**Abstract:** Conservation planning depends on reliable information regarding the geographic distribution of species. However, our knowledge of species’ distributions is often incomplete, especially when species are cryptic, difficult to survey, or rare. The use of species distribution models has increased in recent years and proven a valuable tool to evaluate habitat suitability for species. However, practitioners have yet to fully adopt the potential of species distribution models to inform conservation efforts for information-limited species. Here, we describe a species distribution modeling approach for at-risk species that could better inform U.S. Fish and Wildlife Service’s species status assessments and help facilitate conservation decisions. We applied four modeling techniques (generalized additive, maximum entropy, generalized boosted, and weighted ensemble) to occurrence data for four at-risk species proposed for listing under the U.S. Endangered Species Act (Papaipema eryngii, Macbridea caroliniana, Scutellaria ocmulgee and Balduina atropurpurea) in the Southeastern U.S. The use of ensemble models reduced uncertainty caused by differences among modeling techniques, with a consequent improvement of predictive accuracy of fitted models. Incorporating an ensemble modeling approach into species status assessments and similar frameworks is likely to benefit survey efforts, inform recovery activities, and provide more robust status assessments for at-risk species. We emphasize that co-producing species distribution models in close collaboration with species experts has the potential to provide better calibration data and model refinements, which could ultimately improve reliance and use of model outputs.
Embracing ensemble species distribution models to inform at-risk species status assessments

*Carlos Ramirez-Reyes, Mona Nazeri, Garrett Street, D. Todd Jones-Farrand, Francisco J. Vilella, Kristine O. Evans

C. Ramirez, M. Nazeri, G. Street, K.O. Evans
Quantitative Ecology & Spatial Technologies Laboratory, Department of Wildlife, Fisheries and Aquaculture, Mississippi State University, Box 9690, Mississippi State, MS 39762

D.T. Jones-Farrand
U.S. Fish and Wildlife Service, 302 Natural Resources, University of Missouri, Columbia, MO 65211

F.J. Vilella
U.S. Geological Survey, Mississippi Cooperative Fish and Wildlife Research Unit, Box 9691, Mississippi State, MS 39762

*Corresponding author: cr2066@msstate.edu
Abstract

Conservation planning depends on reliable information regarding the geographic distribution of species. However, our knowledge of species' distributions is often incomplete, especially when species are cryptic, difficult to survey, or rare. The use of species distribution models has increased in recent years and proven a valuable tool to evaluate habitat suitability for species. However, practitioners have yet to fully adopt the potential of species distribution models to inform conservation efforts for information-limited species. Here, we describe a species distribution modeling approach for at-risk species that could better inform U.S. Fish and Wildlife Service’s species status assessments and help facilitate conservation decisions. We applied four modeling techniques (generalized additive, maximum entropy, generalized boosted, and weighted ensemble) to occurrence data for four at-risk species proposed for listing under the U.S. Endangered Species Act (Papaipema eryngii, Macbridea caroliniana, Scutellaria ocmulgee and Balduina atropurpurea) in the Southeastern U.S. The use of ensemble models reduced uncertainty caused by differences among modeling techniques, with a consequent improvement of predictive accuracy of fitted models. Incorporating an ensemble modeling approach into species status assessments and similar frameworks is likely to benefit survey efforts, inform recovery activities, and provide more robust status assessments for at-risk species. We emphasize that co-producing species distribution models in close collaboration with species experts has the potential to provide better calibration data and model refinements, which could ultimately improve reliance and use of model outputs.

Keywords

SDM, listing decisions, prioritization, species survey, conservation planning
Introduction

Species status assessments and their role on listing decisions

Information on the geographic distribution of many at-risk species is often limited (Lomba et al. 2010). Yet, conservation decisions that may affect species persistence are regularly made despite lacking reliable knowledge on status (McDonald-Madden et al. 2008, Martin et al. 2017). Thus, efforts to increase the quality of information, including models to help target surveys, inform recovery planning or assessing the overlap of species distribution and threats, can increase the odds of making better conservation and management decisions for at-risk species (e.g., Rutrough et al. 2019).

Globally, the International Union for Conservation of Nature’s red list of threatened species (1963) has served as the main reference for species conservation status. In the United States, the U.S. Endangered Species Act (ESA 1973, as amended), aims to protect and recover imperiled species (including subspecies or any distinct population segment of any species) and the ecosystems upon which they depend. Since its passage, the ESA prevented the extinction of
>90% of the species under its protection (Greenwald et al. 2019). However, mega-petitions that simultaneously propose hundreds of species for ESA listing as threatened or endangered have been a pervasive challenge given limited resources available to evaluate population status and support field surveys for each petitioned species (Wilde 2014, USFWS 2021). The U.S. Fish and Wildlife Service (USFWS) recently adopted a new standardized framework for conducting species status assessments (SSA) that intends to improve efficiency and rigor in ESA listing and management decisions. The aim of the SSA framework is to provide defensible, transparent, and transferable analytical approaches based on species’ life history requirements, current species condition, and projections for the future of the species under a variety of climate, urbanization and management scenarios (Smith et al. 2018).

An essential component of an SSA is a comprehensive understanding of the ecology of the species considered for ESA listing, including known population locations and current distribution, abundance, and potential for local persistence (McGowan et al. 2017). Obtaining these data can be difficult for species whose distributions and habitat relationships are poorly understood. Therefore, managers rely on limited empirical data (e.g., as few as 20-30 occurrence records), existing literature, and expert knowledge to inform the status of a species. This often limits an individual SSA to basic descriptions of environmental conditions at locations where the species is known to be present, overlooking the conditions of areas where the species may persist undetected or where the species was historically present and may yet recolonize (Rutrough et al. 2019).

