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Comparison of climate envelope models developed using expert-selected variables versus statistical selection

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ABSTRACT

Climate envelope models are widely used to describe potential future distribution of species under different climate change scenarios. It is broadly recognized that there are both strengths and limitations to using climate envelope models and that outcomes are sensitive to initial assumptions, inputs, and modeling methods Selection of predictor variables, a central step in modeling, is one of the areas where different techniques can yield varying results. Selection of climate variables to use as predictors is often done using statistical approaches that develop correlations between occurrences and climate data. These approaches have received criticism in that they rely on the statistical properties of the data rather than directly incorporating biological information about species responses to temperature and precipitation. We evaluated and compared models and prediction maps for 15 threatened or endangered species in Florida based on two variable selection techniques: expert opinion and a statistical method. We compared model performance between these two approaches for contemporary predictions, and the spatial correlation, spatial overlap and area predicted for contemporary and future climate predictions. In general, experts identified more variables as being important than the statistical method and there was low overlap in the variable sets (<40%) between the two methods Despite these differences in variable sets (expert versus statistical), models had high performance metrics (>0.9 for area under the curve (AUC) and >0.7 for true skill statistic (TSS). Spatial overlap, which compares the spatial configuration between maps constructed using the different variable selection techniques, was only moderate overall (about 60%), with a great deal of variability across species. Difference in spatial overlap was even greater under future climate projections, indicating additional divergence of model outputs from different variable selection techniques. Our work is in agreement with other studies which have found that for broad-scale species distribution modeling, using statistical methods of variable selection is a useful first step, especially when there is a need to model a large number of species or expert knowledge of the species is limited. Expert input can then be used to refine models that seem unrealistic or for species that experts believe are particularly sensitive to change. It also emphasizes the importance of using multiple models to reduce uncertainty and improve map outputs for conservation planning. Where outputs overlap or show the same direction of change there is greater certainty in the predictions. Areas of disagreement can be used for learning by asking why the models do not agree, and may highlight areas where additional on-the-ground data collection could improve the models.

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1. Introduction

Climate change is creating new challenges for conservation. Within the next century it is expected to become one of the primary drivers of global biodiversity loss (Sala et al., 2000; Thomas et al., 2004; Urban, 2015). There are documented cases of species range shifts linked to changing climate (Chen et al., 2011; Parmesan and Yohe, 2003; Root et al., 2003) and climate change may have already

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resulted in species extinction (Cahill et al., 2013; McLaughlin et al., 2002; Pounds et al., 2006). The conservation community has recognized that existing strategies for landscape and species protection (including existing protected area networks) may not be effective in the future because of shifting species distributions (Heller and Zavaleta, 2009; Kostyack et al., 2011). Efforts are underway to develop adaptation strategies (Glick et al., 2009) that will help to assess and respond to conservation challenges associated with climate change. Development of successful adaptation plans in the face of uncertainty requires tools for assessing climate change impacts and vulnerabilities of species and habitats. Models are one way to do this, and climate envelope models, a subset of species distribution models, are becoming more widely used in vulnerability assessments and adaptation planning (Franklin, 2013).

Climate envelopes for species are developed by correlating species occurrences with selected climate variables (Beaumont and Hughes, 2002; Berry et al., 2002; Huntley et al., 2010; Pearson and Dawson, 2003; Thuiller, 2003). They can be used to describe historical, current, and future potential climate space for species. The resulting maps of potential climate space are based on two assumptions: 1) climate variables play an important role in defining a species geographic range (Lomolino et al., 2005), and 2) empirical relationships between contemporary distributions of species and climate can be used to forecast species distributions under future climate change scenarios (Araújo and Peterson, 2012; Franklin, 2010). Climate envelope models require relatively little data on the specific biology of a species (they rely on correlating occurrence data with climate variables such as monthly temperatures and precipitation) and therefore can be developed for many species over broad geographic areas fairly rapidly (Lawler et al., 2006). Although climate envelope models can provide useful information, they also have received substantial criticism (Araújo and Guisan, 2006; Araujo and Peterson, 2012; Beale et al., 2008), in part because they do not incorporate specific biological information or consider all relevant factors that determine a species range (Real et al., 2013). There is increasing recognition that different modeling techniques and different inputs can yield different results (Baker et al., 2016; Elith and Graham, 2009; Synes and Osborne, 2011; Watling et al., 2012b), and that there is a need for a better understanding of the strengths, weaknesses, and sensitivity of resulting maps to initial assumptions and inputs (Araujo and Guisan, 2006; Whittaker et al., 2005).

Selection of climate predictor variables is a central step in climate envelope modeling (Austin and Van Niel, 2011; Harris et al., 2013). There are a number of ways to select variables, including automated statistical techniques or *a priori* selection of variables based on expert knowledge, where experts are individuals who have documented extensive knowledge about the subject. An advantage of automated approaches is that many species can be evaluated quickly. A disadvantage is that the resulting variables may be biologically implausible or irrelevant (Heikkinen et al., 2006). Selection of variables using expert knowledge also has advantages and disadvantages. Natural resource managers may be more comfortable with models developed through expert input than with those developed only by statistical methods because they have established relationships with trusted experts or are unfamiliar with statistical techniques (Addison et al., 2013). In addition, expert-selected variables may be more closely tied to empirical biophysical tolerances of species. However, there are shortcomings of using experts, probably the most important ones being bias and functional fixedness (Chi, 2006). Experts may be biased when the species occurs outside of the geographical area with which they are familiar resulting in variables only reflecting a subset of environmental conditions experienced by a species. Experts may become fixated on ideas that are familiar and find it challenging to accept new ideas or consider novel species environmental relationships that might occur with climate change. In addition, consultation with experts takes considerable time, experts may not agree on which variables are important, or experts may not exist for all species that need to be modeled, limiting the number of species that can be modeled in a given timeframe.

