Performance metrics and variance partitioning reveal sources of uncertainty in species distribution models

James I. Watling [a],[*], Laura A. Brandt [b], David N. Bucklin [a], Ikuko Fujisaki [a],
Frank J. Mazzotti [a], Stephanie S. Romañach [c], Carolina Speroterra [a]

[a] University of Florida, Fort Lauderdale Research and Education Center, Fort Lauderdale, FL 33314, United States
[b] U. S. Fish and Wildlife Service, Fort Lauderdale, FL 33314, United States
[c] U. S. Geological Survey, Southeast Ecological Science Center, Fort Lauderdale, FL 33314, United States

A B S T R A C T

Species distribution models (SDMs) are widely used in basic and applied ecology, making it important to understand sources and magnitudes of uncertainty in SDM performance and predictions. We analyzed SDM performance and partitioned variance among prediction maps for 15 rare vertebrate species in the southeastern USA using all possible combinations of seven potential sources of uncertainty in SDMs: algorithms, climate datasets, model domain, species presences, variable collinearity, CO_2 emissions scenarios, and general circulation models. The choice of modeling algorithm was the greatest source of uncertainty in SDM performance and prediction maps, with some additional variation in performance associated with the comprehensiveness of the species presences used for modeling. Other sources of uncertainty that have received attention in the SDM literature such as variable collinearity and model domain contributed little to differences in SDM performance or predictions in this study. Predictions from different algorithms tended to be more variable at northern range margins for species with more northern distributions, which may complicate conservation planning at the leading edge of species' geographic ranges. The clear message emerging from this work is that researchers should use multiple algorithms for modeling rather than relying on predictions from a single algorithm, invest resources in compiling a comprehensive set of species presences, and explicitly evaluate uncertainty in SDM predictions at leading range margins.

© 2015 Published by Elsevier B.V.

1. Introduction

Species distribution models (SDMs) have become one of the most important quantitative tools in conservation biology, and are widely used to forecast ecological effects of climate change, assess invasion risk of exotic species, and prioritize conservation activities (Araújo and Peterson, 2012). As a result of the rapid adoption of SDMs in the last decade, several aspects of SDM use and interpretation are actively evolving, including their application in phylogenetic studies and their ability to predict population density (Alvarado-Serrano and Knowles, 2014; Oliver et al., 2012; Pagel and Schurr, 2012). Many SDM studies compare alternative methodological approaches that help reduce or more accurately characterize uncertainty in the analysis of species–environment relationships

(Dormann et al., 2008; Elith et al., 2006; Gritti et al., 2013; Synes and Osborne, 2011). Much progress has been made towards identifying best practices for individual aspects of niche modeling (Braunisch et al., 2013; Dormann et al., 2013; Shirley et al., 2013), but we lack a robust framework with which to compare the relative importance of the many sources of uncertainty in SDMs. Although some patterns may emerge as a result of convergence across many individual studies, factorial experiments provide a unique opportunity to identify sources of uncertainty in SDMs using a common methodological framework.

Uncertainty in SDMs can arise from many sources that can be grouped into two categories: measurement uncertainty and model uncertainty (Elith et al., 2002). Measurement uncertainty arises from imprecision or errors in obtaining data, and can occur when geographic coordinates of species observations are recorded or transcribed incorrectly, or alternative climate datasets use different weather stations, time periods, and interpolation techniques to create climate maps. Model uncertainty arises from assumptions or limitations of simplified models describing complex processes,

* Corresponding author. Current address: John Carroll University, Department of Biology, University Heights, OH 44118, United States. Tel.: +1 954 577 6316.
E-mail address: watlingj@jcu.edu (J.I. Watling).

such as the models describing future climate conditions, or the algorithms describing species–environment relationships. Previous studies have compared individual sources of uncertainty in predictions from SDMs by comparing predictions from different modeling algorithms using a common suite of species and environmental predictors (Elith et al., 2006) or comparing predictions using a common suite of species and algorithms but varying the identity of predictor variables (Watling et al., 2012; Synes and Osborne, 2011). However, relatively few studies have compared multiple factors in a single framework (Buisson et al., 2010; Dormann et al., 2008; Hanspach et al., 2011; Wenger et al., 2013). One previous study comparing four sources of measurement and model uncertainty on one metric of model performance for a single species found that algorithm was the most important source of uncertainty, followed by uncertainty in the occurrence data and collinearity among predictor variables (Dormann et al., 2008).

Here we generalize from previous observations by reporting on a comprehensive analysis investigating seven sources of uncertainty in SDMs for 15 species, using analyses of two model performance metrics and a variance partitioning of SDM prediction maps. Our perspective is that uncertainty in SDMs results in variation in model performance and predictions, with factors contributing most to uncertainty associated with the greatest variation in SDM performance and prediction maps across levels of that factor. The 15 species included in our analysis are all federally listed threatened or endangered terrestrial vertebrates occurring in peninsular Florida. The species vary from range-limited, habitat specialists endemic to a small part of the Florida peninsula, to species with large geographic ranges in both North and South America. Florida is a national biodiversity hotspot (Blaustein, 2008; Knight et al., 2011; Stein, 2002), but is highly urbanized (www.census.gov), has a growing population (University of Florida, 2014), and is at great risk from negative effects of climate change and sea level rise (Benscoter et al., 2013; Nicholls et al., 2008; Reece et al., 2013). Therefore, our pool of species is highly relevant in the context of SDM development for conservation applications.

Uncertainty in SDM prediction maps can influence conservation planning. For example, estimates of environmental suitability from SDMs for four plant species were used to guide a reserve selection exercise in Australia (Wilson et al., 2005). Five alternative methods for interpreting the probabilistic output from SDMs identifying the most suitable areas for species differed in both the identity of locations selected as reserves, and the total reserve area needed to meet pre-defined conservation targets (Wilson et al., 2005). When using SDMs to understand potential responses to species to climate change, uncertainty in future climate conditions can compound uncertainties associated with other factors such as algorithm selection, presence data, and variable collinearity (Wenger et al., 2013).

Uncertainty in climate change effects on species distributions may have a spatial component. For example, it has been suggested that uncertainty in estimates of climate suitability from SDMs may be greater at range margins than range centers, particularly at the 'trailing' range margin (i.e., the southern range margin in the northern hemisphere; Gritti et al., 2013). Variance partitioning approaches compare estimates of environmental suitability in SDM prediction maps on a pixel-by-pixel basis across different maps, and characterize the proportion of variance in estimates of suitability attributable to individual factors (Diniz-Filho et al., 2009). Variance partitioning can be used to describe uncertainty in SDM prediction maps and help identify high-priority areas for specific conservation interventions. For example, areas identified as being very suitable across multiple models (i.e., those with a high certainty of being suitable) may be high-priority targets for future protected areas. On the other hand, trailing range margins currently occupied by an endangered species but uncertain to be suitable in the future

may represent possible targets for ecosystem restoration that could make marginal areas suitable further into the future, increasing the adaptive capacity of species.

We used a factorial framework to analyze model performance and predictions, quantifying seven sources of uncertainty in SDMs: algorithms, contemporary climate datasets, model domain, comprehensiveness of species presences, collinearity of predictor variables, CO_2 emissions scenarios and general circulation models (Table 1). Our analyses of model performance focused on two metrics commonly used to evaluate SDMs: the area under the receiver operating characteristic curve (AUC), and the true skill statistic (TSS). To describe how the seven factors influenced predictions in different portions of the geographic range, we compared variance in SDM predictions in range margins versus range cores and at leading (northern) versus trailing (southern) range margins. All analyses were conducted for 15 federally threatened and endangered vertebrate species occurring in Florida, USA that are the focus of regional conservation planning efforts (Catano et al., 2014).

2. Materials and methods

2.1. Species and environmental data

We used climate data at a spatial resolution of 10 arc-minutes, or 0.167 decimal degrees, the common resolution of the two contemporary climate data sets. Presence data for 15 species were obtained from online databases, the primary literature, and field surveys (Appendix B). Presence data were obtained from throughout the full geographic range of each species or sub-species. For sub-species, presence data for only the federally listed taxon were included. We removed obviously erroneous observations (e.g., observations of terrestrial species from the middle of large ocean basins), dubious records (e.g., records from zoos or other artificial environments), and presences falling far outside the native range of the species. Presences from coastal areas that fell just outside the terrestrial domain of the climate data were snapped to the nearest terrestrial grid cell, and duplicate observations were removed so that one presence per grid cell was retained for analysis. We used only climate data as predictors in all models because incorporating non-climate predictors into climate-only SDMs did little to improve model performance for many of the species reported on here (Bucklin et al., 2015), probably because non-climate variables such as land cover have their greatest effect at relatively small spatial scales (Luoto et al., 2007).

