Development and Delivery of Species Distribution Models to Inform Decision-Making

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Information on where species occur is an important component of conservation and management decisions, but knowledge of distributions is often coarse or incomplete. Species distribution models provide a tool for mapping habitat and can produce credible, defensible, and repeatable information with which to inform decisions. However, these models are sensitive to data inputs and methodological choices, making it important to assess the reliability and utility of model predictions. We provide a rubric that model developers can use to communicate a model's attributes and its appropriate uses. We emphasize the importance of tailoring model development and delivery to the species of interest and the intended use and the advantages of iterative modeling and validation. We highlight how species distribution models have been used to design surveys for new populations, inform spatial prioritization decisions for management actions, and support regulatory decision-making and compliance, tying these examples back to our model assessment rubric.

Keywords: species distribution model, model assessment rubric, survey design, spatial planning, decision support

Information on species distributions underlies nearly every aspect of managing biodiversity, including efforts to conserve rare species, anticipate problematic invasions, identify biodiversity hotspots, and delimit valued habitat types (Franklin 2010). Information about where individuals of a species are or could exist is a key component to legally binding decisions, such as regulatory actions under the US Endangered Species Act (ESA; Schwartz 2008, Camaclang et al. 2015) and establishment of quarantine zones for invasive species (Robinson et al. 2017). Species distributions also inform management activities, such as those found in state wildlife action plans (Fontaine 2011). Typically, information used for these purposes consists of narrowly delimited point or polygon representations of observed species occurrences, maps based on opinions (*blob maps*, *sensu* Jetz et al. 2008), or maps indicating the presence of a species within a geopolitical boundary, such as a county (figure 1; Jetz et al. 2012). Each of these summaries has substantial limitations. Point observations underestimate the occupied area of a species and conflate sampling biases and underlying distributions (Rondinini et al. 2006). Geopolitical and expert-created maps can overestimate a species' occupied area and often lack transparency and repeatability (Jetz et al. 2008, Peterson et al. 2016). In each of these cases, variation in sampling effort, geopolitical delimitations, and documentation of expert decisions can result in a degree of arbitrariness that may undermine credibility for decision-making (Hurlbert and Jetz 2007).

Species distribution models (SDM) use known locations of a species and information on environmental conditions to predict species distributions. SDM use a variety of algorithms to estimate relationships between species locations and environmental conditions and predict and map habitat suitability (Franklin 2010). The conceptual underpinnings of SDMs originated in the midtwentieth century to describe a species' niche in both environmental and geographic space (Colwell and Rangel 2009). In the early 2000s, the increasing availability of geospatial data and computational resources led to a rapid expansion of analytical methods and case studies exploring the many uses and caveats of SDMs (Elith and Leathwick 2009). More recently, SDMs have matured to a point where the distributions that they predict have found success in numerous on-the-ground conservation efforts (Guisan et al. 2013). SDMs are now easily implemented thanks to well-tested modeling algorithms (e.g., Elith et al. 2006), ever-increasing accessibility of occurrence information, and software and computational resources that facilitate model fitting and visualization (Thuiller et al. 2009,

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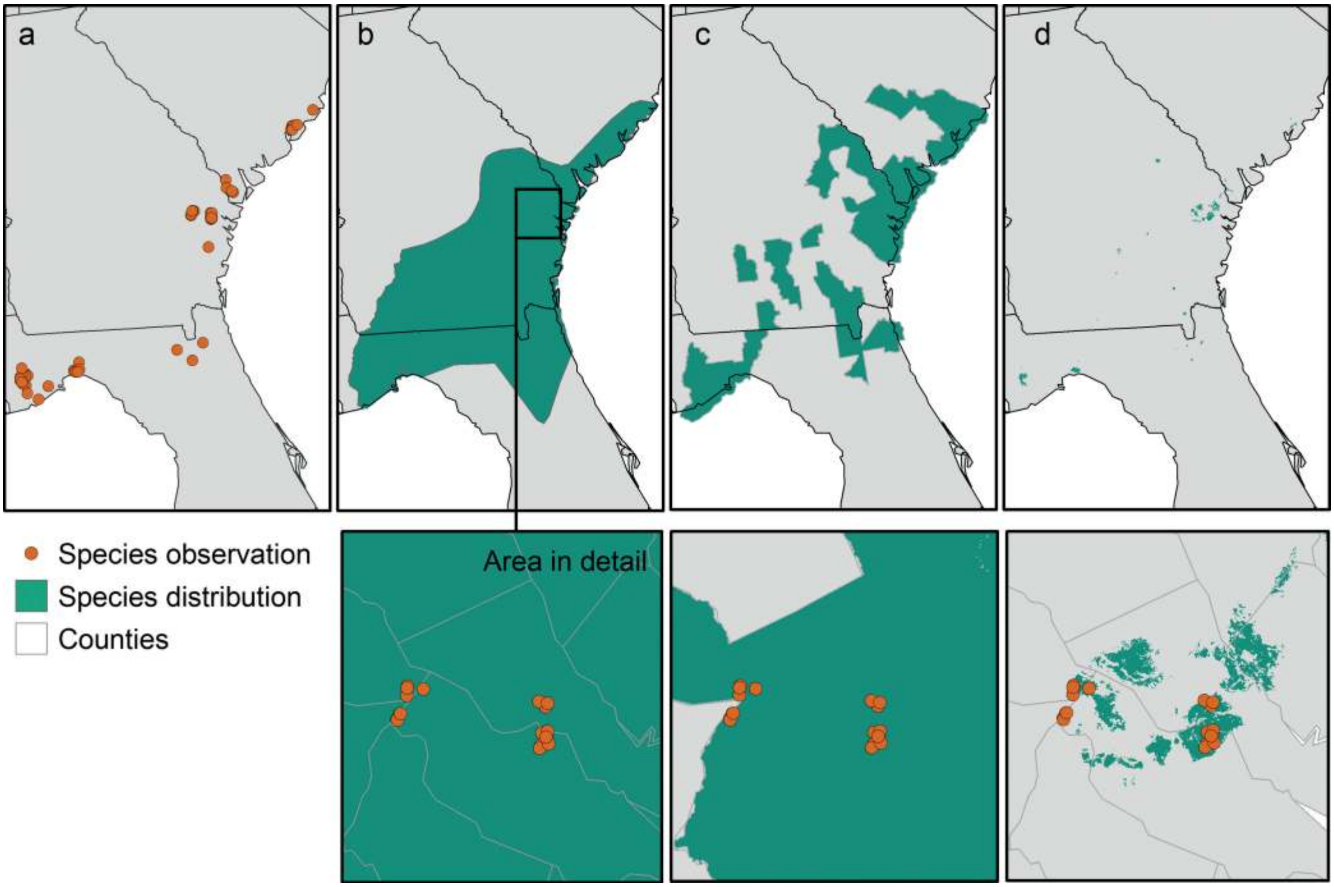

Figure 1. Comparison of data types often used to represent species distributions, shown in the present article for the threatened frosted flatwoods salamander* Ambystoma cingulatum *including (a) species observation points (NatureServe 2017), (b) a range map (International Union for Conservation of Nature et al. 2007), (c) county records (US Fish and Wildlife Service 2018), and (d) predicted suitable habitat from a species distribution model (Florida Natural Areas Inventory 2017).