**An ensemble species distribution modeling approach to inform SSAs**

A better understanding of at-risk species can be facilitated by using species distribution models that can complement existing species information (e.g., Rooper et al. 2016). Species distribution
models (SDMs) have proliferated in multiple aspects of conservation, including identifying biodiversity hotspots, suitable habitat for vulnerable species, and managing invasive species (see reviews by Franklin 2013; Urbina-Cardona et al. 2019). A standard SDM describes empirical correlations between species occurrences and geospatially-explicit environmental variables presumed to affect the species (Franklin 2009). This model can then be projected over different areas to measure their relative habitat suitability for the species. Many algorithms, from regression to machine learning, have been proposed to create those correlations, with multiple reviews highlighting the strengths and weaknesses of individual models (e.g., Elith et al. 2006; Jones-Farrand et al. 2011). This variety of options, however, can be confusing to conservationists working with rare or elusive species, where limited sample size, lack of structured monitoring to include both presence and absence, and limited understanding of species-habitat associations can compound model uncertainties (McCune 2016). An alternative to single SDM algorithms is the simultaneous use of multiple algorithms to generate an ensemble SDM (Araújo and New 2007). This ensemble model approach can be advantageous, as it considers the variability in the predictions made by individual modeling techniques to produce a combined SDM that may improve such predictions (Meller et al. 2014).

While the SDM literature has increased consistently in the last decades (Brotons 2014), these models have not been fully adopted by practitioners developing SSAs. Therefore, we see an opportunity for SDM development that could contribute to multiple aspects of the status assessment process. These contributions include: 1) help managers identify the relative likelihood of occurrence across the species’ geographic range to guide strategic investment of survey efforts and increase the likelihood of detection (Aizpurua et al. 2015); 2) formalize our understanding of species associations with habitat conditions (current status) based on the relationships of species occurrences to the gradient of environmental predictor variables (Guisan
and Thuiller, 2005); 3) inform how species are likely to respond to changing conditions (future status; Elith and Leathwick 2009); 4) inform adaptive management decisions to promote species viability over time (Cassini 2011); 5) identify sites for species reintroductions (D’Elia et al. 2015); and 6) point to gaps in the species range that could signal geographic breaks in the species distribution, which might be important in terms of conserving cryptic genetic diversity. Our objective was to generate a framework to produce ensemble SDMs to inform SSAs for at-risk species. As a case study, we applied four SDM approaches: generalized additive modeling (GAM), generalized boosting modeling (GBM), maximum entropy (MaxEnt) and weighted ensemble to occurrence data for four at-risk species petitioned for ESA listing in the Southeastern U.S. to support SSA development. We discuss the advantages of using this method to strengthen SSAs for these and other species submitted for listing decisions.

Materials and methods

In collaboration with the USFWS Southeastern Region and state agency partners, we identified four at-risk species petitioned for ESA listing and undergoing SSA development. The selected species were (1) Balduina atropurpurea Harper (purple-disk honeycombhead), a plant species associated with wet pine flatwoods and savannas (Chafin 2000); (2) Macbridea caroliniana (Walter) S.F. Blake (Carolina birds-in-a-nest), a plant species associated with swamp forests (Sorrie 2011); (3) Papaipema eryngii Bird (rattlesnake-master borer moth), an insect associated with mesic and wet-mesic prairies (USFS 2003); and (4) Scutellaria ocmulgee Small (ocmulgee skullcap), a plant associated with moist hardwood forests on stream terraces (Chafin et al. 2016). All species nomenclature follow the current Integrated Taxonomic Information System database (ITIS 2021).
SDM approach

We used an ensemble SDM approach to predict potential suitable habitat for each species based on the environmental conditions associated with known populations (Figure 1). We used two sets of data: (a) georeferenced occurrence records for each species; and (b) environmental predictor variables presumed to be associated with species presence in the form of digital raster surfaces. All data were processed using ArcMap 10.5, and statistical analyses conducted using R 3.5.2 (R Core Team 2017).

We collaborated with species experts to delineate a modeling extent for each species based on either their approximate native range (B. atropurpurea - 216,746 km² and M. caroliniana - 368,254 km²) or within administrative units (P. eryngii - 422,406 km² and S. ocmulgee - 199,517 km²) (Figure 2). We identified relevant environmental variables (e.g., climatic, terrain, vegetation) based on available literature and expert knowledge. We obtained these geospatial data from different sources, including WorldClim (Hijmans et al. 2005) for climatic variables, Landsat satellite imagery collections on Google Earth Engine (Gorelick et al. 2017) for digital elevation models, vegetation and surface reflectance variables, Landfire (U.S. Department of Agriculture 2019a) for fire frequency, national hydrography dataset (U.S. Geological Survey 2018) for hydrology data, and SSURGO (U.S. Department of Agriculture 2019b) for soil variables (see complete set of variables in Table 1). All environmental variables had a 30 m resolution with exception to WorldClim climatic variables (1 km), which were resampled to have a consistent 30 m resolution using a bilinear approach (the average value of the surrounding four pixels) and projected to a geographic coordinate system. We ran Pearson’s correlations to select non-correlated environmental variables. If two or more variables were highly correlated to each other (|r|>0.7, Dormann et al. 2013) we retained those that better correspond to expected species ecology based on expert knowledge.
With the help of species experts and data providers, we compiled presence records for each of the four species from state Natural Heritage Programs and USFWS field offices (*B. atropurpurea* n=92, *M. caroliniana* n=200, *P. eryngii* = 66 and *S. ocmulgee* n= 37). We removed records reported prior to 1990, labeled as locally extinct in the databases, or reported with an accuracy >50m. We then applied a spatial filter on the remaining records by randomly selecting one occurrence for each 500 m distance to reduce spatial autocorrelation. Choosing 1 observation per pixel has been used to reduce spatial dependence of points (e.g., Syfert et al. 2013). Given that most of our predictor variables had 30 m resolution and some had 1 km resolution (i.e., Worldclim variables), we decided to use 500 m as the compromise distance to apply this spatial filter. We also used this distance to retain more of the few occurrences available to develop SDMs (Gaul et al. 2020). The final number of presence records per species was *B. atropurpurea* n=67, *M. caroliniana* n=115, *P. eryngii* n=54 and *S. ocmulgee* n=22 (Figure 2). We also modelled habitat suitability for the rattlesnake master plant, *Eryngium yuccifolium* Michx, because it is an obligate host for *P. eryngii*. In this case, we created a habitat suitability ensemble model for rattlesnake master in a similar fashion to the other species and used the resulting model’s predictions as input to model *P. eryngii* (i.e., a hierarchical model; Gelman and Hill, 2007).