2.2. Sources of uncertainty

We identified seven sources of uncertainty in SDMs (Table 1) that we manipulated in a factorial experiment with 288 unique factor combinations. The factorial experiment allowed us to isolate each factor and quantify its relative impact on performance and spatial predictions from SDMs. We included two factors describing measurement uncertainty: differences in contemporary climate datasets and comprehensiveness of the species presences used for modeling, and five factors describing model uncertainty: algorithms, model domain, variable collinearity, CO_2 emissions scenarios, and general circulation models.

2.2.1. Contemporary climate datasets

We compared two different contemporary climate datasets available at the same spatial resolution (0.167 decimal degrees). Both the WorldClim (Hijmans et al., 2005) and Climate Research Unit (New et al., 2002) data sets provide grids of global climate based on interpolation of data from weather stations. We chose to use monthly climate rather than bioclimate variables (Nix, 1986) because the high-resolution global Climate Research Unit data

Table 1
Seven sources of uncertainty affecting species distribution models.

Uncertainty type	Factor	Factor levels	Source of uncertainty
Measurement	Contemporary climate	Two: Worldclim, Climate Research Unit	Different number of weather stations and interpolation technique
	Species presences	Two: Full, 75% subset	Simulating effects of incomplete presence data
Model	Algorithm	Three: Generalized linear models, random forests, maximum entropy	Alternative functional relationships between species occurrence and environment
	Variable collinearity	Two: Uncorrelated subset, random subset	Differential effects of collinearity among environmental predictors
	Model domain	Two: Target group, geographic range	Differences in the environmental background against which climate used by species is compared
	General circulation model	Three: GFDL, NCAR, UKMO	Alternative descriptions of future climate dynamics for projection of climate change effects
	CO_2 emissions scenarios	Two: A1B, A2	Different assumptions about magnitude of climate change

include monthly mean temperature only, rather than the monthly minimum and maximum temperatures needed to calculate some of the bioclimate variables. Previous work for the same group of species indicated little difference in model predictions between SDM constructed with monthly versus bioclimate data (Watling et al., 2012). Both WorldClim and Climate Research Unit data are widely used for niche modeling, and are available at multiple spatial resolutions. The data sets differ in the time frame over which data were collected and identity of the station data included, as well as the interpolation method used to create the final maps (see Hijmans et al., 2005 for more details on WorldClim-Climate Research Unit comparisons).

2.2.2. Comprehensiveness of species presences

We also investigated the effect of incomplete presence data on SDMs. We compared models created from the most comprehensive set of species presences we could obtain, using data from several sources (see Section 2.1) to a random subset of 75% of presences from the full dataset. Our intent in manipulating the size of the presence dataset used for modeling was to simulate two approaches to compiling existing presence data for SDMs, the first a more time-consuming survey of multiple data sources, including literature records, online databases, museum records and expert consultation, and the other a less in-depth survey of data from a single source that is unlikely to include all records available through a more comprehensive search.

2.2.3. Algorithms

The effects of different algorithms on performance of SDMs has been investigated by many authors, and is widely believed to be among the most important factors determining model performance (Dormann et al., 2008; Elith et al., 2006; Guisan et al., 2007). Many different algorithms are used in SDMs (Franklin, 2009), and we focused on three widely-used algorithms. Generalized linear models (GLMs) use link functions to model non-normal response variables (i.e., a binomial presence/non-presence response) as a function of many predictor variables (McCullugh and Nelder, 1989). Random forests (Breiman, 2001; Cutler et al., 2007) partition a response variable such as presence/non-presence into the most homogeneous subsets possible based on the identification of thresholds in the predictor variables that maximize homogeneity of the response. The process is repeated many times (creating a 'forest' of individual regression trees), and average values of the predictors that best categorize the response variable are calculated. An internal cross-validation procedure evaluates predictions in order to maximize performance as trees are being defined. Finally, maximum entropy modeling (Elith et al., 2011; Phillips et al., 2006) calculates the probability of occurrence of a species by comparing

environmental conditions at sites known to be occupied by the species to environmental conditions throughout the study area.

2.2.4. Model domain

We compared two approaches to defining the model domain for each species, one using a modification of the target group approach (Phillips et al., 2009) and the other using a fixed geographic domain. Variation in size of the geographic domain influences the selection of pseudo-absences when survey-based absence data are unavailable (Lobo et al., 2010), and can have significant effects on model performance (VanDerWal et al., 2009; Wisz and Guisan, 2009). There are many possible approaches to defining the geographic domain from which pseudo-absences are acquired (Barve et al., 2011; VanDerWal et al., 2009), and we selected two of many possible approaches, each of which could have different effects on model performance. First, we used a modification of the target group approach (Phillips et al., 2009) to select pseudo-absences for SDMs. A target group is defined as species that are ecologically similar to, and sampled using similar methods as the species being modeled. The original target group approach used presence data for target group species as pseudo-absences for species models (Phillips et al., 2009). We modified the target group approach by selecting pseudo-absences at random from a domain defined by the minimum convex polygon around the target group presences. The selection criteria for all target groups are documented in Appendix A. In a second approach, we defined the model domain as either the contiguous United States (for Florida endemics and species occurring throughout the southeastern United States) or both North and South America for more widely ranging species.

2.2.5. Collinearity of predictor variables

We examined effects of collinearity among predictor variables (Dormann et al., 2013) by creating models using a subset of relatively uncorrelated predictors (mean variable correlation per species, $r = 0.43 \pm 0.08$ [range: $r = 0.30$–0.58]) to a set of variables selected at random without regard to collinearity. The total pool of predictors included 24 possible variables: 12 variables describing mean monthly temperature and 12 describing mean monthly precipitation. The uncorrelated predictors for each species were obtained using the Biomapper software for ecological niche factor analysis (Hirzel et al., 2002). In Biomapper, we generated a cluster diagram of variable correlations for each species, from which we removed the most correlated variables ($r > 0.85$). We retained the single variable in each cluster that that best differentiated climate at sites where species were present from background conditions, resulting in 3–10 uncorrelated predictor variables for each species (Bucklin et al., 2013). The same number of variables per species was selected for inclusion in the random subset.

2.2.6. CO_2 emissions scenarios

The final two sources of model uncertainty were the CO_2 emissions scenarios and general circulation models (GCMs) used to describe future climate. Because the performance of SDM projections under future conditions cannot be validated, uncertainty in the two factors describing future climate data was only included in the variance partitioning analysis. We compared two CO_2 emissions scenarios (A1B and A2; Table 1) from the Intergovernmental Panel on Climate Change family of scenarios (Nakićenović et al., 2000). We chose the two high CO_2 emissions scenarios because actual CO_2 emissions have far exceeded the lower emissions scenarios, making scenarios such as B1 implausible descriptions of future climate (Peters et al., 2013).

2.2.7. General circulation models (GCMs)

Data on future climate conditions were extracted from a global dataset of statistically downscaled projections of twenty-first century climate change (Tabor and Williams, 2010). We used average projections for the years 2041–2060 from three GCMs (the Geophysical Fluid Dynamics Laboratory Coupled Model version 2.0, the National Center for Atmospheric Research Community Climate System Model version 3.0, and the Hadley Center for Climate Prediction, United Kingdom Meteorological Office coupled model version 3.0). The three GCMs were selected because they were included in a dynamically downscaled projection of regional climate (Stefanova et al., 2012) that we have used for other SDM work.

2.3. Uncertainty analysis

We conducted analyses of model performance and variance partitioning of prediction maps to describe the magnitude of uncertainty associated with factors describing both measurement and model error.

2.3.1. Model performance

The analysis of model performance focused on how five factors describing sources of uncertainty in SDMs (algorithm, climate dataset, model domain, species presences and variable collinearity) affected two metrics of model performance: the area under the receiver operating characteristic curve (AUC), and the true skill statistic (TSS). All metrics were calculated as the mean ± 1 SD of 100 replicate model runs, with each replicate using a unique random partition of the occurrence data into a 75–25% training-testing split.