Morisette et al. 2013, Kass et al. 2018). The distributions produced by SDMs can ameliorate some of the mischaracterizations that arise from biased and sparse sampling of natural populations (Phillips et al. 2009), can provide more localized predictions than maps based on geopolitical boundaries, and can be reproducible in a way that maps based on expert opinion are not. Nevertheless, there remains a need to address SDMs' high sensitivity to data inputs and methodological decisions to ensure that models can effectively and efficiently inform conservation and management decisions across both jurisdictional boundaries and a range of legal and social contexts.

Four major criticisms have been leveled against SDMs that have inhibited their use in management decision-making: First, they are overcomplicated and difficult for a broad audience to interpret. They lack expert intuition, particularly when methodological choices are not rooted in relevant natural history knowledge. Variation in the quality of input data and model-development decisions can result in important differences in the predicted distributions. And careful interpretation of model output is necessary when distinguishing correlative representations of potential (i.e., within a species' niche) versus actual (i.e., currently occupied) distributions (Jiménez-Valverde et al. 2008, Araújo and Peterson 2012, Guisan et al. 2013). The first two criticisms are general to many models, and can be best addressed via clear communication, involving experts and end users in the modeling process, and considering the process of structured decision-making (Addison et al. 2013, Guisan et al. 2013, Morisette et al. 2017). The final two criticisms (sensitivity to data and modeling processes, and issues of interpretation) are methodological concerns that speak to the credibility of a particular SDM and its context-dependent utility.

To be used effectively in decision-making, the entire process used to build any model—including an SDM—must be credible, transparent, and reproducible (Guisan et al. 2013, Villero et al. 2016, Morisette et al. 2017). There are numerous decisions that must be made in estimating and interpreting species distribution models, including those about the input data, modeling processes, and depiction of model outputs (Franklin 2010). Modeled responses to environmental variables and mapped model predictions should be scrutinized and not treated as truth, and performance assessments (including enumeration of strengths and weaknesses) should be clearly documented and communicated. Support for the interpretation of model outputs should be accessible to people that lack technical expertise in species distribution modeling for those products to bear on important decisions.

Here, we establish guidelines for model development and communication to provide a framework for assessing the suitability of a given SDM for a particular purpose. We provide an assessment rubric (table 1a–1d) for evaluating and communicating the quality of SDM inputs and modeling methods. This rubric defines the attributes of models important for end users and provides objective criteria for comparing the context-dependent utility of models produced by different researchers, agencies, or organizations. Referencing the SDM assessment rubric (table 1a–1d), we review the use of SDMs for informing three types of decisions: designing field surveys, prioritizing locations and actions for conservation and management, and supporting regulatory decision-making. We provide examples of how SDMs have been applied in these three common decision categories and emphasize the importance of iterative modeling (reestimating models to incorporate new information) and model validation. The generalities of these three decision categories are highlighted by including use cases covering a range of taxonomic groups, geographies, and spatial extents from the United States.

In considering the use of SDMs in decision-making, it is important to recognize that model outputs alone do not determine outcomes, but are combined with expert knowledge, resource constraints, priorities, and other information to inform decisions. In some cases, SDMs may provide limited added value, often because spatial information on the factors that truly limit distributions is unavailable, or because key threats are not represented within SDM inputs (Tulloch et al. 2016). However, given the many situations where the efficacy of species management and conservation actions would benefit from improved distribution information, the SDM rubric outlined in the present article (table 1a–1d) provides a means of evaluating SDMs and improving communication between modelers and practitioners who could benefit from the information SDMs can provide.

Guidelines for model development and delivery

Guidelines for production of SDMs are important because results are often sensitive to methodological decisions, and the intended uses of an SDM's output can alter the decisions made during model development (Guisan and Zimmermann 2000, Araújo et al. 2019). To determine how much to emphasize a model's output in a given decision-making process, end users need accessible information about how a distribution model was produced, and what it should and should not be used for. Does the model conform to basic SDM standards? Were the environmental predictors selected based on taxon-specific natural history information? Have taxonomic or regional experts reviewed the predicted distribution?

We describe the major steps involved in developing a species distribution model along with criteria to classify modeling inputs and procedures as *interpret with caution*, *acceptable*, or *ideal* (table 1a–1d). The criteria in this table offer a rubric for evaluating the scientific uncertainty of SDMs. A model with some criteria classified as *interpret with caution* may still be useful to guide additional field surveys to support iterative modeling (Wisz et al. 2008) or to gain a qualitative understanding of a species' distribution. Conversely, a single criterion classified as *interpret with caution* may undermine the utility of a model for a given application, particularly when the quality of input data is poor. Model attributes classified as *ideal* are developed using current best practices from the academic literature, but those practices are often beyond the scope of what is feasible given limited time and resources, particularly in many resource management situations. Standards for the quality (i.e., *interpret with caution*, *acceptable*, or *ideal*) of model attributes may be higher for models intended to guide decisions at fine spatial resolutions or with important consequences. Producing user friendly, comprehensive summaries of modeling decisions and their implications for appropriate use is a key part of the development of credible and relevant model outputs.

Choices in model development

It is not our intent to duplicate existing publications that have evaluated modeling choices, such as reviewing importance of inputs (Jarnevich et al. 2015) or comparing different statistical algorithms (Elith et al. 2006). Rather, we reiterate that although there is no "best" modeling method for all contexts (Merow et al. 2014, Qiao et al. 2015), there is general agreement over many aspects of producing SDMs (Araújo et al. 2019). Data quality and quantity matter. This includes the number and precision of presence locations (Graham et al. 2008, Wisz et al. 2008), whether a model relies on background or pseudoabsence information versus higher quality absence data (Barbet-Massin et al. 2012, Guillera-Arroita et al. 2015), and the data's biases, including those associated with detection and sampling. Evaluation metrics are most reliable when derived from independent data (table 1a; Roberts et al. 2017). Predictors are best when they are related to factors that govern the distribution of target species and are geographically and temporally matched to occurrence data (table 1b). The use of ensemble methods and visualizations provide ways to recognize explicitly that no single model is likely to be ideal and instead to integrate outputs from multiple models (table 1c; Araújo and New 2007). Comparing and combining outputs from models produced with different predictors, methods, or assumptions provides a tool for decision-making in the face of uncertainty and has the added benefit of being able to readily

Table 1a. Effects of the quantity and quality of species data on model credibility.