When empirical data on species absences are not available, SDMs can be calibrated using a set of randomly generated geographic points where the species is assumed to not be present, or where the species may be present but was not observed (i.e., pseudoabsences). To generate pseudoabsences, we defined both a 2 km and a 50 km buffer around a presence record. We then defined a pseudoabsence sampling area as the polygon created by removing the 2 km buffer from the 50 km buffer (i.e., a torus centered on the recorded location). Omitting the 2 km center accommodates the common practice for Heritage Programs to consider such area as an
approximate area for a unique population. For each species, we generated 500 pseudoabsence points across all pseudoabsence sampling areas for both model training and model evaluation.

**Modeling techniques**

We generated SDMs using three widely used modeling techniques: generalized additive model (GAM; Hastie and Tibshirani 1986); generalized boosted model (GBM; Friedman et al. 2000); and maximum entropy (MaxEnt; Phillips et al. 2006). GBM and MaxEnt are machine-learning methods while GAM is an additive model approach. These models are well documented in the literature (Elith et al. 2006, Phillips and Dudík 2008) and therefore not described here. We used different R libraries to run each model including dismo for MaxEnt (Hijmans et al. 2017), mgcv for GAM (Wood 2018) and gbm for GBM (Greenwell et al. 2018). We ran each modeling algorithm with the same set of environmental predictor variables, presence and pseudoabsence data for each species to capture the influence of predictor variables in the models (Table S1).

Each of the three calibrated models was projected across the species’ study areas to generate three separate predictions of habitat suitability.

Given the small sample size for each species, we used a leave-one-out approach to cross-validate the models that contrasted our set of presence and pseudoabsence records with a set of model-predicted presences and absences. We built a model using all presence and pseudoabsence records minus one observation (i.e., a training dataset of size \( n-1 \)). The omitted observation’s environmental data were then used to solve the estimated model to obtain a predicted value (i.e., a test value). We iterated this process to generate a list of predicted values of size \( n \). These test values were then compared to the observed values to evaluate model performance using the area under the precision-recall curve (AUC-PR). While the area under the receiver operating characteristic curve (AUC-ROC) is the most common metric, AUC-PR works well with small
sample sizes, is robust to broad geographic extents, and is not sensitive to the use of pseudoabsences (Sofaer et al. 2019a). As a robustness check, we also calculated the AUC-ROC and correlation coefficients for each model. The range of each metric varied from 0 (poor model performance) to 1 (good model performance).

Our SDM outputs consisted of three habitat suitability index (HSI) maps for each species with pixel values ranging from 0 (low suitability) to 1 (high suitability). We generated a model ensemble based on weights to minimize uncertainties associated with each modeling approach (Marmion et al. 2009). The weight $w$ of a particular model was calculated by dividing its AUC-PR score by the sum of the three AUC-PR scores (one for GAM, GBM, and MaxEnt). That is, models with greater AUC-PR were assigned larger $w$ in the final ensemble. The final ensemble model prediction $HSI_{ens}$ for a given landscape pixel $j$ was $HSI_{ens,j} = \sum_{i=1}^{3} w_i HSI_{i,j}$ where $w_i$ is the weight of the $i$-th model algorithm (GAM, GBM, or MaxEnt) and $HSI_{i,j}$ is the predicted suitability for the $j$-th pixel from the $i$-th algorithm. The final ensemble model for each species thus consisted of a habitat suitability map with pixel values ranging from 0 (low suitability) to 1 (high suitability) weighted by the relative explanatory power of each modeling algorithm. We calculated the performance metrics (AUC-PR, AUC-ROC, and correlation) for the model ensemble in a similar fashion to individual models. In the resulting ensemble maps, we considered suitable areas all pixels that surpassed the HSI threshold that maximized the sum of sensitivity (proportion of presences correctly predicted) and specificity (proportion of absences correctly predicted) (Liu et al. 2005).
Results

*Balduina atropurpurea*

Individual models predicted different proportions of suitable habitat, with GBM and MaxEnt being the most conservative (8.71 and 10.91% of the study area deemed as suitable, respectively), whereas GAM was the most inclusive with 14.05% of the study area identified as suitable (Figure 2b). Our ensemble habitat suitability map, however, indicated that 10% of the study area could be suitable for the species, with only 0.52% in the highest suitability bin (HSI > 0.8) (Table 2). The explanatory environmental variables that consistently exhibited greater weights in the models were maximum winter temperature and fire frequency, whereas elevation and mean summer temperature had lower weights (Table 1). Among the three SDM approaches, GBM had the highest performance while GAM had the lowest (AUC-PR=0.59 and 0.41, respectively). The ensemble model, however, had an AUC-PR=0.79. Other model performance metrics also showed similar patterns (Table 3). We found that areas deemed as suitable in the three models generally overlapped (59.47% agreement in at least two models, and 32.97% agreement for the three models). The most suitable areas were found in the central and southern portions of the study area (Figure 2b, Figure S1).