The AUC measures the tendency for a random presence grid cell to have a greater probability than a random pseudo-absence grid cell (Fielding and Bell, 1997). Models with greater AUC values are better able to discriminate between sites occupied by a species and sites where occupancy is unknown. Although AUC is widely reported as a metric of model performance in SDMs, its interpretation is problematic for several reasons, including its contingency on model domain (Lobo et al., 2007). The TSS, on the other hand, considers both omission and commission errors in a single metric of classification accuracy (Allouche et al., 2006). The TSS ranges from -1 to 1, with values below 0 indicating classification no better than random, and values approaching 1 indicating high classification accuracy. The TSS has been recommended as a better metric of SDM performance than AUC because its value is independent of prevalence (Allouche et al., 2006), although it is less widely used than AUC. Here we report AUC to maintain consistency with previous studies, in addition to the more robust performance metric, TSS.

We used AICc model selection to identify the most parsimonious subset of factors that best explained variation in model performance, considering models in which $\Delta AICc < 2$ to be equivalent to the best-fitting model (Burnham and Anderson, 2002). We ran separate analyses to identify factors explaining variance in AUC and TSS. For each of the two performance metrics, we tested

11 candidate models: a null, intercept-only model, five single-factor models, a model with all five factors and no interaction, and four models with algorithm plus one other factor and their interaction. We did not test all possible combinations of factors because the large number of candidate models was prohibitive. Rather, in light of the importance of algorithm as a source of uncertainty in SDMs (Elith et al., 2006), we focused on candidate models that included an effect of algorithm along with an additional factor.

2.3.2. Variance partitioning

We used a variance partitioning procedure (Diniz-Filho et al., 2009) to quantify uncertainty in prediction maps attributable to each of seven factors (the five sources of uncertainty described for the analysis of model performance, plus effects of CO_2 emissions scenarios and GCMs). For each species, we created 288 prediction maps, each representing a unique combination of levels of the seven factors (3 algorithms $\times$ 2 climate datasets $\times$ 2 model domains $\times$ 2 sets of species presences $\times$ 2 variable collinearity subsets $\times$ 2 CO_2 emissions scenarios $\times$ 3 GCMs). All prediction maps were clipped to the target group extent for the variance partitioning procedure, but we note that results were qualitatively similar when prediction maps were clipped to each species' geographic range. We ran an analysis of variance (ANOVA) on each individual grid cell across the 288 prediction maps, calculating the proportion of the sum of squares attributable to each factor relative to the total sum of squares. After running the ANOVA analysis for all grid cells in the map, we calculated the species-specific mean (± 1 SD) proportional sum of squares for each factor, and mapped the proportions for the entire study area.

We tested two specific hypotheses regarding the spatial structure of uncertainty in SDMs, focusing specifically on the factor that contributed most to uncertainty across all species. First, we tested whether uncertainty was greater at range margins compared with range cores (Gritti et al., 2013). To do that, we used range maps from the International Union for the Conservation of Nature (http://www.iucnredlist.org) to extract cells from each uncertainty map that intersected the geographic range of each species. We compared the average proportion of variance explained by the factor across all cells comprising the perimeter of the species range (the range margin) to all remaining cells (the range core). We used a linear mixed effects model testing for an effect of range location (margin or core) on the average proportion of variance explained by the factor. Species identity was coded as a random effect. We conducted a follow-up test for a latitudinal trend in uncertainty at range margins versus cores. For that analysis, we calculated the difference in the proportion of variance explained by the most important factor at range margins and cores, and used a linear model to relate that difference to the latitudinal midpoint of the geographic range. If either the overall model or the test of latitude indicated a significant difference in uncertainty between range margins and cores, we calculated mean suitability in the area of highest variation for each species to determine whether uncertainty was concentrated in areas of high, medium, or low suitability. We reasoned that relatively high variation may have less impact on conservation decisions if it occurs in areas of uniformly high or low suitability (i.e., suitability values ranging from 0.01 to 0.33 on a scale of 0–1 are variable, but low suitability supersedes high variability in terms of conservation decision-making). We also used a linear mixed effects model to test whether uncertainty was greater at the trailing (southern) margin of the geographic range by comparing the average proportion of variance explained among edge cells located north or south of the midpoint of the geographic range. The geographic range midpoint was estimated as the midpoint between the latitudinal centroid of the northernmost and southernmost grid cells. We also conducted
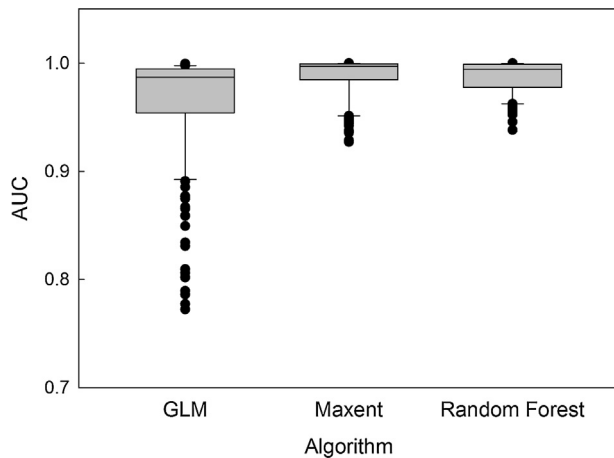
Fig. 1. Boxplots indicating differences in the area under the receiver operating characteristic curve metric of model performance (AUC) among three species distribution modeling algorithms: generalized linear models (GLM), maximum entropy (Maxent) and random forests.

Fig. 2. Differences in the true skill statistic metric of model performance (TSS) among three species distribution modeling algorithms: generalized linear models (GLM), maximum entropy (Maxent) and random forests. Solid lines indicate performance for models constructed using all available presence data, whereas dashed lines indicate performance for models constructed using random subsets of 75% of presence data.

a follow-up test to determine whether there was a latitudinal trend in uncertainty at leading (northern) versus trailing range margins. As before, if either the overall model or the latitudinal test were significant, we assessed suitability across all maps for each species. All statistical analyses were run using the programs SAS (SAS Institute, 2013) or R (R Development Core Team, 2013).

3. Results

3.1. Model performance

For the analysis of SDM performance, we ran 72,000 SDMs (100 replicates × 48 factor combinations × 15 species). There was one best-fit model explaining variance in AUC, and it included the factor describing modeling algorithm (Table 2). Although mean AUC scores were uniformly high, AUC was generally greatest for maximum entropy models and lowest for GLMs. Random forest models had intermediate AUC scores (Fig. 1). Results using TSS as the
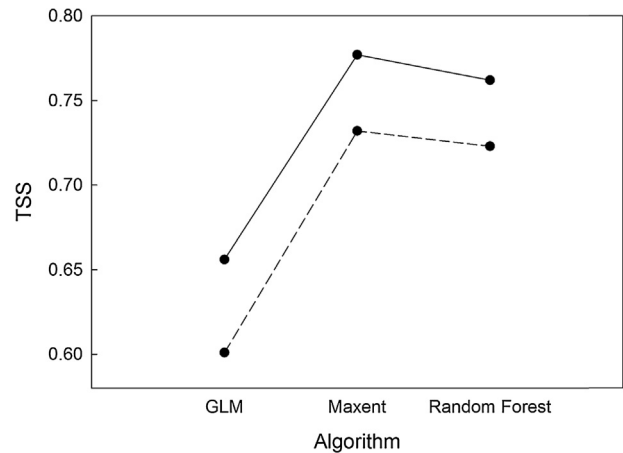
model performance metric were similar to those obtained for AUC, although there were two candidate best-fit models: one including algorithm only, and another including algorithm, presences, and their interaction (Table 2). The effect of algorithm was similar to that seen in the analysis of AUC scores, with TSS greatest using the maximum entropy algorithm, lowest for GLMs, and intermediate for random forests (Fig. 2). The model including the interaction between algorithm and presences indicated that TSS was greater for models including all presences compared with models including a random subset of species presences (Fig. 2). The relative differences among algorithms in the interaction model were as described for the single-factor models.