	Interpret with caution	Acceptable	Ideal	References
Presence data	Poor or unassessed quality of data (precision, taxonomy).	Spatial error in coordinates < spatial grain of model. Correction of taxonomic inconsistencies. Confirmation of outlying presences and spatial thinning as needed.	Verified and spatially precise records or weighting of occurrences to place greater emphasis on locations with lower coordinate error.	Graham et al. 2008, Lozier et al. 2009
Absence/ background data	Background data does not mimic sampling bias in presence locations. Background data across much broader extent than presence data.	Sampling of background points to mimic sampling biases in data and/or sensitivity analyses to evaluate effects of different background data sets.	Design-based sampling of both presence and absence locations. Any combination of data sets done in statistically compatible manner. May require explicit modeling of detection biases.	Phillips et al. 2009, Barbet-Massin et al. 2012, Guillera-Arroita et al. 2015
Evaluation data	Based on training data.	Based on cross-validation of training data (spatial cross-validation preferred).	Based on independent data from separate sampling effort.	Roberts et al. 2017, Fourcade et al. 2018

Table 1b. Attributes of environmental predictors affecting model credibility.

	Interpret with caution	Acceptable	Ideal	References
Ecological and predictive relevance	Arbitrary sets of predictors.	Selection of predictors justified based on natural history.	Predictors represent factors known to govern distributional limits or are direct signals of species presence (e.g., remotely sensed indices).	Guisan and Zimmermann 2000, Petitpierre et al. 2017, Fourcade et al. 2018
Spatial and temporal alignment	Poor coverage of environmental variability and relevant geographic area. Temporal alignment of species data and predictors not considered.	Predictors encompass the study area and time period. Resolution of predictors is appropriate given uncertainty and for the focal species.	Training data encompass environmental variability in focal time and place.	Roubicek et al. 2010

Table 1c. Attributes of the modeling process affecting model credibility.

	Interpret with caution	Acceptable	Ideal	References
Algorithm choice	Models prone to overfitting used for extrapolation, goals of prediction versus explanation confounded.	Selection of algorithm aligned with objectives, including need for actual versus potential distribution.	Selection of algorithm aligned with objectives, including need for actual versus potential distribution. Multiple evaluated.	Qiao et al. 2015
Sensitivity	Single algorithm without evaluation of settings. Ensemble of multiple algorithms based on default settings and without assessment of sensitivity.	Assessment of sensitivity to choice of algorithm(s) and selected settings and input data.	Multiple algorithms with evaluation of model settings and input data, model agreement and uncertainties evaluated via ensemble techniques.	Araújo and New 2007
Statistical rigor	Assumptions not recognized or evaluated.	Assumptions recognized and considered.	Assumptions formally evaluated.	Dormann 2007, Dormann et al. 2013
Performance	Based on single metric, and/or evaluation scores are below generally accepted levels.	Multiple metrics evaluated and evaluation scores are close to generally accepted levels, ecological plausibility evaluated.	Multiple metrics evaluated with scores at or above generally accepted levels, scores connected with implications for intended use considered, ecological plausibility is described and supported with data or references.	Jarnevich et al. 2015
Model review	Model released without review or reviewers have potential conflicts of interest.	Review by regional and taxonomic experts, their comments considered in model revisions or in recommendations for its use.	Regional and taxonomic expert review conducted and model updates considered. Reviews and associated metadata transparent, and no potential conflicts of interest.	Guisan et al. 2013
Iterative	No.	Updated based on expert review and other performance assessments. Not updated based on new field observations.	Updated via targeted field sampling and incorporation of new field data into subsequent model iterations.	

Table 1d. Attributes of the model products affecting model credibility.

	Interpret with caution	Acceptable	Ideal	References
Mapped products	Binary, classified, or continuous map produced without clear description to interpret range of values. If a threshold map is produced, a single default threshold used for all applications. Use of 0.5 as a threshold for poorly calibrated models.	Continuous map with clear description to interpret range of values. Thresholds based on test data (e.g., sensitivity equals specificity) but not necessarily linked to intended use.	Continuous predictions mapped with description or used as basis for derived products (e.g., sampling design). Or, threshold selected based on intended use and model assessment, with exploration of sensitivity. Mapping of uncertainties and extrapolation.	Liu et al. 2005, Owens et al. 2013, Guillera-Arroita et al. 2015, Liu et al. 2016
Interpretation support products	None or inadequate to assess key decisions. Little or no description of predictor variables or methods.	Enough information to evaluate every row in this table. Where explanation is a goal, description of variables and their importance.	Information to easily evaluate every row in this table. Where explanation is a goal, description of predictor variable importance and estimated relationships to response for focal variables. Engagement with user community to help define objectives, guide the development and interpret results.	
Reproducibility	Inputs not saved/published, settings from modeling GUI not saved or code not annotated and saved.	Inputs saved and made available (excepting locations of rare species), scripts, settings, and model results archived.	Inputs saved and made available (excepting locations of rare species). Scripts, settings, model results archived. Species expert and modeler identity known.	

assimilate models developed by different stakeholders, if applicable.

The way in which model outputs are provided can be tailored to the intended use, both for individual models and for ensemble models. Using continuous predictive output from models, in which predictions range from 0 to 1, can have advantages over output classified into a binary map, in which each location is defined as either suitable or unsuitable habitat, because this binary conversion entails the loss of information (Guillera-Arroita et al. 2015). However, many applications of species distribution modeling do use the conversion of a continuous mapped surface into a binary map (Liu et al. 2005). This transition is made by considering continuous values above a selected threshold to be potentially suitable. Practitioners can select a threshold that appropriately reflects the context-specific costs of false positives (predicting habitat where there is none) versus false negatives (not recognizing habitat). Therefore, the same continuous model output can be tailored for a specific intended use (figure 2). Threshold choice depends not only on the context but also on the set of models being considered and the degree to which each model may underpredict or overpredict habitat availability.