*Macbridea caroliniana*

We found that 9.15% of the study area could be suitable for the species according to the ensemble model, while only 0.63% appeared in the highest suitability bin (HSI > 0.8) (Table 2). The most important variable across the three individual models was distance to floodplain. GBM and MaxEnt had higher model performance (AUC-PR=0.6 and 0.55, respectively), and the ensemble led to an AUC-PR=0.9 (Table 3). We detected that 24.79% of suitable area was agreed for three models, and 49.88% agreement for at least two models. Most of the resulting suitable
area in the ensemble model was located in the coastal plain, particularly in areas close to the floodplains (Figure 2b, Figure S1).

**Papaipema eryngii**

For this species, suitable habitat covered 7.22% of the study area in the ensemble model, whereas areas in the highest suitability bin (HIS > 0.8) comprised only 0.38% (Table 2). Environmental predictor variables with greater importance for the models included the enhanced vegetation index, habitat suitability for the obligate host plant *E. yuccifolium* and soil organic matter. Variables that had lower importance in the models were percent silt in soils and tree cover (Table 1). The GBM modeling approach yielded the best performance, while GAM performed the poorest (AUC-PR=0.37 and 0.29, respectively). The ensemble model indicated an AUC-PR=0.63. The tree models had a 14.76% agreement in the area deemed as suitable on their perspective models, while that proportion increased to 38.24% when considering the overlap of at least two models. Most of the areas with high suitability for the species were located towards the central-west and central-south portions of the study area, while other portions of suitable habitat were scattered in the remaining extent (Figure 2b, Figure S1).

**Scutellaria ocmulgee**

The ensemble model for *S. ocmulgee* shows that about 3.19% of the study area was suitable for the species, while only 0.1% had high suitability (Figure 1S, Table 2). The most consistently important environmental predictor variables in the models for this species were temperature, percent sand, and solar radiation, while elevation appeared to be the least important (Table 1). The GBM approach exhibited the greatest model performance and GAM the lowest (AUC-PR=0.32 and 0.2, respectively), while the model ensemble had an AUC-PR=0.67. For this species, the agreement of predicted suitable areas was only 18.18% between the three models but
the percent increased to 45.87% agreement for two models. The model ensemble showed that areas with higher habitat suitability for the species were located in the central part of the study area (Figure 2b, Figure S1).

Discussion

Case studies

In our case studies, we identified potential suitable areas that can be candidates for surveys. Prioritizing locations within areas of greater suitability scores may increase survey efficiency by targeting smaller search areas with the potential for success (Table 2). In addition, during the modeling process we identified the species’ associations with environmental predictor variable gradients that could help describe each species’ ecological (realized) niche (Figure S2). For instance, we confirmed that one of the most relevant predictor variables for *B. atropurpurea* was fire frequency (Table 1). Fire is a determinant for the species as it requires open areas with periodic fire events (Lincicome 1998), and our model captured this trend. Models for *P. eryngii* agreed that habitat suitability for the host species *E. yuccifolium* was a good predictor for the presence of the species. We also noted that the species seemed to prefer areas with intermediate proportions of canopy cover (e.g., 40%) since a complete cover would impede the growth of the host species. Lastly, precipitation was the most important variable in *S. ocmulgee* models, matching the known association of the species with moist forest (Chafin et al. 2016). We found different suitable habitat for the species scattered in the central part of the study region, particularly near rivers, corresponding with the species’ natural history (Chafin et al. 2016). *S. ocmulgee* was the most challenging species to work with given the small number of records available, which impacted model performance. We therefore caution managers to treat predictions with caution. Nevertheless, our model approximated habitat suitability for the species...
based on available data, and our maps can be used to inform additional species surveys, which
would then aid future model refinement.

**Potential of ensemble SDM in species status assessments**

Under the current SSA approach, USFWS personnel have to identify the “best available” data
and complete the assessment within a short time frame (6-9 months). Given the workload
generated from mega-petitions this may represent a limiting factor to the successful completion
of the SSA process. Whereas SDM development is not required for the SSA process, we believe
distribution models can inform multiple aspects of an SSA. First, our results indicate SDMs can
provide reliable, transparent and defensible information on the potential spatial extent of a
species (Villero et al. 2017). As such, our study produced reliable solutions within a geographic
context to inform conservation efforts and benefit the SSA process through the ability to
compare among different modeling approaches. Our ensemble models identified geographical
areas of agreement of individual models (Figure S1), accounted for individual model
performance (by using weights) and consistently ranked higher in model accuracy (Table 3).
Therefore, the use of ensemble SDMs may be an improved approach to guide SSA assessments
of current status. Moreover, ensemble SDMs provide a standardized, transferable modeling
approach that may enhance consistency in the status assessment while making distribution
products comparable across spaces and species (Araújo et al. 2019).

Our results suggest that areas identified as highly suitable in the ensemble SDM would be
recognized as priority sites for conservation efforts. For instance, surveys aiming to detect
additional populations can improve status assessments. Targeting surveys in areas with high HSI
may improve the detection of at-risk species (Meller et al. 2014; McCune 2016) and
consequently, improve the reliability of the information used for listing decisions. Furthermore,
stratifying conservation efforts (e.g., surveys, recovery and translocation planning) based on suitability gradients would indicate where to invest greater effort (i.e., predicted high suitability locations). In this context, SDM outputs used as continuous (0-1) instead of categorical data (suitable/non-suitable) would best avoid loss of suitability information (Guillera-Arroita et al. 2015).