3.2. Variance partitioning

For the variance partitioning exercise, we ran 12,093–403,832 ANOVAs per species (one for each 0.167° grid cell in each species'

Table 2
Models describing effects of five sources of uncertainty in species distribution models (algorithm, climate, domain, presences, variables) on two model performance metrics (area under the receiver-operator curve, AUC, and the true skill statistic, TSS). Models were compared using the Akaike Information Criterion corrected for small samples (AICc). Delta AICc described the difference between the best-fit model with the lowest AICc value and all other models. The AICc weight describes the probability of each model being the best model for each response variable.

| Variable	Covariate	AICc	ΔAICc	AICc weight
	Algorithm	−3188.9	0.0	0.9996
	Algorithm, domain, algorithm × domain	−3173.2	15.7	0.0004
	Algorithm, presences, algorithm × presences	−3160.8	28.1	<0.0001
	Algorithm, variables, algorithm × variables	−3160.2	28.7	<0.0001
	Algorithm climate, algorithm × climate	−3160.0	28.9	<0.0001
AUC	Algorithm, variables, climate, presences, domain	−3157.9	31.0	<0.0001
	Domain	−3058.3	130.6	<0.0001
	Null	−3058.0	130.9	<0.0001
	Presences	−3047.8	141.1	<0.0001
	Variables	−3047.4	141.5	<0.0001
	Climate	−3047.4	141.5	<0.0001
	Algorithm, presences, algorithm × presences	−623.3	0.0	0.5906
	Algorithm	−622.3	1.0	0.3582
	Algorithm, domain, algorithm × domain	−618.4	4.9	0.0509
	Algorithm climate, algorithm × climate	−606.4	16.9	0.0001
	Algorithm, variables, algorithm × variables	−604.9	18.4	<0.0001
TSS	Presences	−548.3	75.0	<0.0001
	Domain	−541.7	81.6	<0.0001
	Null	−538.8	84.5	<0.0001
	Variables	−532.1	91.2	<0.0001
	Climate	−531.9	91.4	<0.0001
	Algorithm, variables, climate, presences, domain	−531.5	91.8	<0.0001
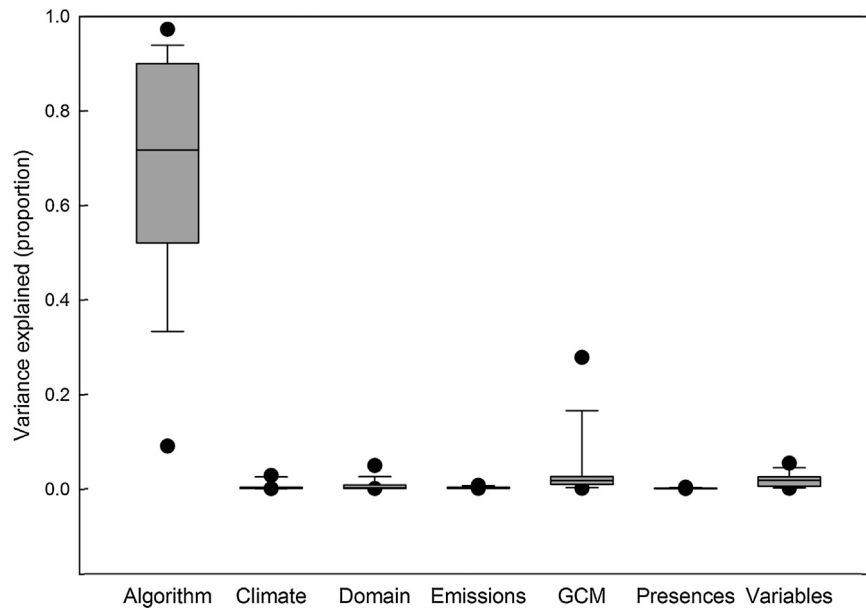
Fig. 3. Boxplots indicating the partitioning of variance associated with seven sources of uncertainty in species distribution models: modeling algorithm, contemporary climate dataset, modeling domain, CO_2 emission scenario, general circulation model, number of presences, and variable collinearity.

target group domain), with 288 replicates each, representing all possible combinations of seven factors. The results were very consistent among species, with almost 70% of variance in spatial predictions attributable to algorithm, between 1 and 5% of variance each attributable to GCM and variable collinearity, and <1% of variance attributable to remaining factors (Fig. 3; Appendix C). Geographic ranges for three species (Florida scrub jay, *Aphelocoma coerulescens*, Florida sand skink, *Neoseps reynoldsi* and Southeastern beach mouse, *Peromyscus polionotus niveiventris*) were all edge, so we were not able to compare the proportion of variance explained by algorithm in range margins versus cores for those species. For the remaining 12 species, the average proportion of variance explained by algorithm was greater in range margins for six species, greater in range cores for four species and equal in range margins and cores for two species (Table 3). Overall, there was no significant difference in the proportion of variance explained by algorithm at range margins ($\bar{x} = 0.31 \pm 0.21$) compared with range cores ($\bar{x} = 0.33 \pm 0.24$; $\chi^2 = 1.23$, df = 1, $P = 0.267$). However, predictions from different algorithms were more variable at range margins than cores for more northerly species ($F_{1, 10} = 16.63$, $P = 0.002$; Fig. 4). Average suitability in range margins varied from 0.20 for the American crocodile, *Crocodylus acutus*, to 0.56 for the Cape Sable seaside sparrow, *Ammodramus maritimus mirabilis*. Mean suitability among all species was 0.40 ± 0.12. The average proportion of variance explained by algorithm was greater at southern range margins for seven species, greater at northern range margins for four species, and equal at northern and southern range margins for one species (Table 3). The difference in variance explained at northern range margins ($\bar{x} = 0.29 \pm 0.17$) versus southern range margins ($\bar{x} = 0.35 \pm 0.28$) was not significant ($\chi^2 = 1.87$, df = 1, $P = 0.172$). However, once again there was a significant effect of latitude on the difference in variability in predictions from different algorithms between northern and southern range boundaries, with greater variability in northern range margins for more northerly species ($F_{1, 10} = 23.87$, $P < 0.001$; Fig. 5). Mean suitability in the northern range margin across all maps ranged from 0.23 in the Bluetail mole skink, *Eumeces egregious lividus* to 0.52 for the Cape Sable seaside sparrow (for all species, mean suitability in northern range margins was 0.40 ± 0.10).
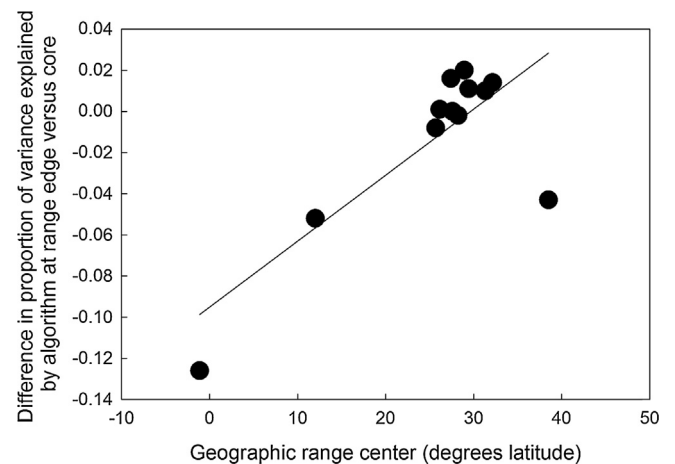

Fig. 4. Differences among algorithms explained more variation in SDM predictions at range margins than range cores for species with northern distributions. Values along the y-axis increase when the proportion of variation explained by algorithm in range margins was greater than in range cores.