Performance metrics such as area under the receiver operating curve (ROC), known as AUC, Cohen's kappa, and TSS (True Skill Statistic) are used to quantify prediction accuracy of model outputs and numerous studies have examined how accuracy is affected by different inputs (see for example, Elith et al., 2006; Guisan et al., 2007; Hernandez et al., 2006; Segurado and Araújo, 2004). However, fewer studies (Bagchi et al., 2013; Baker et al., 2015; Baker et al., 2016; Bucklin et al., 2015; Syphard and Franklin, 2009; Watling et al., 2012b) have examined specifically how spatial configuration (spatial correlation and spatial overlap) of prediction maps varies even when performance metrics are high. Map outputs from models using different inputs might have equally high performance metrics but look different. Because in the context of natural resource management it is often the resulting map that is used for planning and management decisions, variations in spatial characteristics of prediction maps (which areas appear as high suitability) have the potential to result in different planning and management decisions.

We initiated this project to address concerns that models created via statistical variable selection would not be useful because of the belief that they would not reflect the ecology of the species. We did this by examining how climate envelope models and resulting prediction maps for 15 threatened or endangered species in Florida differed between two methods: 1) using predictor variables (temperature and precipitation) selected by experts as most important in describing the species climate envelopes, and 2) using variables selected by a statistical method. We evaluated model performance using traditional performance metrics of AUC and TSS. We projected model results to contemporary and future conditions and analyzed how spatial predictions (correlation of map suitability, spatial overlap, and area of map suitability) differed between the variable selection techniques. We compared similarity between expertly and statistically selected variable sets. We also used information gathered from experts on importance of temperature and precipitation for determining the range of the species and experts' level of confidence in variable selection, to examine if there were differences in confidence in variable selection or model outputs between models produced for species for which experts believed temperature or precipitation were very important compared to species for which they believed temperature or precipitation were not important.

2. Methods

Climate envelope models develop associations between species occurrence and environmental conditions described by climate data. Climate data are described by a set of predictor variables such as average temperature or average precipitation. Once these associations are developed an index of environmental suitability or probability of occurrence for the modeled species can be developed, tested, and projected spatially in the form of a map. Maps can be developed for both contemporary and future conditions. Below we describe how we applied these steps.

2.1. Input data for climate envelope models

2.1.1. Species' occurrence data

Our study species consisted of 15 terrestrial vertebrates classified as federally threatened or endangered species in the United States (Table 1), and contain either all or some of their distribu-

Table 1
Fifteen federally threatened or endangered terrestrial species whose geographic range includes all or part of Florida were used in this study. Common name, scientific name, species code, and number of presence points used in this study are indicated below.

Common name	Scientific name	Species code	Presence records
Mammals			
Florida panther	*Puma concolor coryi*	pucoc	109
Key deer	*Odocoileus virginianus clavium*	odvicl	17
Lower Keys marsh rabbit	*Sylvilagus palustris hefneri*	sypah	12
Birds			
Cape Sable seaside sparrow	*Ammodramus maritimus mirabilis*	amma	17
Florida grasshopper sparrow	*Ammodramus savannarum floridanus*	amsaf	26
Florida scrub jay	*Aphelocoma coerulescens*	apco	208
piping plover	*Charadrius melodus*	chme	867
roseate tern	*Sterna dougallii dougallii*	stdod	104
wood stork	*Mycteria americana*	myam	1601
Audubon's crested caracara	*Polyborus plancus audubonii*	popla	162
snail kite	*Rostrhamus sociabilis plumbeus*	rosopl	106
whooping crane	*Grus americana*	gram	17
red-cockaded woodpecker	*Picoides borealis*	pibo	531
Reptiles			
sand skink	*Neoseps reynoldsi*	nere	21
eastern indigo snake	*Drymarchon corais couperi*	drcoc	278

Table 2
Nineteen bioclimatic variables used in this study (http://www.worldclim.org/bioclim).

Bioclimatic variable code	Description
bio_1	Annual Mean Temperature
bio_2	Mean Diurnal Range (Mean of monthly (max temp − min temp))
bio_3	Isothermality (BIO2/BIO7) (* 100)
bio_4	Temperature Seasonality (standard deviation *100)
bio_5	Max Temperature of Warmest Month
bio_6	Min Temperature of Coldest Month
bio_7	Temperature Annual Range (BIO5-BIO6)
bio_8	Mean Temperature of Wettest Quarter
bio_9	Mean Temperature of Driest Quarter
bio_10	Mean Temperature of Warmest Quarter
bio_11	Mean Temperature of Coldest Quarter
bio_12	Annual Precipitation
bio_13	Precipitation of Wettest Month
bio_14	Precipitation of Driest Month
bio_15	Precipitation Seasonality (Coefficient of Variation)
bio_16	Precipitation of Wettest Quarter
bio_17	Precipitation of Driest Quarter
bio_18	Precipitation of Warmest Quarter
bio_19	Precipitation of Coldest Quarter

tion in the state of Florida. We collected species presences with geographic coordinates from online databases (primarily Global Biodiversity Information Facility, GBIF) and the scientific literature (Watling et al., 2011). We removed duplicate observations, retaining a single presence per grid cell (10 min cells or approximately 325 km^2 to match Worldclim data). Table 1 shows the total number of presence points per species used for our models.

2.2. Climate data

We used spatial layers of contemporary climate data (1950–2000) from the WorldClim database (Hijmans et al., 2005) at the 10 arc-min resolution. We used two commonly available and widely used sets of variables to describe climate: 1) monthly temperature and precipitation averages (for a total of 24 variables), and 2) 19 'bioclimatic' variables (Table 2). Both sets of climate layers are available for download online at the global extent.

Dynamically-downscaled future climate projections were acquired from the Center for Ocean-Atmospheric Prediction Studies (COAPS) at Florida State University, part of the COAPS Land–Atmosphere Regional Ensemble Climate Change Experiment for the Southeast United States (Southeast) at a 10-km resolution (https://floridaclimateinstitute.org/resources/data-sets/regional-downscaling). They employed a dynamical model (Kanamitsu et al., 2010) to create projections for three global circulation models (GCMs; Geophysical Fluid Dynamics Laboratory-GFDL, National Center for Atmospheric Research- NCAR, United Kingdom Meteorological Office- UKMO) using the moderate-high A2 emissions scenario (Stefanova et al., 2012); we acquired data for the period 2041–2060 (referred to as "future"). Precipitation variables were already de-biased by the COAPs group (so no de-biasing was done by us). Temperature variables (mean monthly temperature) were debiased using the "delta change" method, using the consensus of Worldclim and CRU contemporary datasets as a baseline (described in Bucklin et al., 2013).