By relating environmental predictor variables with occurrence data, managers can gain additional quantitative insight into how species respond to environmental gradients (e.g., Figure S2). This is particularly relevant for many rare and at-risk species targeted by SSAs, whose known habitat requirements are mostly limited to descriptive habitat associations. Further, SDM development could also function in a predictive context (future status) by incorporating climate and management scenarios, enhancing the conservation value of SDMs (Wiens et al. 2009, Porfirio et al. 2014, Lyon et al. 2019).

Adopting the use of SDMs in the SSA process would require investments in terms of technical capacity and training. Nonetheless, once the initial investment is complete, work with new species would require less time and resources, something particularly important in the context of mega-petitions. For instance, one major and time-consuming component in developing an SDM is the initial effort to compile relevant environmental predictor variables for a species of interest. Our study indicated that many environmental variables used for one species were also useful for other species (Table 1). This is because our case study species were located in the same region (i.e., Southeastern U.S.) and likely responded to similar environmental factors. Regardless, substantial effort to identify common data layers at regional extents prior to model fitting can simplify the modeling process for multiple species within the same region. Similarly, once the code for generating individual and ensemble models is built for one species,
it will take substantially less time to adapt it for other species. Given the transferability of coding frameworks, we recommend future efforts also focus on development of on-the-fly ensemble model predictions in a web-enabled, user-guided geoplatform.

**Perceived SDM challenges precluding their development**

Although SDM studies have become common in the last decades, they are yet to be fully adopted in conservation planning (Tulloch et al. 2016). In practice, conservation organizations may still consider modeling as challenging for multiple reasons, including that SDM development is technically difficult, not reliable, or expensive (Joppa et al. 2013, Tulloch et al. 2016). In this study we illustrated how generating ensemble SDMs has the potential to inform several aspects of a SSAs and that most perceived challenges can be surmounted. While generating an ensemble SDM requires knowledge of digital data manipulation and programming, there are existing tools and libraries available in the SDM field to facilitate both data manipulation and processing (Ahmed et al. 2015). For instance, the code we developed to generate an ensemble SDM (Text S1) can be adapted for specific needs of other species. There might also be reluctance by practitioners to develop SDMs based on perceived lack of reliability. In this regard, our study confirmed that different model algorithms produced different outputs (Qiao et al. 2015). Importantly, this is one of the strengths of ensemble models. The ensemble model considered individual model agreement and weighted each individual model by its relative model performance (Breiner et al. 2015), thereby increasing objectivity and improving support for the decision-making process.

Another perceived shortcoming of SDMs is that resolution of model inputs might not reflect species’ ecological requirements, but recent developments in the remote sensing community provide environmental variables across large geographic extents at finer spatial and
temporal resolutions (Leitão and Santos 2019). Lastly, practitioners might question the reliability of models built with a limited number of locations. Indeed, despite considerable advancements in tools and techniques, the efficacy of SDMs lies in the quality of data used to build the models, making presence data a major limiting factor (Phillips et al. 2009, Gaul et al. 2020). Conversely, SDMs can produce spatial predictions that may help field biologists target new survey areas (Fois et al. 2018). If an SDM is developed well in advance to the SSA, additional species locations from such model-guided surveys could be used to validate or revise the SDM to increase its reliability for use in the SSA.

Potential limitations

Similar to other conservation methods, there is no single SDM approach that fits the needs and conditions of all practitioners developing SSAs. Whereas our approach was appropriate for our needs, and we hope that SDM developers use it as a guide for their own work in SSAs, this methodology still has room for improvement depending on particular needs and level of information available. For instance, we used an arbitrary distance to restrict the drawing of pseudoabsences given the lack of empirical information on proper biological distances. An improved model for the species could use the dispersal capacity of the species as the distance used to restrict such calibration area. Another avenue of improvement could be calibrating the models using stratified presence/absence samples based on the complexity of environmental conditions in the landscape (Hirzel and Guisan 2002). As such, more (or less) presence and pseudoabsences could be drawn depending on the heterogeneity of environmental conditions. Further, our filtering decision for presence data (i.e., randomly select 1 presence at a distance equal of the largest pixel size of environmental data) was chosen to retain as many records as possible given our relatively small sample sizes. This approach did not take into account other
possible biases in the sample, such as higher survey efforts in areas with easy access. Enhanced analyses can make use of tools to reduce that potential bias to minimize overfitting and increase performance (Boria et al. 2014). In addition, while we aimed to have a balanced sample size for presence and pseudoabsences across individual SDM algorithms and equal data for model validation, MaxEnt is known to perform well with larger numbers of background points. Thus, a MaxEnt only model would be better tuned by including a larger size of background points (Phillips and Dudík 2008). Finally, given that we did not know the range for several species, we extrapolated the model to the political boundaries containing presences (e.g., Figure 1S). Improved extrapolations can use a multivariate environmental suitability surface (MESS) as a measure of the similarity between new environments and those in the calibration sample (Elith et al. 2010).