4. Discussion

Our comprehensive uncertainty analysis indicated that modeling algorithm had by far the greatest effect on SDM performance and spatial predictions. Algorithm was the factor most associated with variance in AUC, was included in both top models for TSS, and explained much more variation in SDM prediction maps than any other factor. The contribution of algorithm to SDM performance has been reported on widely, with many studies comparing multiple algorithms using a standard suite of presence data and environmental predictors (Elith et al., 2006; Jaeschke et al., 2012; Muñoz and Felicísimo, 2004; Oppel et al., 2012). As a result of published methods comparisons (Elith et al., 2006; Tsoar et al., 2007), some algorithms have largely fallen out of favor for constructing SDMs (i.e., early bioclimate algorithms such as BIOCLIM; Booth et al., 2014; Nix, 1986). Among recent comparisons, random forests have been frequently cited as a high-performance algorithm (Elith

Table 3
Summary of variance partitioning for 15 species of threatened and endangered vertebrate species in the southeastern USA. The proportion of variance associated with each of seven factors (columns 3–9) across 288 prediction maps in each species' target group domain (determined individually for each species as the least convex polygon encompassing occurrences of ecologically similar species). Columns 10–11 compare variance associated with differences among three algorithms (generalized linear models, maximum entropy, and random forests) in geographic range margins and cores, and columns 12–13 compare variance among algorithms at northern and southern range margins. Ranges for three species were all edge, so geographic range analyses were not performed.

| Species		Target group analyses							Geographic range analyses			
Scientific name	Common name	Algorithm	Climate	Domain	CO$_2$ emissions scenario	GCM	Presences	Variables	Margin	Core	Northern margin	Southern margin
Ambystoma cingulatum	Flatwoods salamander	0.09	0.03	<0.01	<0.01	0.28	<0.01	<0.01	0.02	0.01	<0.01	0.04
Ammodramus maritimus mirabilis	Cape Sable seaside sparrow	0.97	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.39	0.40	0.37	0.42
Ammodramus savannarum floridanus	Florida grasshopper sparrow	0.52	<0.01	<0.01	<0.01	0.09	<0.01	0.02	0.21	0.21	0.22	0.19
Aphelocoma coerulescens	Florida scrub jay	0.70	<0.01	0.01	<0.01	0.02	<0.01	<0.01	NA	NA	NA	NA
Charadrius melodus	Piping plover	0.72	<0.01	<0.01	<0.01	0.03	<0.01	0.05	0.28	0.32	0.29	0.26
Crocodylus acutus	American crocodile	0.86	<0.01	<0.01	<0.01	0.01	<0.01	0.02	0.71	0.77	0.64	0.85
Drymarchon corais couperi	Eastern indigo snake	0.72	<0.01	<0.01	<0.01	0.02	<0.01	<0.01	0.28	0.26	0.31	0.23
Eumeces egregius lividus	Bluetail mole skink	0.50	<0.01	<0.01	<0.01	0.02	<0.01	0.02	0.41	0.40	0.39	0.44
Mycteria americana	Wood stork	0.76	<0.01	<0.01	<0.01	0.04	<0.01	0.02	0.63	0.75	0.51	0.92
Neoseps reynoldsi	Florida sand skink	0.92	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	NA	NA	NA	NA
Peromyscus polionotus niveiventris	Southeastern beach mouse	0.71	<0.01	<0.01	<0.01	0.02	<0.01	0.03	NA	NA	NA	NA
Picoides borealis	Red-cockaded woodpecker	0.50	0.02	0.049	<0.01	<0.01	<0.01	0.04	0.24	0.23	0.19	0.33
Polyborus plancus audubonii	Audubon's crested caracara	0.69	<0.01	<0.01	<0.01	0.03	<0.01	0.03	0.17	0.15	0.16	0.17
Puma concolor coryi	Florida panther	0.91	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.32	0.31	0.32	0.32
Rostrhamus sociabilis plumbeus	Everglades snail kite	0.9	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.06	0.06	0.11	0.02
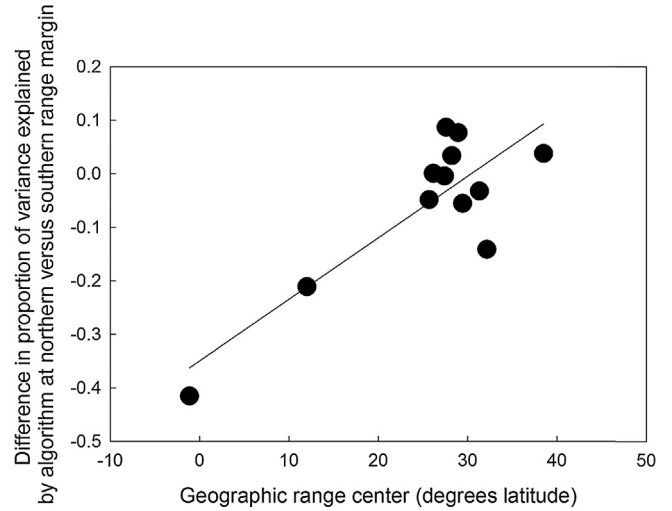
Fig. 5. Differences among algorithms explained more variation in SDM predictions at northern (leading) range margins compared with southern (trailing) range margins for species with northern distributions. Values along the y-axis increase when the proportion of variation explained by algorithm in northern range margins was greater than in southern range margins.

et al., 2008; Kampichler et al., 2010; Valle et al., 2013). Although still evolving, niche models constructed using Bayesian and other approaches (Royle et al., 2012) may one day outperform machine learning algorithms such as maximum entropy and random forests (Fitzpatrick et al., 2013).

The clear implication of the factorial experiment we conducted is that users should compare results from multiple algorithms when constructing SDMs, and use a subset of the highest-performing algorithms for extrapolation. Advances in the software used for modeling make it possible to run models for many algorithms in a single package (e.g., the BIOMOD package for R statistical software, which can create prediction using 10 different algorithms, Thuiller et al., 2014). Given the overwhelming importance of algorithm demonstrated in this and other studies, use of a single algorithm without explicitly comparing its performance to others may easily lead to spurious predictions. Ensembles of high-performing algorithms often have higher performance than any one component algorithm (Marmion et al., 2009). However, even high-performing algorithms may have different characteristic behaviors when extrapolated in space and time. For example, maximum entropy can be prone to overprediction (Fitzpatrick et al., 2013), whereas random forest models often have high specificity (Bucklin et al., 2015). It is probably best to use a subset of multiple algorithms for which preliminary model performance metrics indicate high performance for the species being modeled (Marmion et al., 2009).

A previous study compared uncertainty associated with four factors: the reliability of the occurrence data, collinearity among environmental predictors, algorithm, and variable selection techniques on SDM predictions for the Great Grey Shrike (Lanius excubitor) in east-central Germany (Dormann et al., 2008). For that one species in a relatively small region (~17,000 km^2), differences among algorithms contributed to approximately 50% of the variation in model performance (AUC), with differences in the reliability of occurrence data and variable collinearity explaining most of the rest of the variation in AUC in roughly equal proportions. Alternative variable selection approaches contributed negligibly to differences in AUC in that study. Our results are consistent with those of the previous study (Dormann et al., 2008) insofar as we also found that algorithm explained most of the variance in SDM performance. However, our study of 15 species and seven sources

of uncertainty revealed that factors other than algorithm explained relatively little variation in SDMs, especially in the analysis of prediction maps. Although the species pool used for our analyses is relevant from the perspective of applied conservation, more work with different species in varying geographical contexts is needed to generalize the results of the current study.

In contrast with the overwhelming effect of algorithm on SDM performance and predictions, many putative sources of uncertainty contributed little to variation among model runs in the experiment. For example, several recent studies have focused on variable collinearity as a major source of uncertainty in SDMs (Braunisch et al., 2013; Cruz-Cárdenas et al., 2014; Dormann et al., 2013; Heikkinen et al., 2006). Machine learning algorithms may be more tolerant of collinearity than other modeling methods (Dormann et al., 2013), so we may have seen greater effects of collinearity if we had used a different group of algorithms for comparison. Nonetheless, regardless of the algorithm used, it is best to take precautions against collinearity, and simply using a single variable to represent multiple correlated variables can be a good approach (Dormann et al., 2013). Another well-known source of variation in SDMs is different descriptions of future climate. A previous study suggested that high variation in SDM predictions among GCMs precluded the ability to evaluate alternatives associated with different CO_2 emissions scenarios (Real et al., 2010). Our study suggests that even more caution is necessary when evaluating alternative future conditions, because differences in spatial predictions among GCMs and emissions scenarios are swamped by differences among algorithms.

We found that the number of presence observations included in models was a factor, along with algorithm, in one of two candidate best-fit models explaining variance in TSS. We found that models constructed from a random subset of 75% of all species presences had lower performance than models using the full presence dataset (Fig. 2). The decrease in TSS was consistent among algorithms. A previous study investigating variously sized subsets of presence data for rare species in California found that even models using 50% of presences performed comparably to models constructed with the complete training dataset (Hernandez et al., 2006). The same study found that different algorithms responded somewhat differently to variation in the size of the presence dataset used for SDM training. It is possible that the more dramatic decline in TSS seen in the reduced models we created may be a result of smaller initial sample sizes for some of the species we tested (nine out of 15 species in the current study had fewer than the minimum 150 presences used in the California study; Hernandez et al., 2006). It is also possible that the effects of presence subsets are more apparent using the TSS performance metric. Presences were not a factor in best-fit models for AUC in our study. Few studies report results using TSS, however, so it is difficult to know how our observations compare with other comprehensive studies. Given the potential importance of species presences observed in this study, and the possibility of erroneous predictions resulting from sampling bias in the presence data (Fourcade et al., 2014; Phillips et al., 2009), we suggest that care be invested in compiling the most robust presence datasets possible.