It is critical to assess model performance and uncertainty in a manner guided by the focal application. For example, even models based on irrelevant predictors can yield reasonable distributions in the region of the training data but will perform poorly if extrapolated to new areas (Fourcade et al. 2018). Tools for quantifying and visualizing model extrapolation are available (Owens et al. 2013), but assessing extrapolation performance requires independent data. Prediction of future range expansion and contraction is similarly challenging, and SDMs may not be reliable for identifying either the species likely to exhibit the greatest change in range size, nor the locations in which such changes may occur (Rapacciuolo et al. 2012, Sofaer et al. 2018). Assessment of models should include computation of performance metrics selected according to the intended use (Jarnevich et al. 2015, Sofaer et al. 2019). For example, minimizing false negatives is likely to be important in ESA consultations, while minimizing false positives may increase success when surveying for the location of new populations. The model assessment should also include an evaluation of ecological plausibility (Elith and Leathwick 2009), ideally based on criteria identified a priori. This will generally be a qualitative assessment by taxonomic and regional experts, focusing on whether modeled relationships between predictor variables and habitat suitability align with knowledge of the species' natural history and physiology, and whether the spatial pattern of predicted suitability reasonably reflects known and likely occurrence locations (table 1c).

Iterative modeling for decision support

An iterative process that reflects collaborations between modelers, species experts, and practitioners can increase model relevance and utility. Using existing occurrence data from open-access repositories and best practices, modelers

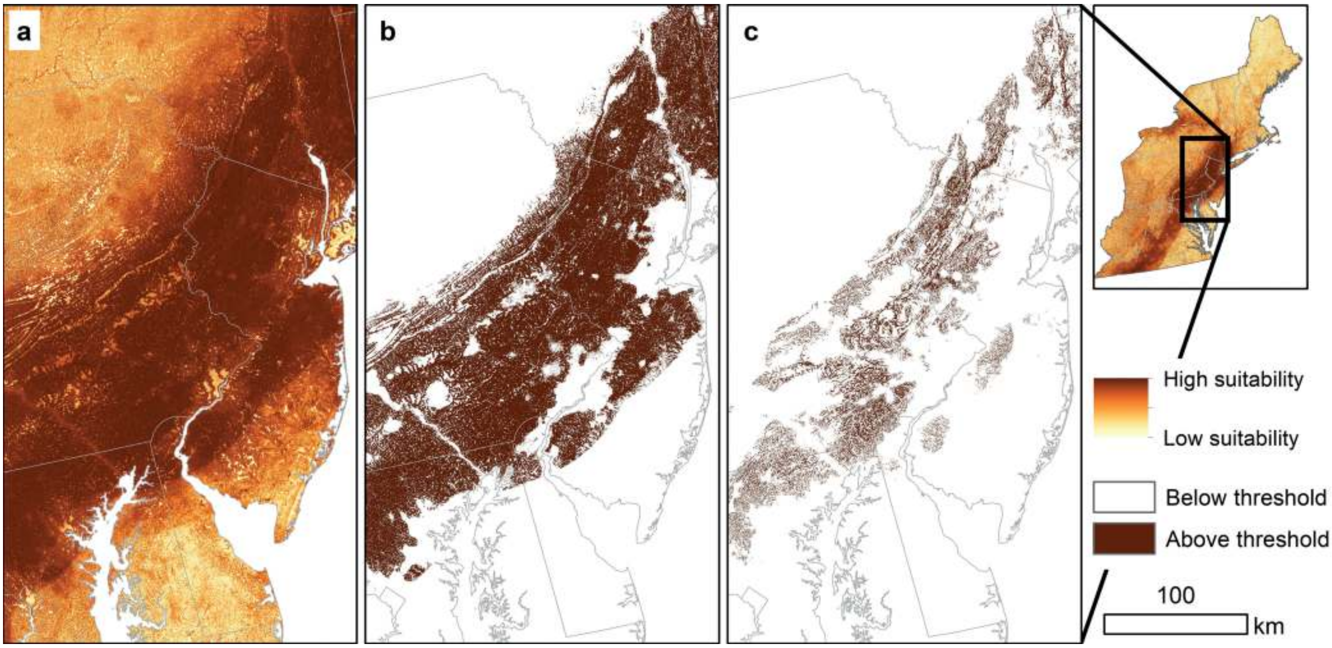

Figure 2. Species distribution map products for the Bog Turtle (*Glyptemys muhlenbergii*), a federally threatened species (New York Natural Heritage Program 2017). (a) Continuous surface showing the full range of predicted habitat suitability. (b) Map with a conservative threshold applied, which includes a higher proportion of the landscape so that potentially suitable sites are unlikely to be missed. (c) Map with a higher threshold applied so that the shaded areas have much higher likelihood of representing suitable habitat.

can often reach the *acceptable* criteria for relatively well-known taxa, such as vascular plants and vertebrates. Moving from *acceptable* to *ideal* will often require the acquisition of new field data and collaborations between species experts, modelers, and end users. Open and clear communication can both improve models and promote uptake of model outputs into decision-making processes (Addison et al. 2013). New field efforts can increase the quantity, relevance, accuracy, and resolution of species and environmental data. Visualizing maps and response curves can help experts understand what aspects of a species' ecology a model appears to have captured appropriately, and expert knowledge of a species' natural and life-history traits can be used to suggest additional or alternative predictors. In turn, iterative modeling can increase understanding of species ecological requirements. Iterative modeling provides a means to move from left to right in table 1a–1d, and to compare the impact of different modeling decisions in the context of the intended use.

Model development for decision support occurs in the context of continual changes in on-the-ground distributions, environmental conditions, information availability, statistical methods, and computational capacity. These ongoing changes present both opportunities and challenges in interpreting model output. How should we interpret modeled distributions in a world where both the models and the reality behind them may be in flux? The frequency of iterative model updates can be related to the timing of management decisions, species' population dynamics, and patterns of environmental variability. Locality information, environmental predictors, modeling methods, summaries of model outputs, and stipulation of appropriate uses can all be updated iteratively. An iterative modeling approach can reflect species' changing distributions, provide a better understanding of key limiting factors, and increase buy-in from experts and end users. Surveys conducted within an iterative modeling process can also target locations of high model uncertainty and disagreement (Crall et al. 2013), and sensitivity analyses can reveal important sources of uncertainty to help guide subsequent field and modeling efforts. New locations—and absence records reflecting nondetections—can then be integrated into subsequent models to refine distributions (figure 3). Decision-making structures based on adaptive management are particularly well poised to benefit from iterative modeling, because clear objectives and recognition of key uncertainties can guide model improvements, and decisions can be revisited as information improves.