Despite the vast number of ways to create SDMs, SSAs developers should evaluate their model needs before selecting a particular approach. This is important, because SDMs can become very complex and require significant investment in familiarity with SDM tuning options. For instance, a model aimed to have high sensitivity (even if it generates overprediction) can be preferred for identifying additional sites for surveys, while a model aimed to have high specificity (choosing areas where the species is highly likely to be present) would be preferred when designing reserves (Barbet-Massin et al. 2012). In our work we aimed to have a balance of model sensitivity and specificity so that model outputs could be relevant for wide range of uses in SSAs (e.g., improving surveys, finding translocation sites, finding species and habitat relationships, and determining status, especially for species with limited data. Further, our models provide a foundation for building our knowledge and understanding of rare and vulnerable species. Ultimately, the model choice and calibration settings can be adapted depending of the decision context (Villero et al. 2017).
Simple but effective models that address model study objectives, consider the attributes and limitations of the data used, and provide a framework for how these interact with the underlying biological processes, are useful tools for conservation decision-making (Merow et al. 2014, Sofaer et al. 2019b). As such, we aimed to create an approach to develop ensemble models with relatively simple calibration settings for individual algorithms that can guide novice SDM developers and be useful for at-risk species. Others have argued that single, high-tuned models can yield results as good or even better than ensemble models (Hao et al. 2020). However, in the decision context of SSAs to support ESA listing decisions, legal and workload constraints often demand that models be developed rapidly with the data in hand. We believe that use of an ensemble SDM produces a more transparent and defensible decision because the ensemble model encapsulates the current state of knowledge of the species with clear assumptions and balances the biases inherent in individual modeling approaches. In any case, we recommend identifying the strengths and limitations of the SDM in a transparent way. For instance, Sofaer et al. (2019b) developed a rubric for communicating the credibility of SDMs for decision making (e.g., see this table for our case studies in Table S2). In addition, it is useful for decision-makers to recognize the variation of individual or ensemble models. For instance, we provided maps showing areas with higher predicted likelihood of suitability across models (e.g., Figure S1). Finally, it is important to consider that even if a model has a good discriminatory accuracy (e.g., high AUC-ROC scores for correctly predicted occurrences during model testing), this does not guarantee that models reflect a good functional accuracy (e.g., a model’s ability to make continuous estimates of relative habitat suitability). Making sure that models are simple and reflect known biology for the species can close the gap between these two types of accuracy and improve the usability of the SDM outputs (Warren et al. 2020).
Concluding remarks on developing effective ensemble SDMs

Developing an effective SDM requires close collaboration between multiple model participants, and preferably those involved in the decision process, which can also improve use (Sofaer et al. 2019b). In our project, these participants included conservation agencies and organizations responsible for the species SSA, a modeling team, data providers, and experts with local knowledge of the species’ biological needs (Figure 3). Although not all SSAs require generation of novel SDMs, the structure used here provides a useful model for effective co-production of SDMs, and science in general. The decision-making organization facilitates coordination of participants to obtain the necessary resources and sustain appropriate communication among other participants. Modelers provide the technical expertise to compile, harmonize and process data and create model outputs. Species experts are essential to inform model development, because they can help model developers select relevant environmental variables that reflect the species’ natural history and also help locate additional calibration data. Later on, species experts can also help other participants assess iterative model outputs. Finally, the decision-making organization coordinates and verifies that model outputs are archived and delivered to practitioners.

Mechanisms to promote effective collaboration will require funding for initial and subsequent model development, clear communication about the existence and performance of the model, and perennial free access to modeling code and outputs. In the spirit of a co-production approach, a close and iterative collaboration among participants will help ensure that the outputs of SDM lead to actionable outcomes (Guisan et al. 2013; Sofaer et al. 2019b). Finally, this collaborative approach should be initiated such that it results in the timely development of SDMs (i.e., in time to inform the decision). Specifically for SSAs, modelers should, at a minimum, be involved in the early planning stages to help weigh the appropriateness of modeling and help
determine the most appropriate approach within the decision context (e.g., budget, timeline, capacity). The earlier in the process that models can be generated the better, as it allows more time for review and revision. This will ensure that the best possible model is readily available to support SSA development and ultimately policy and management decisions for the target species.

In summary, SDMs have the potential to improve the listing decision process but these models have not been fully adopted as standard practice when developing SSAs. We suggest that using ensemble SDMs can benefit the SSAs or other similar processes by providing objective and defensible information about species and habitat relationships, as well as a spatial characterization of the species suitable habitat. This information can then be used to optimize species surveys, relocate or reintroduce individuals, strategic planning for current and future climate and management threats, and used with external partners for habitat conservation planning. Policies for conservation of at-risk species in other regions may also benefit from this approach. However, these benefits require that a specific ensemble SDM adequately addresses stakeholder needs in a timely manner via model co-production, and that stakeholders commit to updating the model over time to reflect what they have learned through the model’s application.
Supplemental materials

Table S1. Microsoft excel file containing the environmental predictor values for each presence and pseudoabsence points used to create habitat suitability maps. Each of the tabs corresponds to each of the four at-risk species in the Southeastern U.S. for which we created habitat suitability map in support of species status assessments.

Table S2. Description of model quality for each at-risk species for which we developed habitat suitability maps in the Southeastern U.S. in support of species status assessments. The model categories and scores are based on Sofaer et al. (2019) guidelines to report SDM models for decision-making.

Figure S1. Large output figures for each modeling technique used to create habitat suitability maps for four at-risk species in the Southeastern U.S. in support of species status assessments. For each species and modeling technique, we show (1) a set of maps of predicted habitat suitability index and (2) a set of maps with a binary suitable and non-suitable areas defined by their model-specific maximum sum of sensitivity and specificity threshold. We also include a compound map showing how many times individual models identified a specific pixel as suitable.

Figure S2. MaxEnt response curves for the environmental predictor variables used to model habitat suitability. We present these curves for each of the four at-risk species in the Southeastern U.S. for which we created habitat suitability map in support of species status assessments US.