We found that variation in SDM predictions at range margins, particularly leading (northern) range margins, was greater for northern species compared with southern species. Climate suitability in northern range margins was moderate, averaging 0.42 ± 0.09 among all species. The observation that different algorithms vary in their predictions at the leading end of the geographic ranges in areas of moderate suitability suggests potential ambiguity when using SDMs to forecast climate-induced range shifts for northern species. High variability around a value (0.42) near the middle of a distribution (suitability ranges from 0 to 1) suggests that some maps will predict high suitability in the northern range margin, and others will predict low suitability, resulting in a moderate estimate

of suitability, on average. If we consider the scenario just described when using SDM prediction maps to locate new protected areas in areas of high future suitability for species at risk for negative effects of climate change (Carroll et al., 2010), we can see that the optimal reserve design may be highly contingent on the algorithm used to estimate suitability. It is important to select a subset of high-performing algorithms when using SDMs for conservation decision-making, and consider average predictions across an ensemble of models to reduce uncertainty (Marmion et al., 2009). However, this study suggests that even high-performing algorithms can vary in their spatial predictions, with high uncertainty concentrated in leading range margins for species with more northern distributions. We note that although we documented greater uncertainty in prediction maps at leading range margins for species with more northern distributions, the species we modeled are concentrated in the southern USA, and we do not know if the latitudinal trends we describe here apply to species in the rest of the country.

4.1. Conclusions

In summary, our comprehensive factorial experiment identified modeling algorithm as the most importance source of uncertainty in performance and predictions from SDMs, outstripping importance of other factors such as the choice of GCM or CO_2 emissions scenario. There was also an indication that the comprehensiveness of the presence dataset used for modeling can consistently influence performance of SDMs. The results of this study suggest that SDM users will be well-served by (1) use multiple algorithms for modeling rather than relying on predictions from a single algorithm, (2) compiling the most comprehensive dataset of species presences possible, acquiring records from multiple sources including the primary literature, expert consultation, and multiple museum databases, and (3) explicitly evaluating uncertainty in SDM predictions at leading range margins. When using SDMs for spatial prioritization of conservation actions, it is best to describe environmental suitability based on areas where predictions from multiple algorithms intersect, given the wide variation in spatial predictions from different algorithms.

Acknowledgments

Appendix A.

Target group definition of the modeling domain for 15 species of threatened or endangered terrestrial vertebrate species in the southeastern USA. Shapefiles of target group masks are available upon request from the first author.

We used a modification of the target group approach (Phillips et al., 2009) to define an ecologically relevant domain for model development because recent work has shown that predictions from climate envelope models may be affected by the arbitrary selection of modeling domain (VanDerWal et al., 2009). Briefly, the target group approach specifies that the 'absence' data used to define species-environment relationships be obtained using presences of ecologically similar species sampled using similar methods as the focal species being modeled (Phillips et al., 2009). In order to

keep the number of 'absences' used for modeling constant across species (using the commonly-invoked number of 10,000 pseudo-absences), we modified the target group approach. Rather than using target group occurrences as 'absences' in our species models, we compiled the occurrences of target group species, drew a minimum convex polygon around those absences, and sampled 10,000 pseudo-absences at random within the minimum convex polygon.

We defined the target group area for the Florida panther as the composite range of all New World felids. The target group for the Cape Sable seaside sparrow was defined as the full range of *A. maritimus*, for the Florida grasshopper sparrow as the range of full species *Ammodramus savannarum*, for the Florida scrub jay as the composite range of all *Aphelocoma* spp, for the piping plover as the composite range of all New World species of the genus *Charadrius*, for the wood stork as the composite range of New World storks (family Ciconiidae), for the Audubon crested caracara as the combined range of the northern and southern caracara (*Caracara cheriway* and *Caracara plancus*), for the Everglades snail kite as all New World species of the subfamily Milvinae, for the whooping crane as the composite range on New World species of the suborder Grui (e.g., the New World cranes, limpkins and trumpeters), and the red-cockaded woodpecker as the composite range of closely-related *Picoides villosus* and *P. albolarvatus* based on a recent *Picoides* phylogeny (Weibel and Moore, 2002). The target group range for the American crocodile was defined as the composite range of all New World crocodilians, for the bluetail mole skink and sand skink as North American species of the *Eumeces + Neoseps* clade from a recent skink phylogeny (Brandley et al., 2005), and for the eastern indigo snake as the composite range of closely related species (*Coluber constrictor, Spilotes pullatus, Phyllorynchus decurtatus, Masticophis flagellum* and *Drymarchon corais*) as determined from two recent phylogenies (Lawson et al., 2005; Alfaro et al., 2008).

We chose more exclusive taxonomic groupings for the definition for some species because the family-level range would result in a domain covering most of the Western Hemisphere, an area much larger than the observed range of the species. Georeferenced observations of all target group species were obtained from a single online database (the Global Biodiversity Information Facility, www.gbif.org), data were preprocessed as described above, and the 100% minimum convex polygon defining each target group was calculated.

References

Alfaro, M.E., Karns, D.R., Voris, H.K., Brock, C.D., Stuart, B.L., 2008. Phylogeny, evolutionary history, and biogeography of Oriental-Australian rear-fanged water snakes (Colubroidea: Homalopsidae) inferred from mitochondrial and nuclear DNA sequences. Molecular Phylogenetics and Evolution 46, 576–593.

Brandley, M.C., Schmitz, A., Reeder, T.W., 2005. Partitioned Bayesian analyses, partition choice, and the phylogenetic relationships of scincid lizards. Systematic Biology 54, 373–390.

Lawson, R., Slowinski, J.B., Crother, B.I., Burbrink, F.T., 2005. Phylogeny of the Colubroidea (Serpentes): new evidence from mitochondrial and nuclear genes. Molecular Phylogenetics and Evolution 37, 581–601.

VanDerWal, J., Shoo, L.P., Graham, C., Williams, S.E., 2009. Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? Ecological Modelling 220, 589–594.

Weibel, A.C., Moore, W.S., 2002. Molecular phylogeny of a cosmopolitan group of woodpeckers (Genus *Picoides*) based on *COI* and *cyt b* mitochondrial gene sequences. Molecular Phylogenetics and Evolution 22, 65–75.

Appendix B.

The number and source of species observations used for model construction is included in the following table:

Species	N	Source								
		GBIF	BERDS	ORNIS	HerpNet	Zip Code Zoo	FLMNH	Literature	Field observations	FWRI
Mammals										
Florida panther	109	4				3		14		88
Southeastern beach mouse	14	2					6	6		
Birds										
Cape Sable seaside sparrow	17			2		2		13		
Florida grasshopper sparrow	26	4						22		
Florida scrub jay	209	122		3				1		83
Piping plover	867	749				95		23		
Wood stork	1601	1464		125				12		
Audubon crested caracara	162	149				13				
Everglades snail kite	106	106								
Red-cockaded woodpecker	531	531								
Amphibians and reptiles										
Flatwoods salamander	9	4						5		
American crocodile	124	37	2		1			72	12	
Bluetail mole skink	20									20
Sand skink	21	10				2		9		
Eastern indigo snake	278	3						275		

GBIF: Global Biodiversity Information Fund: www.gbif.org.
Zip Code Zoo: www.zipcodezoo.com.
FWRI: Fish and Wildlife Research Institute: research.myfwc.com.
MANIS: Mammal Networked Information Service: www.manisnet.org.
BERDS: Biodiversity and Environmental Resource Data System of Belize: www.biodiversity.bz.
HerpNet: www.herpnet.org.
ORNIS: Ornithology Networked Information Service: www.ornisnet.org.
FLMNH: Florida Museum of Natural History: www.flmnh.ufl.edu.

Appendix C.

Maps for 15 species of threatened or endangered terrestrial vertebrate species in the southeastern USA illustrating the proportion of variance in species distribution model predictions attributable to differences among three modeling algorithms: generalized linear models, maximum entropy, and random forests. The model domain illustrated used a mask created by clipping the smaller of two layers: the target group training area, or the fixed extent area for each species model. Each species' geographic range is indicated by a black outline.