2.3. Predictor variables

Predictor variables using both monthly and bioclimatic variables were selected by two methods: expert opinion and statistical.

2.3.1. Expert opinion

For the purpose of this study we defined a "species expert" as an individual who met one or more of the following criteria:

1) A minimum of three years of experience in a job that requires knowledge of the life history traits of the species
2) A minimum of three years of experience conducting ecological or natural history studies of the species
3) Authorship (either first author or coauthor) of at least one peer-reviewed publication on the species
4) A recommendation from an individual who has authored at least one peer-reviewed publication on the species

Based on these criteria we identified three experts for each of the 15 species in our study, with the exceptions of Audubon's crested caracara (for which we were only able to identify two experts,) and roseate tern (for which we had four experts). Experts were initially contacted via email with a description of the project, explanation that they were identified as a species expert, and a request to complete a brief online questionnaire. Follow-up phone calls were made as necessary (59 experts were contacted, 8 experts did not respond, 44 experts agreed to participate [one individual was an expert for 2 species], and 6 experts declined).

Experts who agreed to participate were emailed a link to an online questionnaire in March 2012 via SurveyMonkey.com (paper-based questionnaires were available upon request). After reminder emails were sent three weeks after the initial mailing, all 44 experts who said they would participate responded for a total of 46 surveys (one individual was an expert for two species and one expert completed surveys for two populations of whooping crane). Note

The questionnaire elicited experts' opinions on the importance of climate variables in determining the species' geographic range and climate envelope. Questions were structured as categorical measures and ranks because these measures are easily interpreted, can be elicited remotely (e.g., by a web survey), and can be clearly synthesized for multiple experts (Kuhnert et al., 2010). Categories and ranks are "indirect" elicitation methods which can reduce bias because they are less abstract and draw more on experts' practical knowledge compared to direct measures such as quantities and probabilities (Choy et al., 2009). To clarify the concept of a species' 'climate envelope' we included the following text in the instructions and text of the questionnaire: "Here and throughout the survey, please consider the importance of climate in the maintenance of a viable species population. For species with complex life histories, please consider the importance of climate on the life history stage most likely to contribute to overall population viability." The questionnaire was divided into the following four sections (see Appendix A in supplementary data for full questionnaire).

2.3.1.1. Overall importance of climate factors. First, experts were asked to rate the overall importance of temperature and precipitation, respectively, on a four-point scale ("not at all important" to "very important") in determining the geographic range of the species. The frequency of "very important" responses were summarized to determine the frequency with which experts believed temperature, precipitation, or both were important in determining a species geographic range. A count was used to assess how many experts felt there were factors more important than temperature and precipitation in determining a species geographic range.

Experts were then asked if they believe there are factors more important than these in determining the range, and if so to describe those factors.

2.3.1.2. Selection of monthly climate variables. Experts were asked to consider only the species climate envelope (regardless of whether they thought temperature and precipitation were important in determining the species geographic range) and to rate the importance (on a four-point scale [very important to not at all important]) of each of 12 monthly temperature variables (average monthly temperature) and 12 monthly precipitation variables (total monthly precipitation) in determining the species climate envelope. Next, they were asked to select up to three of the 24 monthly temperature and precipitation variables that they thought were most important in determining the climate envelope for the species. They were asked how confident they were that the variables they selected were the most important (very high confidence [at least 9 out of 10 chance of being correct], high confidence [about 8 out of 10 chance], medium confidence [about 5 out of 10 chance], low confidence [about 2 out of 10 chance], very low confidence [less than 1 out of 10 chance]). This section concluded with a space for the expert to provide comments if desired.

2.3.1.3. Selection of bioclimatic variables. Experts were provided a list of 19 bioclimatic variables (Table 2) that represented annual trends, seasonality, and extreme or limiting environmental factors. They were asked to select up to three of these variables that they thought were most important in determining the climate envelope. As above, they were asked to indicate their level of confidence in their choices and were provided a space for comments.

We selected variables (both bioclimatic and monthly) to use in the climate envelope modeling based on the criterion that at least one expert per species identified a variable as one of the most important. This resulted in a possible range of three to nine variables when all experts agreed on the three most important variables and when all experts disagreed on the three most important variables, respectively.

2.3.1.4. Comparison of monthly and bioclimatic variables. Finally, the questionnaire asked experts which of the two sets of variables that they selected (up to three monthly climate variables or up to three bioclimatic variables) better described the climate envelope of the species (four response categories: "monthly climate variables are better," "bioclimatic variables are better," "the two sets of variables are equally good," "I am not sure"). They were given space to make comments on this question as well as space to provide any general comments on the study.

The questionnaire was approved by University of Florida's Institutional Review Board and pretested prior to implementation on four scientists with specialization in wildlife and endangered species ecology.

2.3.2. Statistical-based selection

We used a variable importance function from the randomForest package (Liaw and Wiener, 2002) in the statistical programming language 'R' (R Core Team, 2013) to select predictor variables. This function compares the full random forest model (including 24 climate variables for the monthly set, and 19 for the bioclimatic set) to a series of models in which values of a single predictor variable are randomly permuted, while values of all other variables remain untouched. The process is repeated 24 times for the monthly variable set and 19 times for the bioclimatic set, so that values of each variable are randomly permuted once. The difference in model accuracy between the full model and the model in which values of a variable are randomly permuted is called the mean accuracy index, and is interpreted as a measure of variable importance. Important variables will result in large decreases in model accuracy compared to the full model, whereas when values of unimportant variables are randomly permuted, there will be little difference in model accuracy compared with the full model. Additional details on the variable importance function are described in the randomForest package documentation (Liaw and Wiener, 2002). In order to replicate the expert selection process, we ran the variable importance function three times for each species (to represent the three species experts) and selected the three highest ranking variables from each run based on the mean accuracy index (to represent the selection by experts of the three most important variables). This resulted in between three and nine variables for each species, depending on how much overlap there was in the variables among the three runs. We determined the proportion of variables selected by experts that were also selected by the statistical selection procedure for both monthly and bioclimatic variables.

