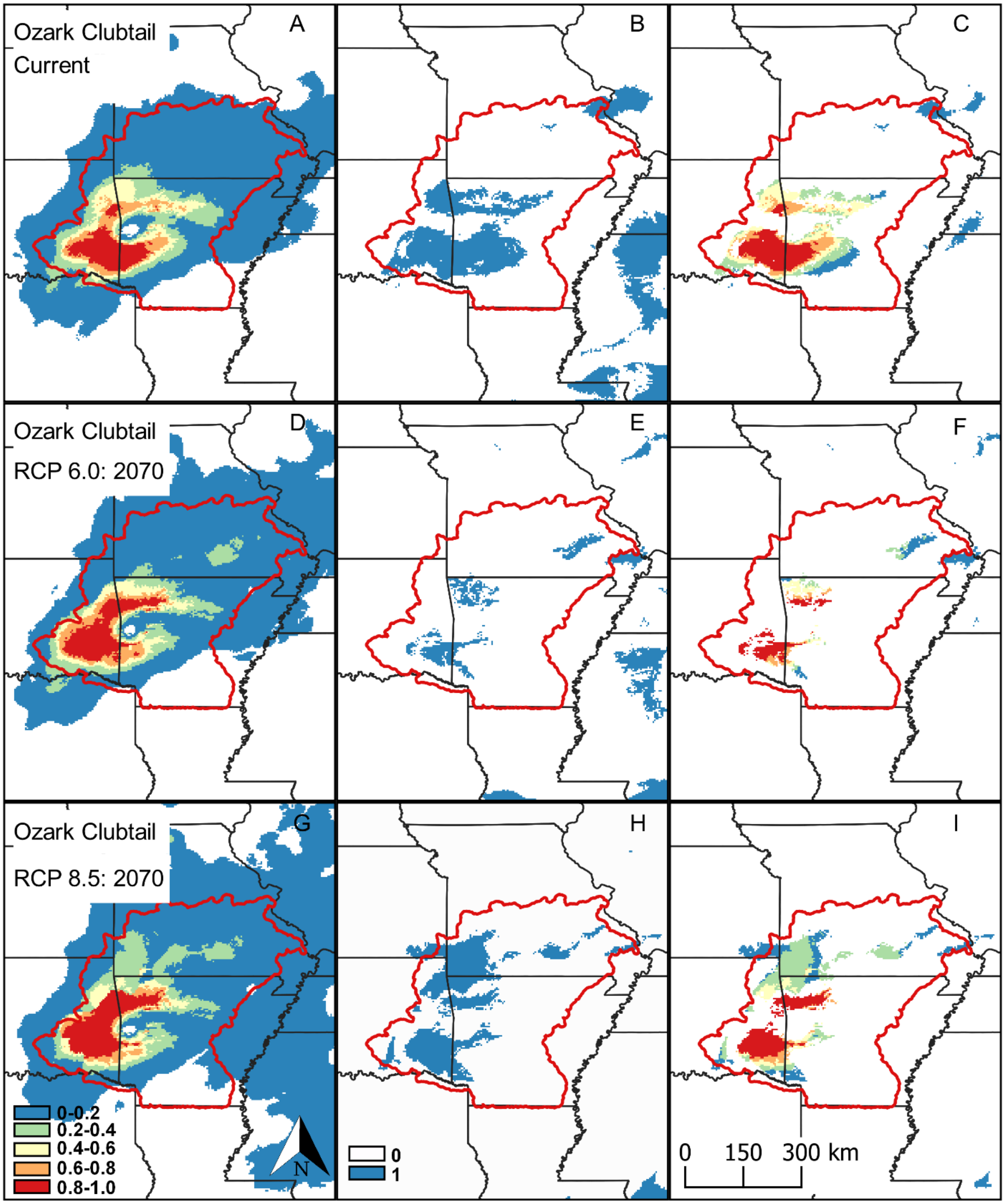

Figure 3. Current (top row) and future (middle and bottom row) predictions of the Ozark Clubtail using bioclimatic variables. Panels A, D, and G contain MaxEnt predictions, panels B, E, and H contain Random Forest predictions, panels C, F, and I contain combined model predictions. Ozark-Ouachita Interior Highlands region outlined in red.