Decisions informed by species distribution models

Decisions that can be informed by species distribution modeling generally fall into three categories: designing surveys for new populations and individuals, identifying priority locations and actions for conservation and management, and supporting regulatory decisions and streamlining compliance. The type of decision an SDM is intended to support

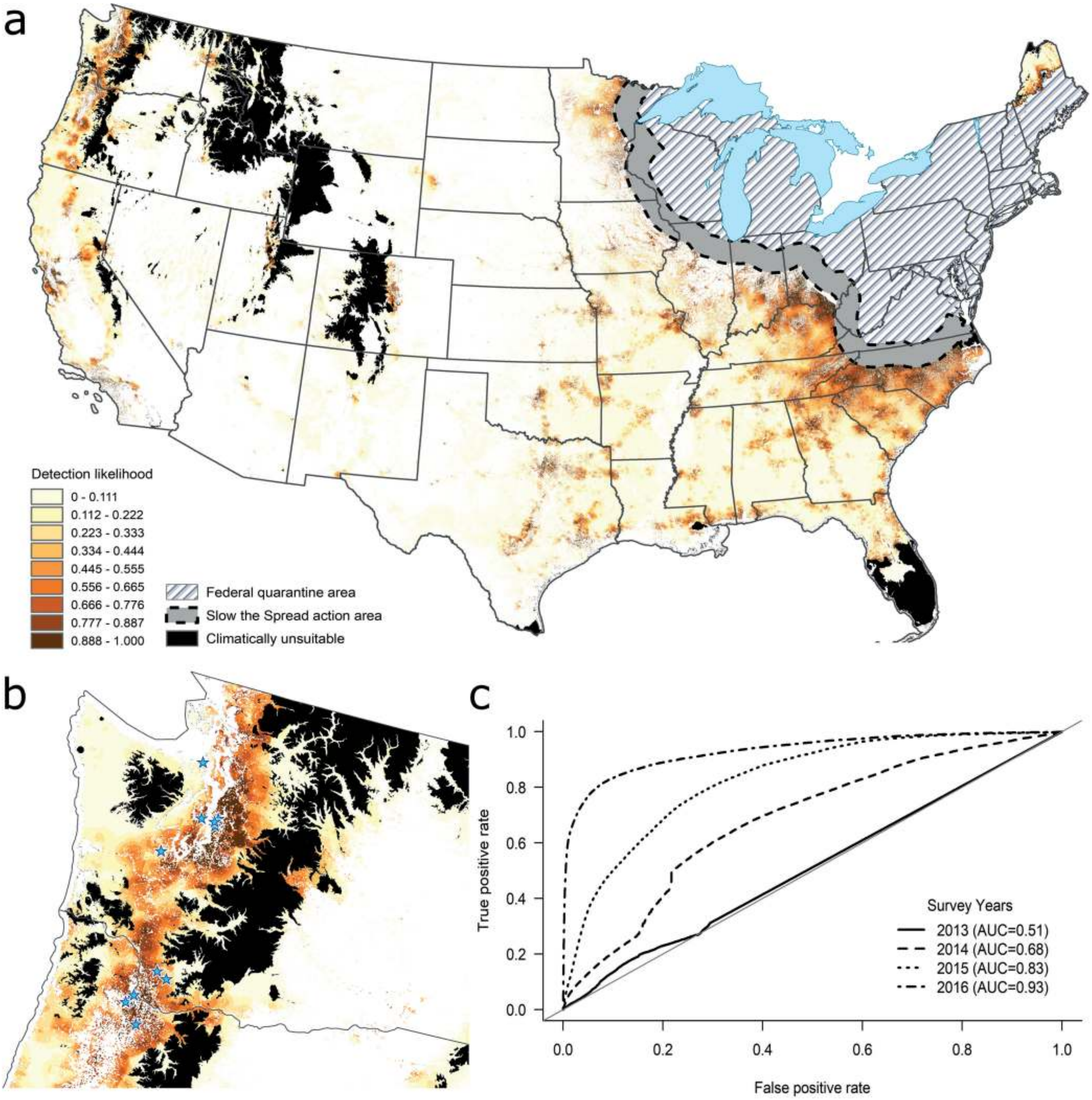

Figure 3. USDA APHIS surveillance efforts for European gypsy moth (*Lymantria dispar dispar*) are guided by a species distribution model that is updated annually. (a) Distribution model output for beyond the federal quarantine and active spread areas for the 2015 survey year. (b) The risk map in the Pacific Northwest, overlaid with subsequent positive detections for that year, shown with stars. The model was used to guide survey effort, and successfully led to the detection of new populations, which were then eradicated. (c) Receiver operating curve showing iterative modeling improved model performance each year; this program exemplifies the operational use of iterative modeling (table 1c). The first model development in 2013 was an expert opinion, GIS-weighted overlay model. This model did not perform better than random (AUC = 0.5) in predicting positive detections. In 2014, the first statistical species distribution model was developed, which divided the study area into two management regions. The next iteration in 2015 explicitly tested spatial stationarity and objectively divided the study into model regions on the basis of changes in the importance of different spread pathways. The most recent model in 2016 retained the 2015 approach, but added the most recent outbreak detections in the Pacific Northwest.

will shape the best practices for model development and interpretation (Guillera-Arroita et al. 2015). Despite these differences related to intended use, there are commonalities about how to rank models that are applicable across taxa and geographies (table 1a–1d). We provide examples of SDMs that have been used to inform these three types of decisions, and we complete an assessment of the quality of those models (table 2a–2d, supplemental table S1) to demonstrate how the SDM rubric summarized in the present article can concisely communicate the credibility of SDMs applied to a variety of species management contexts.

Designing surveys for new populations and individuals

Species distribution models can effectively guide surveys for new populations of rare species (Guisan et al. 2006, McCune 2016). Distribution models have been shown to improve the efficiency of search efforts, with the number of new populations discovered exceeding that from searches guided by expert opinion (Aizpurua et al. 2015). Use of SDMs to discover new or larger populations can lead to delisting petitions under the ESA (Deseret milkvetch *Astragalus desereticus*, 2017 Federal Register 82: 45,779–45,793) or contribute to the decision to not list a species under state and federal endangered species laws. For example, starting with just nine occurrence records, the Wyoming Natural Diversity Database developed an initial SDM for the Wyoming pocket gopher (*Thomomys clusius*) in 2006. The model was used to guide subsequent field surveys, an appropriate use for a model in the *interpret with caution* category because of low sample size (table 1a). New occurrence records were incorporated into a series of model iterations and refinements (Keinath et al. 2014), shifting the models out of *interpret with caution* categories (table 1a, 1d). These field and modeling efforts located 34 new occurrences and contributed to a 2010 decision not to list the species under the federal ESA (2010; Griscom et al. 2010 Federal Register 75:19,592–19,607).