2.4. Climate envelope models

We used the biomod2 package (Thuiller et al., 2013) in R (R Core Team, 2013) to implement the Random Forest algorithm (Breiman, 2001), using the classification mode and the default selection of 500 trees for each model run. As with the vast majority of correlative models, Random Forest requires two major data inputs: occurrence data (species presence/absence) and predictor variables (in our case the climate data). Because records of true absence are nearly impossible to establish given many limitations in the ways we currently collect data on species occurrences, the selection of pseudoabsences in grid cells that are not occupied by a presence point is a common practice when creating correlative models of species distributions (Watling et al., 2012a). However, the model domain from which pseudoabsences are selected can have a large effect on model performance and predictions (Phillips et al., 2009). We defined the model domain for each species separately using a variation of the "target-group" approach (Phillips et al., 2009) wherein the domain was delineated by convex polygons circumscribing occurrences for at least three phylogenetically related and similar species (Watling et al., 2012a). We masked the original climate layers to the target group extent for each species and randomly selected 10,000 pseudoabsences within the model domain. For each of the 15 species there were four possible models based on how predictor variables were selected: monthly expert, monthly statistical, bioclimatic expert, bioclimatic statistical. This yielded a total of 60 models. We cross-validated each of the 60 models by running 10 replicate partitions of the occurrence dataset into 75%/25% (training/testing) subsets. Models were evaluated using two performance metrics (area under the receiver operating characteristic (ROC) curve (AUC) and true skill statistic (TSS), calculating the average values across the 10 replicates for each model. AUC values range from 0 to 1; an AUC above 0.8 is considered to have 'good' discrimination abilities (Swets, 1988). The TSS accounts for both omission and commission errors, and ranges from −1 to +1, where +1 indicates perfect agreement and 0 represents a random fit (Allouche et al., 2006). We evaluated how model performance was affected by variable selection technique for contemporary models by using paired *t*-tests to compare model evaluation statistics of AUC and TSS for the predictions based on the expert-selected variables compared to models created from statistically selected variables.

The 60 resulting models were projected to contemporary and future spatial climate data in order to obtain 'probabilistic suitability maps' for contemporary and future conditions. Probability maps provide a continuous (0–1) scale of landscape suitability. We used this information to also create 'binary suitability maps' by applying a numeric threshold to the probabilistic maps. The threshold (which can range from 0 to 1) establishes that probability values in the probabilistic map below which cells are considered 'unsuitable' areas (coded 0 in the binary map) and above which cells are considered 'suitable' (coded as 1 in the binary map). For each model, we selected a threshold value corresponding to the point closest to the top-left part of the receiver operating characteristic (ROC) plot (the point indicating a perfect classification); therefore, threshold values among the 60 models can be different. We used the probabilistic suitability maps to calculate correlation (Pearson's correlation coefficient) between models created with expert-selected versus statistically selected variables. These correlations are cell by cell comparisons of suitability values between different model outputs. Spatial correlations of expert-selected versus statistically selected variables were compared between monthly and bioclimatic maps using a paired *t*-test to assess if there were differences in spatial correlations resulting from the use of different variable formats. We used the binary maps to calculate spatial overlap between models. Spatial overlap shows where cells are predicted to be suitable by two models. These were calculated for models generated by expert compared to statistically chosen variables for both monthly and bioclimatic formats, and contemporary and future periods. Similarity of spatial overlap between expert variable maps and statistical variable maps for monthly and bioclimatic formats was compared using a paired *t*-test. Because we do not know what the "right" distribution is in the future we cannot directly assess if models constructed using expert-selected variables are better than those constructed using statistically selected variables; however, we can examine where the direction and magnitude of predictions are consistent. In addition, area (number of cells) identified in expert variable maps compared to statistical variable maps for contemporary and future projections were compared using paired *t*-tests.

3. Results

3.1. Expert opinion

3.1.1. Overall importance of climate factors

Across all 46 surveys, 59% of the time, experts said that either temperature or precipitation was "very important" in explaining the species range (28% said temperature was very important and 46% said that precipitation was very important). For four species (Florida panther, Florida scrub jay, Lower Keys marsh rabbit, and red-cockaded woodpecker) no expert indicated that temperature or precipitation was very important. For seven species (Cape Sable seaside sparrow, whooping crane, key deer, wood stork, Audubon crested caracara, piping plover, and Everglades snail kite) experts indicated that both temperature and precipitation were very important in determining the species geographic range.

3.1.2. Expert variable selection

The number of monthly climate variables selected by all experts combined as "most important" in determining the species climate envelope ranged from four (Florida panther) to nine (key deer, Table 3). The maximum number of variables that could be selected was nine, which occurred when each of three experts selected three different variables. Fifty-six percent of monthly variables selected were precipitation variables, and 44% were temperature variables. Experts selected three (Florida panther) to nine (sand skink) bioclimatic variables per species as "most important" in determining the climate envelope (Table 4). Sixty-four percent of bioclimatic variables selected were precipitation variables, and 34% were temperature variables. Average level of confidence that the monthly variables selected were the most important ones for determining the climate envelope for a species ranged from 2.7 (Low confidence: Florida scrub jay, red-cockaded woodpecker, Florida panther, Lower Keys marsh rabbit, Florida sand skink, wood stork) to 7.5 (Medium confidence: whooping crane). Average level of confidence for bioclimatic variables ranged from 2.3 (Low confidence: Florida panther) to 8.3 (High confidence: Cape Sable seaside sparrow). Confidence scores were significantly lower for the four species (Florida panther, Florida scrub jay, Lower Keys marsh rabbit, and red-cockaded woodpecker) where experts did not indicate that temperature or precipitation were very important for determining the species range compared to the seven species where experts indicated temperature or precipitation was important (2.7 [Low confidence] compared to 5.9 [Medium confidence], $t = -3.76$, $p = 0.002$).