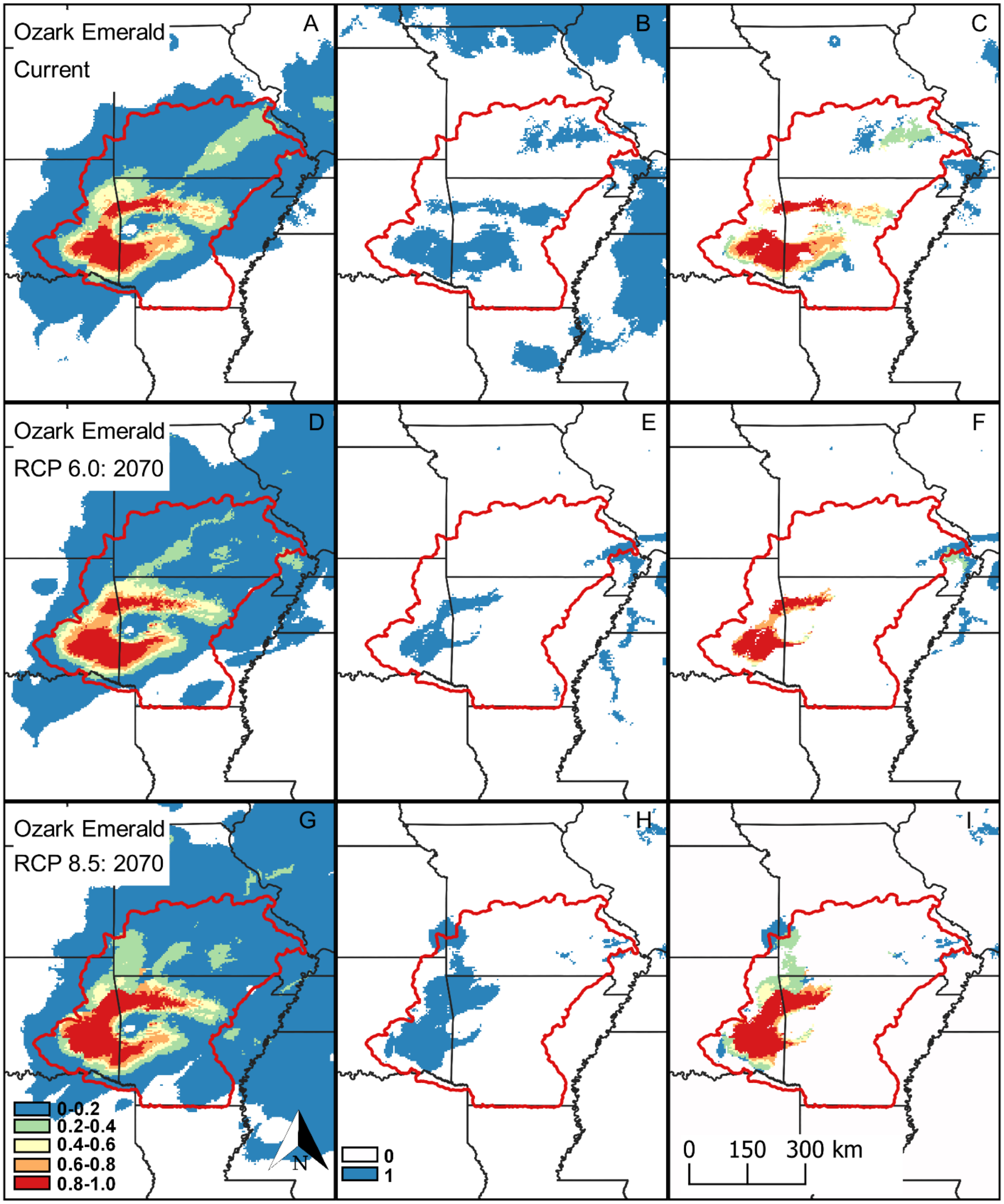

Figure 4. Current (top row) and future (middle and bottom row) predictions of the Ozark Emerald using bioclimatic variables. Panels A, D, and G contain MaxEnt predictions, panels B, E, and H contain Random Forest predictions, panels C, F, and I contain combined model predictions. Ozark-Ouachita Interior Highlands region outlined in red.

CONCLUSION

Species distributions have been of interest to biogeographers for centuries. A number of ecological and evolutionary processes shape where a species can be found, which in turn shapes these processes for other species it interacts with. Some persistent patterns that have been uncovered are that most species are limited in their distributions with only a few being widespread, and that widespread species tend to be more abundant than restricted species. These two paradigms have been applied to conservation biology as a means to rank species on level of conservation need. Species with restricted distributions, such as regional endemics, are thought to be of high conservation need due to narrow environmental tolerances and presumably low abundances. However, rare or cryptic species may be difficult to detect and thus lacking in distributional data. Furthermore, conservation designations are typically assigned within geopolitical boundaries and may not accurately reflect the current status of a species over its entire range.

This study helped address these issues by providing extensive field surveys and distribution modeling for two endemic dragonflies of the Interior Highlands region listed as SGCN within the state of Arkansas. I demonstrated the use of SDMs in guiding field surveys and increasing detections of cryptic or rare species. Any new detection points for rare taxa are valuable and can better inform conservation assessments for species of concern. Further, these models can be projected into the future and serve as a resource to develop conservation plans in light of different climate change scenarios. Projections of these two dragonflies suggest that not all regional endemics are particularly vulnerable to changes in future climate as there are still areas of high predicted suitability under two levels of climate change severity. In addition, SDMs can help facilitate cross-boundary collaborations since species ranges often span multiple jurisdictions. Finally, in the case of SDM predictions showing species shifting their ranges out of a region, we caution against using these methods to forego conservation action as there are limitations to the interpretation of these models and other factors such as dispersal and biotic interactions certainly play a role in shaping species distributions.