Text S1. Example of code used to generate individual (GAM, GBM, MaxEnt) and Ensemble models. The code was used to generate habitat suitability maps for four at-risk species in the
Southeastern US in support of species status assessments. The code is written in R programming language.

Reference S1. USFS. 2003. Conservation assessment For Eryngium root borer (Papaipema eryngii).

Reference S2. Lincicome DA. 1998. The rare perennial Balduina atropurpurea (Asteraceae) at Fort Stewart, Georgia.

Archived material:

All the high-resolution ensemble suitability maps created for four at-risk species in the Southern US in support of species status assessments have been archived and can be found at ScienceBase:

https://www.sciencebase.gov/catalog/item/5f5117f082ce4c3d12385940
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Figure 1. Schematization of the ensemble species distribution modeling approach. The approach was used to create habitat suitability maps for four at-risk species in the Southeastern U.S. in support of species status assessments: (a) Occurrence point locations for a given species, and associated data for environmental factors influencing it. We show both the calibration area where we draw pseudoabsences and the total area of model projection; (b) Relationships between environmental data and point locations are created using three known mathematical algorithms; (c) Individual model validation metrics are calculated for each algorithm; (d) The calibrated model is applied to the full area of interest; (e) An ensemble model is created using weights based on the individual model validation performances.

Figure 2. Study area and habitat suitability model outputs. We created these outputs for four at-risk species in the Southeastern US in support of species status assessments. (a) Study area for the case study species and location of the occurrence data used. (b) Model outputs using three algorithms and the resulting ensemble. Areas that consistently had higher habitat suitability scores in individual model approaches are carried out to the ensemble model, while areas deemed as suitable in only one approach are not represented in the ensemble. Higher detail for these maps is available in Figures S1.

Figure 3. Schematization of the effective co-production strategy. This approach was used to create habitat suitability maps for four at-risk species in the Southeastern US in support of species status assessments. Iterative communication among the participants will yield better and
more useful model outputs. The width of each arrow represents the level of involvement among participants. The dashed lines represent optional links among participants.
Tables

Table 1. Relative importance of environmental predictor variables in each habitat suitability modeling approach. These variables were used to create habitat suitability maps for four at-risk species in the Southeastern US in support of species status assessments. Since each model algorithm (GAM, GBM, and MaxEnt) calculated its own model contribution index, we included the approximate importance of variables in terms of p-values for GAM, where smaller values indicate variables that better inform the model. We also included the relative influence of the model variable (GBM), and the percent contribution to the model (MaxEnt), where larger values denote more informative variables in the respective model.

Table 2. Proportion of the landscape (% of the study area) predicted by individual modeling algorithms. These algorithms were used to create habitat suitability maps for four at-risk species in the Southeastern US in support of species status assessments. The proportions are presented in five equal intervals for the habitat suitability index range.

Table 3. Individual model performance metrics. These metrics were produced for each algorithm used to predict habitat suitability for four at-risk species in the Southeastern US in support of species status assessments. We present the model evaluation using the AUC-PR, AUC-ROC and correlation coefficient for each species and each model algorithm.
b) Modeling algorithms:
1. Generalized additive model (GAM)
2. Gradient boosting model (GBM)
3. Maximum Entropy model (MaxEnt)

c) Model validation
Precision recall
AUC (AUC-PR)

d) Suitability maps

M1
M2
M3

AUC-PR_1
AUC-PR_2
AUC-PR_3

Low
High

e) Ensemble map

AUC-PR_E
Figure 2 SDM study area and outputs

- **Balduina atropurpurea**
- **Macbridea caroliniana**
- **Papaipema eryngii**
- **Scutellaria ocmulgee**

State boundaries

Species occurrences

Habitat suitability index

0 (Very low) to 1 (Very high)

Ensemble

GAM

GBM

MaxEnt
Participants in the species distribution modeling process

**Lead conservation organization**
- Identifies focal species candidate for SDM
- Supervises the development of SDM
- Serves as liaison between different stakeholders
- Identifies funding for the project