3.1.3. Comparison of monthly and bioclimatic variables

Twenty-five experts (56%) believed that the bioclimatic variables were better than the monthly variables at describing a species climate envelope. Experts who believed that bioclimatic variables were better were more confident (average confidence score of 6.3) in their selection of bioclimatic variables than they were in their choice of monthly variables (average confidence score of 5.4; $p = 0.01$, $df = 24$, $t = -2.32$). The same pattern was true for the eight experts (17%) who believed monthly variables were better: they had more confidence in their monthly variable selection (average confidence score of 5.4) than their bioclimatic selection (average confidence score of 4; $p = 0.03$; $df = 7$; $t = 2.31$). 4 experts (9%) thought that monthly and bioclimatic variables were equally good at defining the climate envelope, and 8 experts (17%) were not sure which set of variables was better.

Table 3
Monthly temperature and precipitation variables selected by experts (E) and statistical (S) approaches as being most important in determining a species climate envelope. See Table 1 for species codes.

	amma	amsaf	apco	chme	drcoc	gram	myam	nere	odvicl	pibo	popla	pucoc	rosopl	stdod	sypah
jan_temp	E, S			E	E, S	S		E, S	E, S	E	E, S	S	E, S		E, S
feb_temp	E	S	E, S	E, S	E, S	S		S	S		S	S	E, S	S	E, S
mar_temp	E		E	E	E, S			E					E		E
apr_temp	E	S						E			S	S	E	E	
may_temp	E	E			S			E		E				E	
jun_temp	S							E		E				E	
jul_temp														E	
aug_temp				S											E
sep_temp				S			S			S	S				
oct_temp		S		S			S			S					
nov_temp	S	S	S				S		E, S	S	S	E, S	S	S	
dec_temp			S	E	E, S	S		S	E, S			S	E, S	S	S
jan_prec						E	E		E						
feb_prec		E	E	E			E								
mar_prec	E		E, S	E									E		
apr_prec	E		E	E	E					E				E	
may_prec	E	E					E	E	E	E					
jun_prec	S	E				E			E	E			E		E
jul_prec		E				E	E		E		E	E			E
aug_prec		E	E				E		E		E	E			E
sep_prec			E				E				E	E			
oct_prec						E			E		E				
nov_prec						E									
dec_prec						E	E								
Expert	8	6	7	7	5	6	7	6	9	6	5	4	7	5	7
Statistical	4	4	4	4	5	3	3	3	4	3	5	5	4	3	3
Both	1	0	2	1	4	0	0	1	3	0	1	1	3	0	2

Table 4
Bioclimatic variables selected by experts (E) and statistical (S) approaches as being most important in determining a species climate envelope.

	amma	amsaf	apco	chme	drcoc	gram	myam	nere	odvicl	pibo	popla	pucoc	rosopl	stdod	sypah
bio_1	S	E		S	E		S			E, S	S	S		E, S	E
bio_2								E						E	
bio_3				S	S				S		S		S	S	
bio_4	E	E, S		S	S	S	S	E		E	S	S	S	E	E, S
bio_5		E	E					E						E, S	E
bio_6	S	S		E	E				E, S		E		S		S
bio_7								E					E	E	S
bio_8	E		S		S									S	
bio_9	S	E, S				S		E		S				E	
bio_10	S						S	E		E				E	
bio_11	S	S	E, S	E	E	E, S	S	E	S	S		S	E, S	S	
bio_12	E			E	E		E	E	E	E, S	E	E	E		E
bio_13				E	E	S		S				E			E
bio_14	S		E					E	E				E		E
bio_15	E	E	E	E		E	E		E	E	E		E		
bio_16		E	E	E		E, S	E	S	E		E	E	E		
bio_17	E, S	E	E, S	E		E			E	S	E		E	E	E
bio_18	E	E	E, S					S		E	S				
bio_19			E			E	E			E					
Expert	6	8	8	7	5	5	4	9	6	7	5	3	7	8	7
Statistical	7	4	4	3	3	5	4	3	3	5	4	3	4	5	3
Both	1	2	3	0	0	2	0	0	1	2	0	0	1	2	1

3.2. Statistical variable selection

Statistical variable selection resulted in three (Cape Sable seaside sparrow, wood stork, sand skink, red-cockaded woodpecker, Lower Keys marsh rabbit) to five (indigo snake, Audubon's crested caracara, Florida panther) monthly climate variables (Table 3) and three (piping plover, indigo snake, sand skink, Key deer, Florida panther, Lower Keys marsh rabbit) to seven (Cape Sable seaside sparrow) bioclimatic variables (Table 4).

Proportion of monthly variables that experts selected that were also represented in the statistically selected variables ranged from 0 to 0.8 for monthly variables and 0–0.4 for bioclimatic variables (Table 3 & 4). Experts selected a higher proportion of precipitation variables for both monthly and bioclimatic data than were selected using the statistical approach (mean = 0.56 and 0.03 for monthly expert and statistically selected variables, respectively; $p < 0.001$, df = 17, t = 6.754; mean = 0.64 and 0.19 for bioclimatic expert and statistically selected variables, respectively; $p < 0.001$, df = 27, t = 4.582).

3.3. Comparison of models

3.3.1. Contemporary climate

AUC values for all models were >0.80. Ten of the 60 TSS values (1 expert monthly, 2 expert bioclimatic, 4 statistical monthly, and 3 statistical bioclimatic) were <0.80, but all were >0.70 (Appendix A in supplementary data). Models developed using expert selection of monthly variables had statistically higher values for AUC and TSS than models created using statistically selected monthly variables though differences were small (mean = 0.98 ± 0.012 SD and 0.96 ± 0.031, $p = 0.03$, $df = 14$, $t = 2.401$for AUC, respectively; mean 0.94 ± 0.026 and 0.89 ± 0.063, $p = 0.03$, $df = 14$, $t = 2.144$ for TSS, respectively; Appendix A in Supplementary data). There were no statistically significant differences in AUC or TSS for models created using expert-selected bioclimatic variables compared to models created from statistically selected bioclimatic variables.