For invasive species, distribution models have been used to inform surveillance efforts for risk assessment and early detection and rapid response (EDRR) programs. For species not yet introduced or established in a given country or region, risk assessments use models of potential distributions to evaluate whether the climatic conditions in the given area may be suitable for the potential invader (Venette et al. 2010). Because these models often include extrapolation to novel regions with new environmental conditions, they are most credible when they are based on a clear understanding of limiting factors for the focal species (table 1b).

Another method to support EDRR is to integrate dispersal vectors as predictors, to reflect propagule pressure. For example, the US Department of Agriculture Animal and Plant Health Inspection Service (USDA APHIS) is charged with preventing the introduction, establishment, and spread of the European gypsy moth (*Lymantria dispar dispar*) into uninfested areas of the United States. APHIS currently develops iterative, annual spread-risk models that forecast the likelihood of detecting gypsy moth outside the federal quarantine area the next survey year (figure 3). Prior to using species distribution models to guide surveillance, field managers relied on state surveyors to interpret guidance from qualitative categories in a program manual to allocate traps to high-risk areas. The first attempt to standardize surveillance nationally was an expert-created, weighted GIS layers model, an approach characterized by low repeatability and performance (table 2a–2d, table S1, figure 3). Poor model performance motivated a second and more objective model iteration: a species distribution model. USDA APHIS collaborated with the US Geological Survey and the USDA Forest Service to develop statistically rigorous and defensible methodologies (table 2a–2d, table S1). The model was regionalized to capture the transitions in mechanisms of spread (natural to human assisted) across space (Cook et al. 2019). In 2015, the risk model correctly predicted an outbreak of gypsy moth in the Pacific Northwest that was subsequently eradicated (figure 3). The surveillance program uses the updated statistical model output to prioritize trap surveillance nationally for the next year, and by utilizing continuous predictions, follows ideal practices for table 1d. The field observations of presence and absence are then used to validate and improve the next year's model, thus improving the quality of the model (table 2a–2d) and successfully integrating iterative modeling into an operational context.

Prioritizing locations and actions for conservation and management

On-the-ground conservation and management requires selecting a set of actions and deciding where on the landscape to implement them. SDMs can be used to understand a species' responses to attributes of land use and land cover that can be influenced by management and inform the selection of management actions. Spatial predictions from SDMs can be used to direct management and conservation actions to priority locations. For example, a model developed by West and colleagues (2017) used remotely sensed indices as environmental predictors within an SDM to predict locations that had high cheatgrass (*Bromus tectorum*) cover in recently burned forest land in Wyoming. In this case, the environmental predictors were chosen to reflect the management need to identify locations with high cheatgrass cover rather than locations with potential for high cheatgrass cover, tailoring the model to its intended use (table 1b). This model used best practices, with no *interpret with caution* classifications (table 2a–2d, table S1), making it suitable for use in guiding the desired management activity: weed control. The Medicine Bow National Forest and Wyoming Game and Fish presented model results to partner agencies and organizations to obtain funding for control efforts and then to guide the resulting aerial herbicide application, with the goal of restoring habitat for native species (figure 4).

There are often relatively high costs associated with management and conservation actions, so model outputs with few false-positive errors can be useful in the context

Table 2a. Example overview of model attributes (intended use) for case studies presented in our figures.

	Flatwoods salamander	European gypsy moth (2013 GIS version)	European gypsy moth (2016 statistical version)	Cheatgrass	Uinta Basin hookless cactus	Bog turtle
Intended use	Incorporation into regional conservation plan to support conservation and management needs for a diverse stakeholder group	Guide APHIS surveillance program	Guide APHIS surveillance program	Guide herbicide application for control	Guide premanagement survey locations in relation to proposed energy extraction locations	To support environmental review conducted by agencies and species recovery efforts

Table 2b. Example overview of model attributes (species data) for case studies presented in our figures.

	Flatwoods salamander	European gypsy moth (2013 GIS version)	European gypsy moth (2016 statistical version)	Cheatgrass	Uinta Basin hookless cactus	Bog turtle
Presence data quality	Ideal	Interpret with caution	Ideal	Ideal	Ideal	Ideal
Absence/ background data	Acceptable	Interpret with caution	Ideal	Ideal	Acceptable	Acceptable
Evaluation data	Acceptable	Interpret with caution	Ideal	Ideal	Ideal	Acceptable
Ecological and predictive relevance	Acceptable	Interpret with caution	Ideal	Ideal	Ideal	Acceptable
Spatial and temporal alignment	Acceptable	Interpret with caution	Ideal	Ideal	Ideal	Acceptable

Table 2c. Example overview of model attributes (modeling process) for case studies presented in our figures.

	Flatwoods salamander	European gypsy moth (2013 GIS version)	European gypsy moth (2016 statistical version)	Cheatgrass	Uinta Basin hookless cactus	Bog turtle
Algorithm choice	Ideal	Interpret with caution	Ideal	Ideal	Ideal	Ideal
Sensitivity	Acceptable	Interpret with caution	Ideal	Ideal	Ideal	Acceptable
Statistical rigor	Acceptable	Interpret with caution	Ideal	Ideal	Ideal	Acceptable
Performance	Acceptable	Interpret with caution	Ideal	Ideal	Ideal	Acceptable
Model review	Ideal	Acceptable	Ideal	Ideal	Ideal	Ideal
Iterative	Acceptable	Interpret with caution	Ideal	Acceptable	Ideal	Acceptable

Table 2d. Example overview of model attributes (model products) for case studies presented in our figures.

	Flatwoods salamander	European gypsy moth (2013 GIS version)	European gypsy moth (2016 statistical version)	Cheatgrass	Uinta Basin hookless cactus	Bog turtle
Mapped products	Acceptable	Interpret with caution	Acceptable	Acceptable	Ideal	Acceptable
Interpretation support products	Ideal	Interpret with caution	Ideal	Ideal	Ideal	Ideal
Reproducibility	Acceptable	Interpret with caution	Ideal	Ideal	Ideal	Acceptable