Variance attributable to algorithm

Low   High
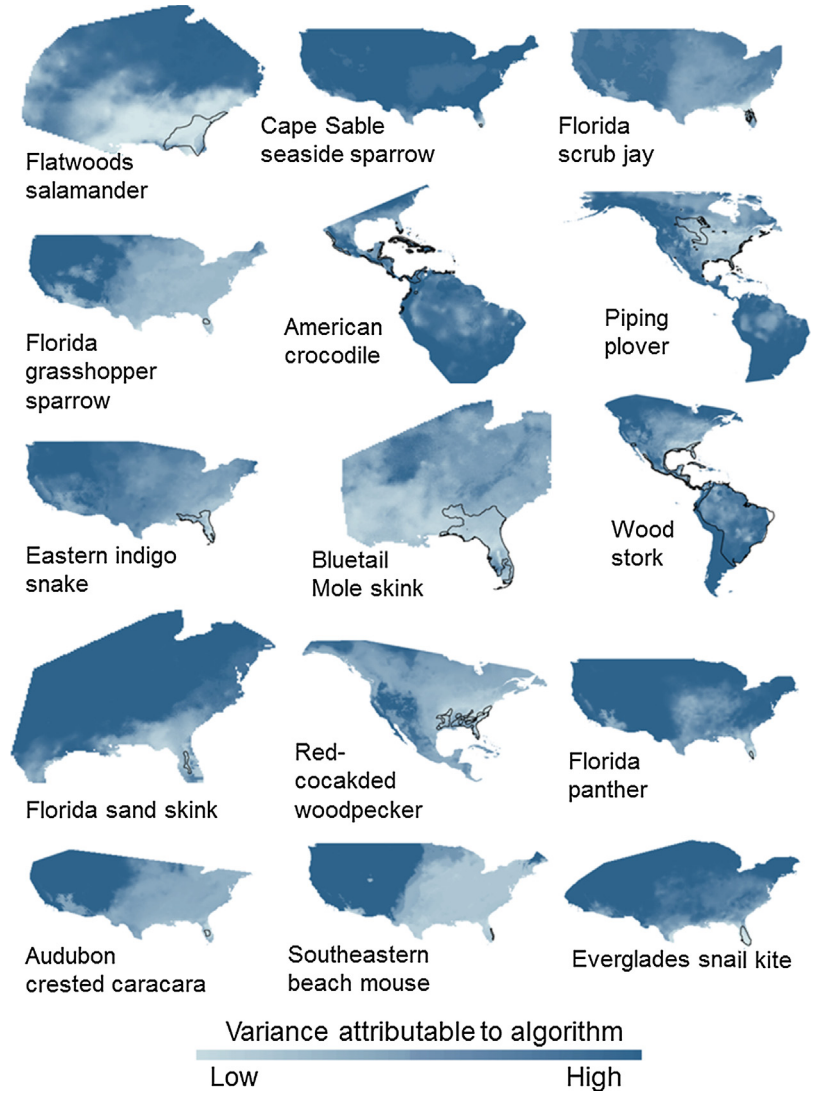
References

Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J. Appl. Ecol. 43, 1223–1232.

Alvarado-Serrano, D.F., Knowles, L.L., 2014. Ecological niche models in phylogeographic studies: applications, advances and precautions. Mol. Ecol. Resour. 14, 233–248.

Araújo, M.B., Peterson, A.T., 2012. Uses and misuses of bioclimatic envelope modeling. Ecology 93, 1527–1539.

Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S.P., Peterson, A.T., Soberón, J., Villalobos, S., 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecol. Model. 222, 1810–1819.

Benscoter, A.M., Reece, J.S., Noss, R.F., Brandt, L.A., Mazzotti, F.J., Romañach, S.S., Watling, J.I., 2013. Threatened and endangered subspecies with vulnerable ecological traits also have high susceptibility to sea level rise and habitat fragmentation. PLoS ONE 8, e70647.

Blaustein, R.J., 2008. Biodiversity hotspot: the Florida panhandle. Bioscience 58, 784–790.

Booth, T.H., Nix, H.A., Busby, J.R., Hutchinson, M.F., 2014. BIOCLIM: the first species distribution modelling package, its early applications and relevance to most current MaxEnt studies. Divers. Distrib. 20, 1–9.

Braunisch, V., Coppes, J., Arlettaz, R., Suchant, R., Schmid, H., Bollman, K., 2013. Selecting from correlated climate variables: a major source of uncertainty for predicting species distributions under climate change. Ecography 36, 971–983.

Breiman, L., 2001. Random forests. Mach. Learn. 45, 15–32.

Bucklin, D.B., Basille, M., Benscoter, A.M., Brandt, L.A., Mazzotti, F.J., Romañach, S.S., Speroterra, C., Watling, J.I., 2015. Comparing species distribution models constructed with different subsets of environmental predictors. Divers. Distrib. 21, 23–35.

Bucklin, D.B., Watling, J.I., Speroterra, C., Brandt, L.A., Mazzotti, F.J., Romañach, S.S., 2013. Climate downscaling effects on predictive ecological models: a case study for threatened and endangered vertebrates in the southeastern United States. Reg. Environ. Change 13, 57–68.

Buisson, L., Thuiller, W., Casajus, N., Lek, S., Grenouillet, G., 2010. Uncertainty in ensemble forecasting of species distribution. Glob. Change Biol. 16, 1145–1157.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information–Theoretic Approach. Springer, New York, USA.

Carroll, C., Dunk, J.R., Moilanen, A., 2010. Optimizing resiliency of reserve networks to climate change: multispecies conservation planning in the Pacific Northwest, USA. Glob. Change Biol. 16, 891–904.

Catano, C.P., Romañach, S.S., Beerens, J.M., Pearlstine, L.G., Brandt, L.A., Hart, K.M., Mazzotti, F.J., Trexler, J.C., 2014. Using scenario planning to evaluate the impacts of climate change on wildlife populations and communities in the Florida Everglades. Environ. Manage., http://dx.doi.org/10.1007/s00267-014-0397-5

Cruz-Cárdenas, G., López-Mata, L., Villaseñor, J.L., Ortiz, E., 2014. Potential species distribution modeling and the use of principal component analysis as predictor variables. Rev. Mexicana Biodiver. 85, 189–199.

Cutler, D.R., Edwards Jr., T.C., Beard, K.H., Cutler, A., Hess, K.T., Gibson, J., Lawler, J.J., 2007. Random forests for classification in ecology. Ecology 88, 2783–2792.

Diniz-Filho, J.A.F., Bini, L.M., Rangel, T.R., Loyola, R.D., Hof, C., Nogués-Bravo, D., Araújo, M.B., 2009. Partitioning and mapping uncertainties in ensembles of forecasts of species turnover under climate change. Ecography 32, 897–906.

Dormann, C.F., et al., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36, 27–46.

Dormann, C.F., Purschke, O., García Márquez, J.R., Lautenbach, S., Schröder, S., 2008. Components of uncertainty in species distribution analysis: a case study of the Great Grey Shrike. Ecology 89, 3371–3386.

Elith, J., Burgman, M.A., Regan, H.M., 2002. Mapping epistemic uncertainties and vague concepts in predictions of species distribution. Ecol. Model. 157, 313–329.

Elith, J., et al., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29, 129–151.

Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. J. Anim. Ecol. 77, 802–813.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists. Divers. Distrib. 17, 43–57.

Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24, 38–49.

Fitzpatrick, M.C., Gotelli, N.J., Ellison, A.M., 2013. MaxEnt versus MaxLike: empirical comparisons with ant species distributions. Ecosphere 4, 55.

Fourcade, Y., Engler, J.O., Rodder, D., Secondi, J., 2014. Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. PLoS ONE 9, e97122.

Franklin, J., 2009. Mapping Species Distributions. Cambridge University Press, Cambridge.

Gritti, E.S., Duputié, A., Massol, F., Chuine, I., 2013. Estimating consensus and associated uncertainty between inherently different species distribution models. Meth. Ecol. Evol. 4, 442–452.

Guisan, A., Zimmerman, N.E., Elith, J., Graham, C.H., Phillips, S., Peterson, A.T., 2007. What matters most for predicting the occurrences of trees: techniques, data, or species characteristics? Ecol. Monogr. 77, 615–630.