Spatial correlation for contemporary prediction maps for the Southeast between expert and statistical variables ranged from 0.67 to 0.97 and averaged 0.84 ± 0.095 for monthly variables and ranged from 0.56 to 0.99 and averaged 0.86 ± 0.120 for bioclimatic variables (Appendix A in supplementary data). Spatial overlap ranged from 31% to 91% and averaged 61% for monthly variables and 21% to 92% (average 66%) for bioclimatic variables (Fig. 1). Spatial overlap was not significantly different for monthly and bioclimatic maps. Number of cells (area) projected under contemporary conditions for the Southeast was not statistically different between models created with expert-selected compared to statistically selected variables for either monthly or bioclimatic variable sets. There was a great deal of variation across species with percent difference in area projected ranging from −120% (Key deer, more area in statistical) to 45% (whooping crane and roseate tern, more area in expert) with an absolute average of 23% for monthly variables and a range of −183% (Key deer) to 42% (piping plover) with an absolute average of 31% for bioclimatic variables (Fig. 2).

3.3.2. Future climate

Spatial correlations between future prediction maps across all three GCMs using expert and statistical variables ranged from −0.39 to 0.88 with an absolute average of 0.43 ± 0.22 for monthly variables and ranged from −0.05 to 0.89 with an absolute average of 0.29 ± 0.24 for bioclimatic variables. Spatial overlap between expert and statistical future prediction maps averaged $32\% \pm 29$ and $26\% \pm 24$ where two and three GCMs predicted suitable climate space, respectively for monthly variables (Fig. 3 and Appendix A in supplementary data). Bioclimatic variables showed a similar pattern, with averages of $33\% \pm 30$, and $26\% \pm 24$ where there was overlap of predictions of suitable climate space from two and three GCMs, respectively.

Number of cells (area) where 2 and 3 GCMs predicted suitable climate space were not significantly different between expert and statistical models for either monthly or bioclimatic variables. For nine of the species both the expert and statistical prediction models suggested the same direction of area change ranging from complete loss of climate space to an increase of over 150% (Fig. 4).

4. Discussion

Models constructed from expert-selected variables and statistically selected variables performed similarly with high model performance statistics, high spatial correlation, and similar amounts of predicted suitable climate spaces. These results are similar to what has been found by others who have examined whether incorporation of expert opinion into species distribution models improves performance. Seoane et al. (2005) found that predictive performance of models of bird distribution constructed using an automated statistical method (requiring little expert input) were as good or better than those with expert input. Pearce et al. (2001) found that predictive accuracy was not improved by incorporating expert input into models of 16 faunal species, and Charney (2012) found that incorporation of habitat suitability information from an expert panel in models to predict distribution of spotted salamanders (*Ambystoma maculatum*) actually made the models worse. These authors all concluded that statistical methods of model development provide an adequate and cost-effective way of creating regional-scale models based primarily on standard map performance metrics.

Standard map performance metrics of AUC and TSS are important, but it is often the map output that natural resource managers use for planning. Differences in spatial patterns on the maps have potential to affect conservation decisions. In our study spatial overlap, which compares the spatial configuration of maps, between maps constructed using the different variable selection techniques, was moderate overall (about 60%) with a great deal of variability across species. Our spatial correlations were high overall (83 and 84% for monthly and bioclimatic models, respectively), also with a great deal of variability across species (but with none <0.65). This is similar to what Watling et al. (2012b) found in a study comparing models created using monthly variables to models created using bioclimatic variables; models constructed using monthly or bioclimatic variables had similar performance and similar spatial predictions (as measured by spatial correlations), but for some species there were discrepancies in spatial predictions even when AUC was high. Watling et al. (2012b) also compared spatial correlation for maps created using uncorrelated predictor variables with maps created using biologically relevant predictor variables. The spatial correlation between monthly and bioclimatic models was higher (0.91 ± 0.081) for the uncorrelated predictor variables than it was for the biologically relevant predictor variables (0.83 ± 0.228) suggesting as in our study, that models created with statistically selected variables perform as well or better than models with expert-selected variables.

Difference in spatial overlap was even greater under future climate projections, indicating additional divergence of model outputs from different variable selection techniques when projected into the future. Because we do not know what the "right" distribution is in the future we cannot directly assess if models constructed using expert-selected variables are better than those constructed using statistically selected variables; however, we can examine where the direction and magnitude of predictions are consistent and use that information in conservation planning. For example, for nine species percent change in area in future prediction maps was in the same direction (Fig. 4) and in five cases fairly close in magnitude, indicating more certainty in predictions despite different variable inputs.

In addition, we can examine differences between variables selected by experts compared to variables selected statistically and how the different variable sets affect map outputs. In general, climate predictor variables selected by experts were different than those selected by the statistical method; however, there was no clear pattern as to the relationship between percent agreement of the variable sets and percent of spatial overlap. Models with no overlapping variables had spatial overlap ranging from 31 to 84%. In addition, patterns of spatial overlap were similar for species for which experts indicated temperature and precipitation were not important and those for which they indicated temperature and precipitation were important (Fig. 5). Since these models use only temperature and precipitation it is logical to think that species for which temperature and precipitation were more important might behave differently than those for species where other factors are more important in determining their range. The only outstanding difference between the two variable sets was that experts selected more precipitation variables than were selected by the statistical variable selection method. This difference may reflect the greater uncertainty in the WorldClim precipitation data where there is greater variation in cross validation in precipitation compared to temperature (Hijmans et al., 2005). Thus more effort should be committed to improving precipitation datasets both for current and future conditions, as GCMs are not as good at simulating precipitation as they are at simulating temperature (Obeysekera et al., 2015). The differences in percent of precipitation variables selected