**SDM modeling team**
- Offers technical capacity to compile and analyze species and ecological variables
- Creates SDM

**Species expert**
- Guides species’ habitat requirements
- Validates models

**Data providers**
- Provide access to species location archives
- Provide spatial data libraries

**Conservation partners**
- Participants in the species distribution modeling process
Table 1

| Variables | *Balduina atropurpurea* | *Macbridea caroliniana* | *Papaipema eryngii* | *Scutellaria ocmulgee* |
|-----------|--------------------------|-------------------------|---------------------|------------------------|
|           | GAM  | GBM  | MaxEnt | GAM  | GBM  | MaxEnt | GAM  | GBM  | MaxEnt | GAM  | GBM  | MaxEnt |
| Maximum winter temperature<sup>1</sup> | <0.001 | 21.88 | 40.7   | 0.25  | 5.54  | 5.3    | <0.01 | 4.22  | 1.3    | 0.15  | 3.45  | 19.2   |
| Mean summer temperature<sup>1</sup> | 0.04  | 9.42  | 22.3   | <0.01 | 17.3  | 5.5    | 0.07  | 2.17  | 4.3    | <0.01 | 17.04 | 35.2   |
| Mean annual precipitation<sup>1</sup> | 0.36  | 4.55  | 2.5    | 0.19  | 4.9   | 6.8    | 0.77  | 4.02  | 2.2    | 0.32  | 1.21  | 0      |
| Mean summer Landsat surface temperature<sup>2</sup> | 0.59  | 7.82  | 3      | 0.28  | 8.48  | 7.9    | <0.01 | 2.85  | 7.7    | 0.35  | 3.99  | 10.5   |
| Tree canopy cover<sup>2</sup> | 0.52  | 4.88  | 0.4    | 0.07  | 2.13  | 3      | 0.01  | 5.85  | 4      | 0.05  | 5.82  | 0      |
| Elevation<sup>2</sup> | 0.06  | 9.39  | 5.7    | 0.12  | 9.42  | 2.8    | 0.05  | 27.41 | 6.2    | 0.01  | 13.54 | 4.3    |
| Soil available water content<sup>3</sup> | 0.06  | 12.06 | 5.2    | 0.31  | 15.9  | 2.9    | 0.47  | 14.56 | 5.5    | 0.05  | 13.54 | 4.3    |
| Soil percent silt<sup>3</sup> | 0.08  | 5.03  | 0.3    | 0.05  | 3.78  | 0.7    | 0.05  | 5.82  | 0      |       |       |        |
| Soil percent sand<sup>3</sup> | 0.07  | 2.13  | 3      | 0.01  | 5.85  | 4      |       |       |        |       |       |        |
| Soil organic matter<sup>3</sup> | 0.08  | 5.03  | 0.3    | 0.05  | 3.78  | 0.7    | 0.05  | 5.82  | 0      |       |       |        |
| Soil pH<sup>3</sup> | <0.001 | 14.59 | 17.9   |       |       |        |       |       |        |       |       |        |
| Mean summer enhanced vegetation index - EVI<sup>2</sup> |       |       |        |       |       |        | <0.01 | 21.55 | 26.1   |       |       |        |
| Mean summer normalized difference vegetation index - NDVI<sup>2</sup> | 0.03  | 10.32 | 2      | 0.17  | 9.11  | 0.3    | 0.11  | 2.73  | 11.6   |       |       |        |
| Fire frequency<sup>2</sup> |       |       |        |       |       |        | <0.001 | 14.59 | 17.9   |       |       |        |
| Solar radiation<sup>2</sup> |       |       |        |       |       |        |       |       |        | 0.03  | 24.46 | 9.2    |
| Distance to streams<sup>4</sup> |       |       |        |       |       |        |       |       |        | 0.04  | 9.9   | 1.7    |
| Distance to floodplain<sup>5</sup> |       |       |        |       |       |        | <0.01 | 13.31 | 63.2   |       |       |        |

*Eryngium* suitability<sup>6</sup> |       | <0.001 | 36.4  | 48.8  |       |       |       |       |        |       |       |        |

<sup>1</sup>WorldClim (Hijmans et al. 2005); <sup>2</sup>Landsat satellite imagery collections on Google Earth Engine (Gorelick et al. 2017); <sup>3</sup>SSURGO (U.S. Department of Agriculture 2019b); <sup>4</sup>National Hydrography Dataset (U.S. Geological Survey 2018); <sup>5</sup>Landfire (U.S. Department of Agriculture 2019a); <sup>6</sup>Derived from SDM modeling.
### Table 2

|                | **Balduina atropurpurea** | **Macbridea caroliniana** | **Papayema eryngii** | **Scutellaria ocmulgee** |
|----------------|---------------------------|---------------------------|----------------------|--------------------------|
|                | GAM GBM MaxEnt Ensemble   | GAM GBM MaxEnt Ensemble   | GAM GBM MaxEnt Ensemble | GAM GBM MaxEnt Ensemble |
| HSI 0.0-0.2    | 88.66 89.25 69.24         | 84.31 87.69 79.94         | 92.48 90.91 71.12     | 97.1 97.98 92.03         |
| HSI 0.2-0.4    | 4.42 5.98 14.79           | 8.67 5.26 4.79           | 10.5 8.22 3.22       | 4.69 16.01 8.02         |
| HSI 0.4-0.6    | 2.87 2.95 9.14            | 3.57 3.15 5.67           | 3.73 1.8             | 2.27 6.78 2.83         |
| HSI 0.6-0.8    | 2.34 1.42 5.06            | 2.13 2.32 2.06           | 3.1 1.99 1.34       | 1.44 3.65 1.09         |
| HSI 0.8-1      | 1.71 0.39 1.77            | 0.52 1.57 1.93           | 0.79 0.63 1.16       | 0.69 2.45 0.38         |

Downloaded from http://meridian.allenpress.com/jfwm/article-pdf/doi/10.3996/JFWM-20-072/2801986/jfwm-20-072.pdf by guest on 03 April 2021
| Species                  | AUC-PR | AUC-ROC | COR | AUC-PR | AUC-ROC | COR | AUC-PR | AUC-ROC | COR | AUC-PR | AUC-ROC | COR |
|--------------------------|--------|---------|-----|--------|---------|-----|--------|---------|-----|--------|---------|-----|
| Balduina atropurpurea    | 0.41   | 0.83    | 0.68| 0.59   | 0.9     | 0.6 | 0.49   | 0.85    | 0.55| 0.79   | 0.95    | 0.81|
| Macbridea caroliniana    | 0.49   | 0.86    | 0.75| 0.6    | 0.88    | 0.92| 0.55   | 0.88    | 0.68| 0.9    | 0.99    | 0.84|
| Papaipema eryngii        | 0.29   | 0.81    | 0.63| 0.35   | 0.85    | 0.67| 0.37   | 0.85    | 0.53| 0.63   | 0.95    | 0.72|
| Scutellaria ocmulgee     | 0.2    | 0.5     | 0.63| 0.32   | 0.77    | 0.63| 0.26   | 0.9     | 0.52| 0.67   | 0.98    | 0.8 |
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