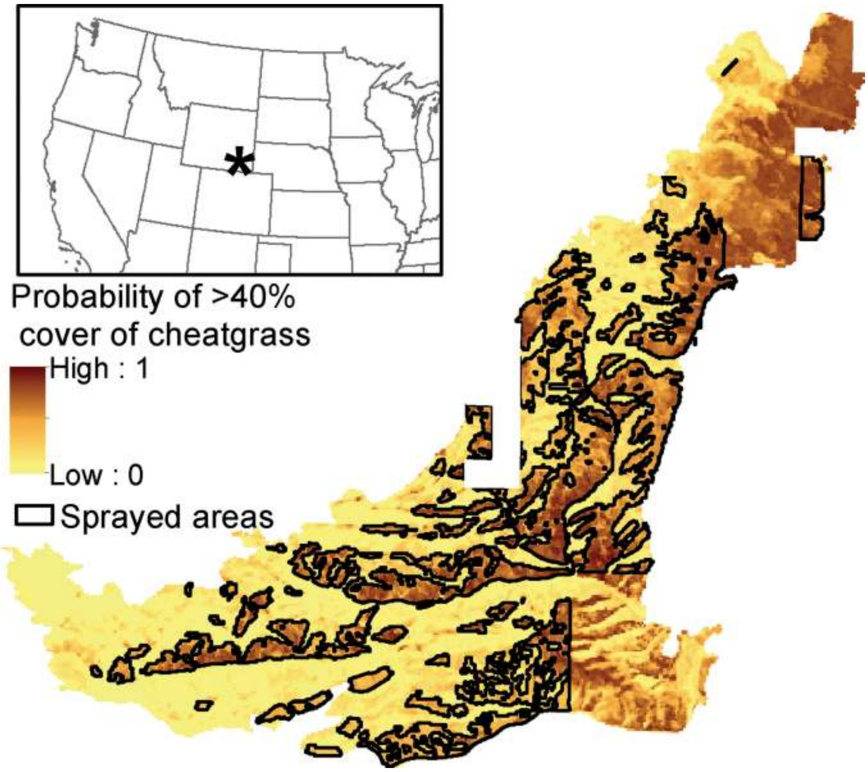

*Figure 4. Probability of cheatgrass (***Bromus tectorum***) cover at least 40% within the boundaries of the Squirrel Creek wildfire in the Medicine Bow National Forest in Wyoming. A species distribution model was created linking field plot data to remotely sensed imagery and topographical indices (West et al. 2017). Model development was based on field-collected absence information (table 1a), included iteration based on expert review (table 1c), and illustrated the appropriate selection of predictors for the desired use because remotely sensed spectral indices captured where the species was abundant (table 1b). The model was used to delineate patches of at least two acres with a up to 50% probability of having cheatgrass cover over 40%, and these mapped outputs were successfully used to guide weed control. Black polygons show areas treated via helicopter application of an herbicide. The entire colored area reflects the fire perimeter, whereas variation in ownership within the burned area also contributed to the boundaries of sprayed polygons.*

of spatial planning (Loiselle et al. 2003). SDMs can provide an efficient means to identify candidate areas for protection and focus inventory efforts to confirm species presence. The costs of implementing management and conservation strategies also make it important to ground-truth modeled distributions (table 1c). Reserve design algorithms have combined outputs from SDMs with information about costs to optimize selection of conservation investments (Moilanen 2005); these methods are flexible in the number of species that can be considered. Similarly, distribution modeling can guide and support green certifications. For New York's state forests, distribution model outputs were used to guide timber harvest strategies and to ensure management compatible with the ranges of rare species. The resulting forest management plans were components of annual reviews by the Forest Stewardship Council and the Sustainable Forestry Initiative, leading to dual sustainability certifications for all state forests in New York (SCS Global Services 2016).

Regulatory decisions and streamlining compliance

Regulatory decisions, such as those governed by the ESA, can be associated with substantial costs and great scrutiny. Knowledge of a species' current distribution is one part of complex analyses designed to evaluate likely persistence, and refined distribution maps can inform multiple aspects of ESA implementation. For petitioned species, SDMs have been used to locate additional populations and estimate the extent of available habitat (Griscom et al. 2010). For listed species, SDMs have been used with other information to evaluate potential effects from proposed land-use actions, assess spatially explicit threats, identify critical habitat, and otherwise direct recovery efforts to areas with optimal conditions for species persistence (Guisan et al. 2013). SDMs have helped streamline initial site assessments in support of consultations under section 7 of the ESA, in which federal agencies assess whether an action they carry out, fund, or permit may affect a listed species. For example, an ensemble of distribution models for the threatened Uinta Basin hookless cactus (*Sclerocactus wetlandicus*) was used to determine where within a proposed energy lease area to require a prelease survey for the species (figure 5, table 2a–2d; Edwards et al. 2016). In this case, because multiple rare plant species are located within an area with high energy potential, SDMs were built for each species and collectively used to guide compliance and siting decisions. Again, given the type of decision, the models used to inform decisions had all attributes classified in the *ideal* or *acceptable* categories (table 2a–2d).

Beyond the ESA, SDMs can also inform other decisions that require compliance. For example, SDMs were one of four lines of evidence used to establish the potential invasiveness of large snakes for the US mainland (Reed and Rodda 2009). This assessment was a key piece of evidence in the regulation of importation and movement of four snake species in the United States (2012 Federal Register 77: 3330). For the Burmese python (*Python bivittatus*), models estimated a broad potential distribution throughout the continental United States (Reed and Rodda 2009, Rodda et al. 2009). This result was challenged by another SDM