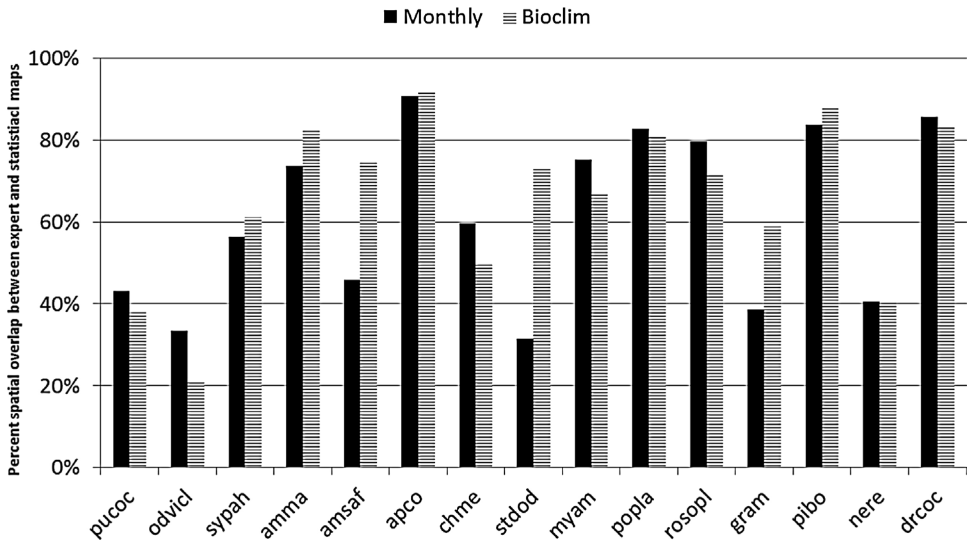

Fig. 1. Percent difference in spatial overlap between prediction maps created by models using variables selected by experts or a statistical method. Solid bars are maps using monthly variables. Striped bars are maps using bioclimatic variables. See Table 1 for species codes.

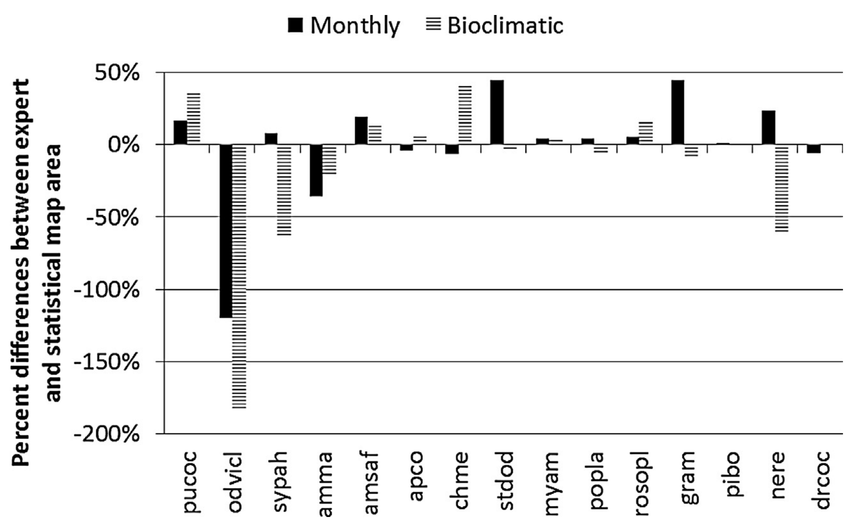

Fig. 2. Percent difference in area between prediction maps created by models using variables selected by experts or a statistical method. Negative values indicate more area in the statistical variable map. See Table 1 for species codes.

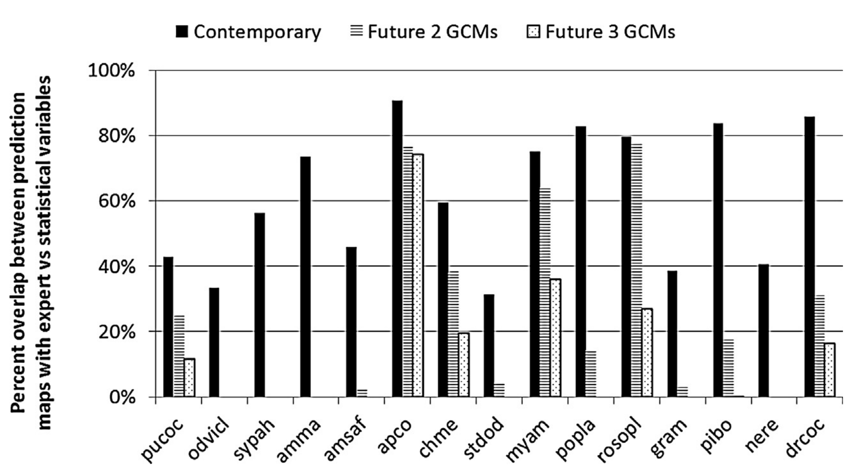

Fig. 3. Percent spatial overlap between prediction maps created by models using monthly variables selected by experts or a statistical method. Solid bars are for contemporary prediction maps. Striped bars are for future prediction maps were 2 GCMs overlap and dotted bars are for future prediction maps where 3 GCMs overlap. See Table 1 for species codes.

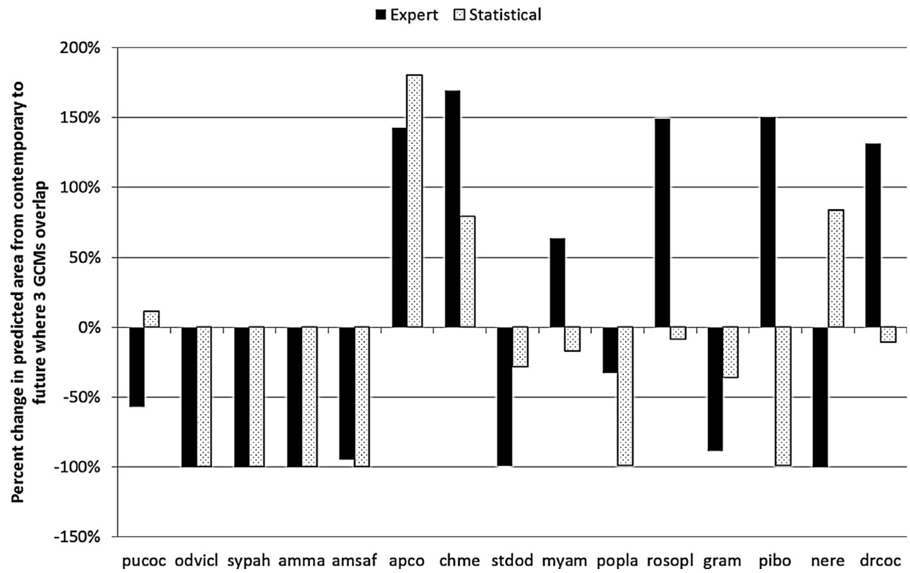

Fig. 4. Percent change in predicted area from contemporary to future where 3 GCMs overlap. Solid bars are for models using expert-selected variables. Dotted bars are for models using statistically selected variables.