Hanspach, J., Kühn, I., Schweiger, O., Pompe, S., Klotz, S., 2011. Geographical patterns in prediction errors of species distribution models. Glob. Ecol. Biogeogr. 20, 779–788.

Heikkinen, R.K., Luoto, M., Araújo, M.B., Virkkala, R., Thuiller, W., Sykes, M.T., 2006. Methods and uncertainties in bioclimate envelope modeling under climate change. Prog. Phys. Geogr. 30, 751–777.

Hernandez, P.A., Graham, C.H., Master, L.L., Albert, D.L., 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography 29, 773–785.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Clim. 25, 1965–1978.

Hirzel, A.H., Hausser, J., Chessel, D., Perrin, N., 2002. Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? Ecology 83, 2027–2036.

Jaeschke, A., Bittner, T., Jentsch, A., Reineking, B., Schlumprecht, H., Beierkuhnlein, C., 2012. Biotic interactions in the face of climate change: a comparison of three modelling approaches. PLoS ONE, e51472.

Kampichler, C., Wieland, R., Calmé, S., Weissenberger, H., Arriaga-Weiss, S., 2010. Classification in conservation biology: a comparison of five machine-learning methods. Ecol. Inform. 5, 441–450.

Knight, G.R., Oetting, J.B., Cross, L., 2011. Atlas of Florida's Natural Heritage – Biodiversity, Landscapes, Stewardship, and Opportunities. Florida State University, Tallahassee.

Lobo, J.M., Jiménez-Valverde, A., Real, R., 2007. AUC: a misleading measure of the performance of predictive distribution models. Glob. Ecol. Biogeogr. 17, 145–151.

Lobo, J.M., Jiménez-Valverde, A., Hortal, J., 2010. The uncertain nature of absences and their importance in species distribution modelling. Ecography 33, 103–114.

Luoto, M., Virkkala, R., Heikkinen, R.K., 2007. The role of land cover in bioclimatic models depends on spatial resolution. Glob. Ecol. Biogeogr. 16, 34–42.

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K., Thuiller, W., 2009. Evaluation of consensus methods in predictive species distribution modelling. Divers. Distrib. 15, 59–69.

McCullugh, P., Nelder, J.A., 1989. Generalized Linear Models, second edition. Chapman and Hall, New York, New York, USA.

Muñoz, J., Felicísimo, A.M., 2004. Comparison of statistical methods commonly used in predictive modelling. J. Veg. Sci. 15, 285–292.

Nakicenović, N., et al., 2000. Intergovernmental Panel on Climate Change Special Report on Emissions Scenarios. Cambridge University Press, United Kingdom, Cambridge.

New, M., Lister, D., Hulme, M., Makin, I., 2002. A high-resolution data set of surface climate over global land areas. Clim. Res. 21, 1–25.

Nicholls, R.J., Hanson, S., Herweijer, C., Patmore, N., Hallegatte, S., Corfee-Morlot, J., Chateau, J., Muir-Wood, R., 2008. Ranking port cities with high exposure and vulnerability to climate extremes: exposure estimates. Environment working paper no. 1. Organization for Economic Co-operation and Development, Paris.

Nix, H.A., 1986. A biogeographic analysis of Australian elapid snakes. In: Longmore, R. (Ed.), Atlas of elapid snakes if Australia: Australian flora and fauna series 7. Bureau of Flora and Fauna, Canberra, pp. 4–15.

Oliver, T.H., Gillings, S., Giardello, M., Rapacciuolo, G., Brereton, T.M., Siriwardena, G.M., Roy, D.B., Pywell, R., Fuller, R.J., 2012. Population density but not stability can be predicted from species distribution models. J. Appl. Ecol. 49, 581–590.

Oppel, S., Meirinho, A., Ramírez, I., Gardner, B., O'Connell, A.F., Miller, P.I., Louzao, M., 2012. Comparison of five modelling techniques to predict spatial distribution and abundance of seabirds. Biol. Conserv. 156, 94–104.

Pagel, J., Schurr, F.M., 2012. Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. Glob. Ecol. Biogeogr. 21, 293–304.

Peters, G.P., Andrew, R.M., Boden, T., Canadell, J.G., Ciais, P., La Quéré, C., Marland, G., Raupach, M.R., Wilson, C., 2013. The challenge to keep global warming below 2 °C. Nat. Clim. Change 3, 4–6.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190, 231–259.

Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecol. Appl. 19, 181–197.

R Development Core Team, 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Austria, Vienna, http://www.r-project.org (accessed 20.05.13).

Real, R., Márquez, A.L., Olivero, J., Estrada, A., 2010. Species distribution models in climate change scenarios are still not useful for informing public policy: an uncertainty assessment using fuzzy logic. Ecography 33, 304–314.

Reece, J.S., Noss, R.F., Oetting, J., Hoctor, T., Volk, M., 2013. A vulnerability assessment of 300 species in Florida: threats from sea level rise, land use and climate change. PLoS ONE 8, e80658.

Royle, J.A., Chandler, R.B., Yackulic, C., Nichols, J.D., 2012. Likelihood analysis of species occurrence probability from presence-only data for modelling species distributions. Methods Ecol. Evol. 3, 545–554.

SAS Institute, 2013. SAS 9.4 User's Guide. Cary, NC.

Shirley, S.M., Yang, Z., Hutchinson, R.A., Alexander, J.D., McGarigal, K., Betts, M.G., 2013. Species distribution modeling for the people: unclassified landsat TM imagery predicts bird occurrence at fine resolutions. Divers. Distrib. 2013, 1–12.

Stefanova, L., Misra, V., Chan, S., Griffin, M., O'Brien, J.J., Smith III, T.J., 2012. A proxy for high-resolution regional reanalysis for the southeast United States: assessment of precipitation variability in dynamically downscaled reanalyses. Clim. Dynam. 38, 2449–2466.

Stein, B.A., 2002. States of the Union: Ranking America's Biodiversity. NatureServe, Arlington, VA.

Synes, N.W., Osborne, P.E., 2011. Choice of predictor variables as a source of uncertainty in continental-scale species distribution modelling under climate change. Glob. Ecol. Biogeogr. 20, 904–914.

Tabor, K., Williams, J.W., 2010. Globally downscaled climate projections for assessing the conservation impacts of climate change. Ecol. Appl. 20, 554–565.

Thuiller, W., Georges, D., Engler, R., 2014. Package 'biomod2': Ensemble Platform for Species Distribution Modeling, Available at cran.r-project.org/web/packages/biomod2/.

Tsoar, A., Allouche, O., Steinitz, O., Rotem, D., Kadmon, R., 2007. A comparative evaluation of presence-only methods for modelling species distribution. Divers. Distrib. 13, 397–405.

University of Florida, 2014. Florida Population Studies, Bulletin 168, April 2014. University of Florida Bureau of Economic and Business Research, Gainesville, FL.

Valle, M., van Katwijk, M.M., de Jong, D.J., Bouma, T.J., Schipper, A.M., Chust, G., Benito, B.M., Garmendia, J.M., Borja, A., 2013. Comparing the performance of species distribution models of *Zostera marina*: implications for conservation. J. Sea Res. 83, 56–64.

VanDerWal, J., Shoo, L.P., Graham, C., Williams, S.E., 2009. Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? Ecol. Model. 220, 589–594.

Watling, J.I., Romañach, S.S., Bucklin, D.N., Speroterra, C., Brandt, L.A., Pearlstine, L.G., Mazzotti, F.J., 2012. Do bioclimate variables improve performance of climate envelope models? Ecol. Model. 246, 79–85.

Wenger, S.J., Som, N.A., Dauwalter, D.C., Isaak, D.J., Neville, H.M., Luce, C.H., Dunham, J.B., Young, M.K., Fausch, K.D., Rieman, B.E., 2013. Probabilistic accounting of uncertainty in forecasts of species distributions under climate change. Glob. Change Biol. 19, 3343–3354.

Wilson, K.A., Westphal, M.I., Possinghamn, H.P., Elith, J., 2005. Sensitivity of conservation planning to different approaches to using predicted species distribution data. Biol. Conserv. 122, 99–112.

Wisz, W.S., Guisan, A., 2009. Do pseudo-absence selection strategies influence species distribution models and their predictions? An information-theoretic approach based on simulated data. BMC Ecol. 9, 8.