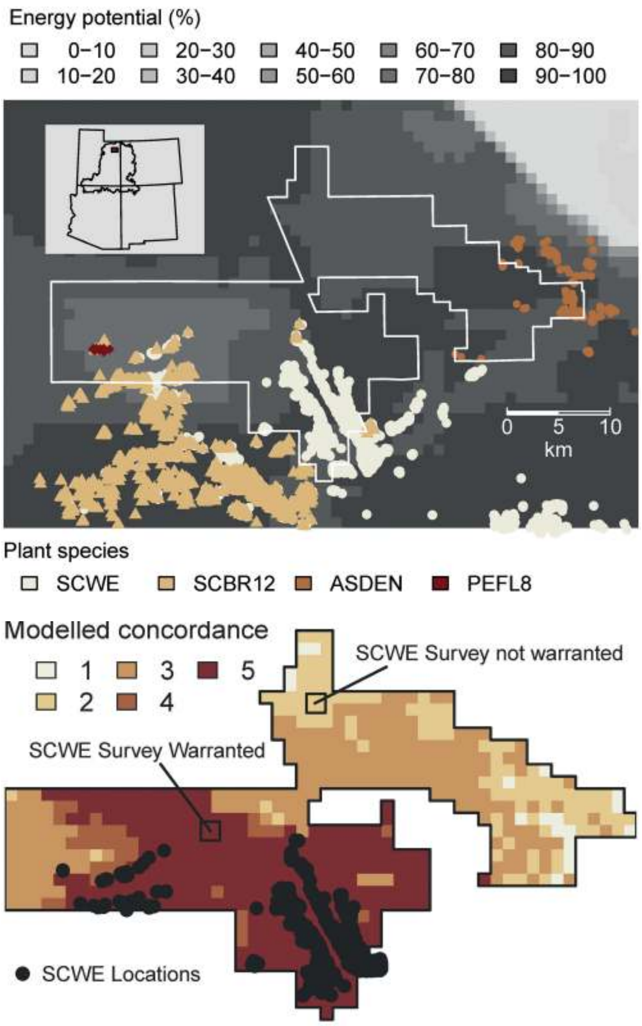

Figure 5. Top panel shows known locations of four rare plant species (SCWE: Uinta Basin hookless cactus **Sclerocactus wetlandicus***; SCBR12: Pariette cactus* **Sclerocactus brevispinus***; ASDEN: Elizabeth's milkvetch* **Astragalus desperatus***; PEFL8: Flowers' beardtongue* **Penstemon flowersii***) in relation to energy potential and the boundary of a proposed energy lease area in the Colorado Plateau ecoregion of western North America (Edwards et al. 2016). The lower panel highlights the use of statistical ensembles (table 1c–d). It depicts the ensemble of five distribution models for the Uinta Basin hookless cactus, a federally threatened species, with maximum concordance (5) indicating all five distribution models predict presence in the same pixel location. Lower concordance values indicate fewer models predict presence at a given location. The concordance is one output from ensemble SDMs that, for this example, can provide the basis for decisions regarding whether prelease surveys for the plant are or are not warranted in a given location within the proposed energy lease area.*

suggesting a much more restricted potential distribution (Pyron et al. 2008). However, evaluating the Pyron and colleagues (2008) model highlighted attributes with an *interpret with caution* classification, including problematic selection of background data (table 1a) and a likely technical issue (overfitting; table 1c). Specifically, Rodda and colleagues (2011) compared models with *interpret with caution* and *acceptable* attributes and showed the choices made by Pyron and colleagues (2008) resulted in underpredicting potential habitat. Such contradictory predictions among models provided a cautionary tale, reinforcing the need for guidelines for developing SDMs, particularly when used for sensitive decisions (Jarnevich and Young 2015).

Moving forward

The examples explored in the present article demonstrate how SDMs have been, and could be, integrated into many types of conservation and management decisions. It is important to continue to improve the transparency and credibility of models used to inform decisions, and to integrate new capacities and innovations into the rubrics that guide model development and assessment (Araújo et al. 2019). Users of model outputs must be able to easily access and interpret information on input data quality, modeling processes, and appropriate use of model outputs. We suggest that model developers produce user-friendly overviews of key data inputs and modeling or methodological decisions that underlie model credibility (e.g., table 1a–1d, table S1). These summaries can provide a framework for assessing model outputs objectively, both for comparisons of multiple models for a single species, and for comparisons of distributional information quality across species. For the models underlying the visualizations shown in the present article, we apply our assessment rubric to provide a quality score for each aspect of the modeling process (table 2a–2d). These models have all been used in guiding management decisions, and the only use of a model with any *interpret with caution* classification was to survey for new locations, which were then used to improve the model via an iterative process.

Two different issues limit the use of SDMs for informing species management decisions: The first is developing credible and repeatable distribution models for many species and the second is accessibility of model inputs and outputs and their respective descriptions. The sheer number of species of management interest is a challenge because model credibility for decision-making benefits from, and may require, species-specific covariate selection, model evaluation, field validation, model iteration, and peer review. Nevertheless, developing credible SDMs for many species could be facilitated by centralized open access repositories for model ingredients, such as validated species occurrence data, tools to filter occurrence data by its quality, and relevant geospatial environmental layers.

Compilation of data inputs is one of the most time-consuming stages of modeling, and information accessibility, rather than biological relevance, often drives selection of data sources. Several repositories for occurrence data exist, with the Global Biodiversity Information Facility (GBIF) being the largest globally, with several nodes such as the US Biodiversity Information Serving Our Nation (BISON). Accessibility of occurrence data and other inputs is a critical component of model reproducibility, although precise locality information for rare and sensitive species may not be made available publicly in many cases. A major need is to develop and make available environmental layers that more directly drive range limits for groups of taxa. In one scenario for efficient and credible modeling, open access repositories of high quality data inputs could be combined with species-specific expertise via collaborations between government agencies, academics, nongovernmental organizations, natural heritage programs, and local stakeholders.

Open access repositories for model inputs and outputs could aid in model evaluation and incorporation into decision-making, just as input data repositories, code repositories (e.g., GitHub), and customizable tools for model fitting and evaluation (e.g., Thuiller et al. 2009, Morisette et al. 2013, Kass et al. 2018) are useful for species-specific and multispecies modeling. For each species, model outputs created by a variety of modelers for diverse purposes could be displayed and compared, along with objective information on the quality of model attributes, as in table 2a–2d and table S1. SDMs already exist for many taxa and geographies, but many are not easily discoverable. Even when discovered, decisions underlying a model's scientific rigor and credibility may not be documented, making it difficult to determine their appropriateness for a management decision. A repository including model output along with an assessment rubric such as the one presented in the present article could facilitate discoverability and interpretation of existing SDMs. Furthermore, it would allow for outputs of models developed via code to be compared and integrated with those developed via graphical user interfaces. A customizable visualization platform could make model outputs more accessible and interpretable to decision-makers, while also accommodating iterative modeling efforts that improve our knowledge over time and maintain the relevance of model outputs in the context of global change.

Conclusions

Species distribution models can provide a repeatable and defensible basis for informing a broad range of species management decisions. The case studies we present in the present article illustrate the use of distribution model output by state and federal government agencies, often reflecting public–private partnerships. There are many opportunities to leverage distribution models more broadly, because many common species management decisions are currently based on subjective, coarse, and incomplete distributional information. We present guidelines for model development and communication, which should enhance the utility of SDMs for decision support, while still enabling decision-makers to determine how model outputs are used and integrated with other information. We encourage model developers to aim for decision quality in their modeling process and to develop user friendly interpretive products that are based on a consistent model evaluation rubric to enhance their applicability to a broader range of users (table 1a–1d). Systematic support for iterative modeling and field validation efforts will improve the quality of available input data and the degree of confidence in model predictions. Continental and global-scale efforts to improve species' occurrence information, available predictors, and computational platforms will increase the efficiency of species–specific model development. The guidelines we present in the present article apply to a broad suite of decisions and can be used to generate credible knowledge of species distributions.

Supplemental material

Supplementary data are available at *BIOSCI* online.

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