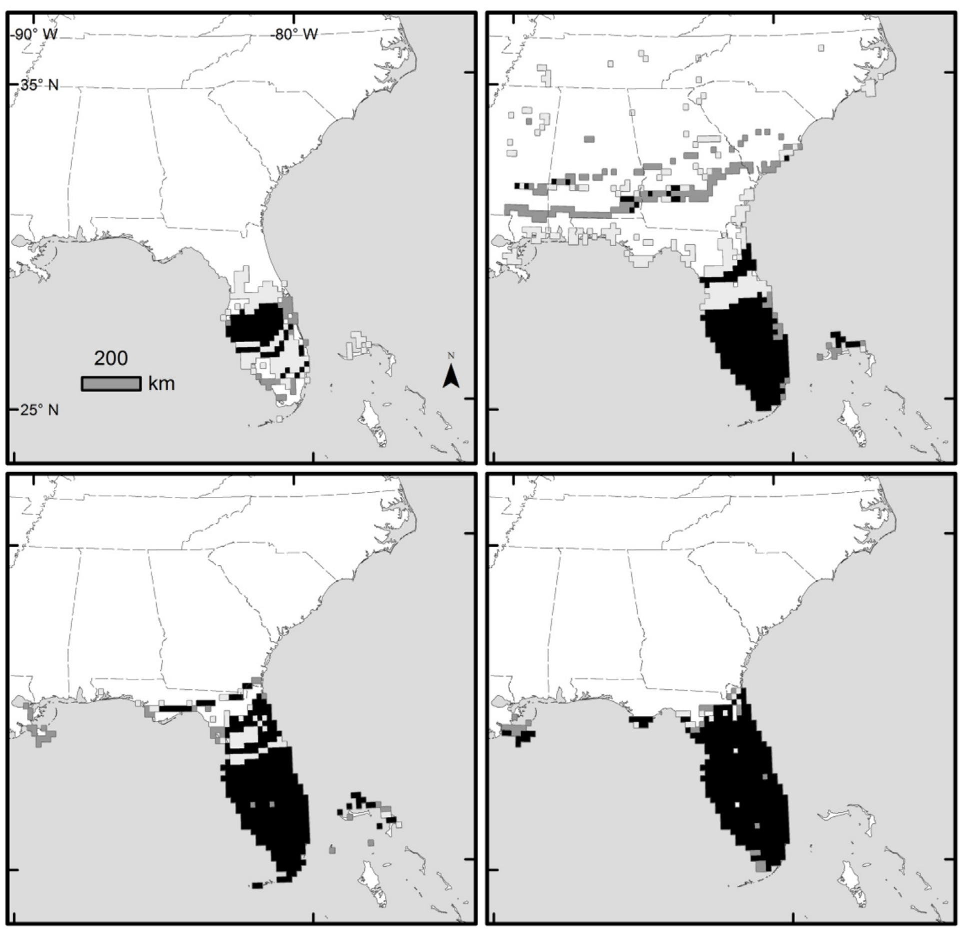

Fig. 5. Examples of low spatial overlap (top) for species that experts believe that temperature or precipitation were important for determining range (whooping crane, 39%, left) and where experts believe that neither temperature nor precipitation were important for determining range (Florida panther, 43%, right). Examples of high spatial overlap (bottom) for species that experts believe that temperature or precipitation were important for determining range (snail kite, 80%, left) and where experts believe that neither temperature nor precipitation were important for determining range (Florida scrub jay, 91%, right). Overlap of expert and statistical is black, expert only light grey, statistical only dark grey.

by experts compared to the statistical method also could reflect that the statistical method uses a single value for each occurrence cell obscuring smaller scale biologically relevant patterns while experts may be integrating their more local knowledge into their assignment of variable importance. This has implications for use of the models with future climate projections where precipitation may become more variable.

We initiated this project to address experts' concerns that models created via statistical variable selection would not be useful because of the belief that they would not reflect the ecology of the species. The assumption is that incorporation of expert input resulting in thoughtful selection of predictor variables reduces inclusion of spurious relationships (Seoane et al., 2005), hence producing better models. However, for this to happen, experts must have a good idea of what the biologically relevant relationships are at the scale of the modeling. In this study we constructed regional models to highlight broad-scale patterns and constrained experts to either monthly summaries of temperature and precipitation or the bioclimatic variables that incorporate annual trends, seasonality, and extreme or limiting environmental factors, thus potentially asking experts for input outside of their experiences. We did not have a direct measure of expert expertise, but did ask experts to express their level of confidence in their variable selection. Overall experts were not very confident in their variable selection and had less confidence in their variable selection for species where they indicated that temperature and precipitation were not important. They were more confident in their variable selection for the format (bioclimatic vs. monthly) that they felt better represented variables affecting the species, indicating a level of internal consistency.

In summary, our work is in agreement with other studies which have found that for broad-scale species distribution modeling, using statistical methods of variable selection is a useful first step, especially when there is a need to model a large number of species or expert knowledge of the species is limited. Future approaches that combine statistical methods with expert input are likely to lead to the most useful models. Statistical variable selection, as we have done here, could be done to create models for a large number of species to identify which ones are most likely to show large changes in predicted suitable climate space under different climate scenarios. Those species would be the ones for which more detailed/focused modeling could be completed. Experts could be consulted to get their input on which variables they believe are most important and to provide feedback on the outputs of the statistical models. Through and interactive process, models for this subset of species can be refined as needed to meet the goals of model creation. Our study also emphasizes the importance of using multiple models to reduce uncertainty and improve map outputs for conservation planning (Jones-Farrand et al., 2011; Marmion et al., 2009; Watling et al., 2015). Where outputs overlap or show the same direction of change there is greater certainty in the predictions. Areas of disagreement can be used for learning by asking why the models do not agree, and may highlight areas where additional on-the-ground data collection could improve the models.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2016.11.016.

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