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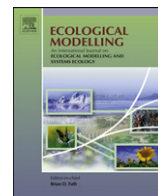
Do bioclimate variables improve performance of climate envelope models?

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ABSTRACT

Climate envelope models are widely used to forecast potential effects of climate change on species distributions. A key issue in climate envelope modeling is the selection of predictor variables that most directly influence species. To determine whether model performance and spatial predictions were related to the selection of predictor variables, we compared models using bioclimate variables with models constructed from monthly climate data for twelve terrestrial vertebrate species in the southeastern USA using two different algorithms (random forests or generalized linear models), and two model selection techniques (using uncorrelated predictors or a subset of user-defined biologically relevant predictor variables). There were no differences in performance between models created with bioclimate or monthly variables, but one metric of model performance was significantly greater using the random forest algorithm compared with generalized linear models. Spatial predictions between maps using bioclimate and monthly variables were very consistent using the random forest algorithm with uncorrelated predictors, whereas we observed greater variability in predictions using generalized linear models.

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1. Introduction

Climate envelope models (CEMs) are an important tool for assessing species vulnerability to climate change and developing adaptation strategies for at-risk species. The general approach is to circumscribe the range of climate conditions currently experienced by a species (the climate envelope) and forecast the future spatial distribution of the climate envelope according to projections of twenty-first century climate change, assuming the contemporary species-climate relationship will hold true (Franklin, 2009). Although CEMs are capable of predicting range shifts in response to climate change (Araújo et al., 2005) and can make predictions similar to those of more complex biophysical models (Kearney et al., 2010), concerns remain about their ability to forecast species responses to environmental change (Austin, 2002; Araújo and Guisan, 2006; Chapman, 2010).

Climate envelope models are generally constructed either from variables describing monthly climate (e.g., mean monthly temperature and precipitation) or 'bioclimate' variables largely derived from seasonal relationships between precipitation and temperature (Table 1). It is generally believed that the most robust models are constructed from variables that affect species most directly (Austin, 2002; Araújo and Guisan, 2006). Bioclimate variables describe seasonal conditions and climate extremes, so it stands to reason that they may be more directly limiting to species than monthly climate variables, and that CEMs constructed from bioclimate variables perform better than models drawing on monthly variables. However, at least one study has found that CEMs made using bioclimate variables perform more poorly than models using monthly climate inputs (Stankowski and Parker, 2010). Few studies systematically compare CEMs constructed from bioclimate or monthly variables, and we lack a thorough understanding of the consequences of variable identity for model performance and spatial predictions; we aim to fill that gap with the current study.

Here we determine whether CEMs built from bioclimate variables differ in performance and spatial predictions from models made using monthly climate variables for twelve species of vertebrates in the southeastern USA (Table 2). We focus on CEM performance and predictions using contemporary rather than future climate data because standard model performance metrics provide a means of evaluating the ability of CEMs to discriminate between areas known to be occupied by species and areas of unknown status. Of the twelve species modeled, some are expected to be strongly affected by climate change (e.g., the American crocodile, an ectotherm whose northern range limit is southern Florida, and the Everglades snail kite, a species

Table 1
Variables used to construct climate envelope models for twelve species of threatened and endangered vertebrates. All 19 bioclimate variables are listed, but superscripts indicate whether variables were included in the subset of uncorrelated predictors ([1]) or the user-defined subset of biologically relevant variables ([2]). Only monthly climate variables included in one of the two data subsets are listed.

Bioclimate variables	Monthly variables
Annual Mean Temperature	January mean temperature[1,2]
Mean Diurnal Range (Mean of monthly (max temp–min temp))[1]	January precipitation[1,2]
Isothermality (annual mean temperature/mean diurnal range × 100)	April precipitation[1]
Temperature Seasonality (variation across 12 months)	May precipitation[1]
Maximum Temperature of Warmest Month[1]	June mean temperature[1]
Minimum Temperature of Coldest Month[1]	June precipitation[1]
Temperature Annual Range (Max temperature of warmest month–min temperature of coldest month)	July mean temperature[2]
Mean Temperature of Wettest Quarter[1]	July precipitation[2]
Mean Temperature of Driest Quarter	September precipitation[1]
Mean Temperature of Warmest Quarter[2]	October precipitation[1]
Mean Temperature of Coldest Quarter[2]	
Annual Precipitation	
Precipitation of Wettest Month	
Precipitation of Driest Month[1]	
Precipitation Seasonality (variation across 12 months)[1]	
Precipitation of Wettest Quarter[1]	
Precipitation of Driest Quarter	
Precipitation of Warmest Quarter[1,2]	
Precipitation of Coldest Quarter[1,2]	

specialized for life in warm seasonal wetlands), whereas other species are threatened primarily by non-climate stressors. However, all focal species are federally listed as threatened or endangered in the United States and are therefore widely viewed as high-priority candidates for the use of climate envelope

models to assess species vulnerability and prioritize policy responses to climate change (Povilitis and Suckling, 2010; Rowland et al., 2011).

2. Material and methods

Models were created for twelve species using two different algorithms (random forest, RF (Cutler et al., 2007) and generalized linear models, GLMs (McCullugh and Nelder, 1989)), two sets of predictor variables (monthly climate and bioclimate) and two approaches to model selection (one using a subset of relatively uncorrelated predictor variables, and the other using a user-defined set of variables expected to be biologically relevant for target species). The 19 bioclimate variables (Table 1) and 24 monthly variables (mean temperature and total precipitation for each month of the year), were obtained from the WorldClim dataset (Hijmans et al., 2005). For each set of predictor variables, two different model selection criteria were used. In the first subset, we removed highly correlated ($r > 0.85$) variables from the analysis. This procedure resulted in a pool of nine relatively uncorrelated ($r < 0.85$) bioclimate variables, and eight relatively uncorrelated monthly variables (Table 1). We defined the second subset of variables based on environmental conditions known to be biologically relevant to organisms in peninsular Florida, where all modeled species co-occur. Because the distribution of many species in Florida is associated with relatively warm year-round temperatures (with extended cold resulting in widespread mortality of both native and exotic organisms, Hallac et al., 2010; Mazzotti et al., 2010), we selected variables describing warm- and cold-season temperatures. Much of peninsular Florida also experiences a seasonal distribution of rainfall, with about 75% of annual rainfall occurring between May and October, and only about 25% between November and April (Duever et al., 1994). Because key life history traits of many of our target species are associated with the seasonal distribution of precipitation (e.g., wood
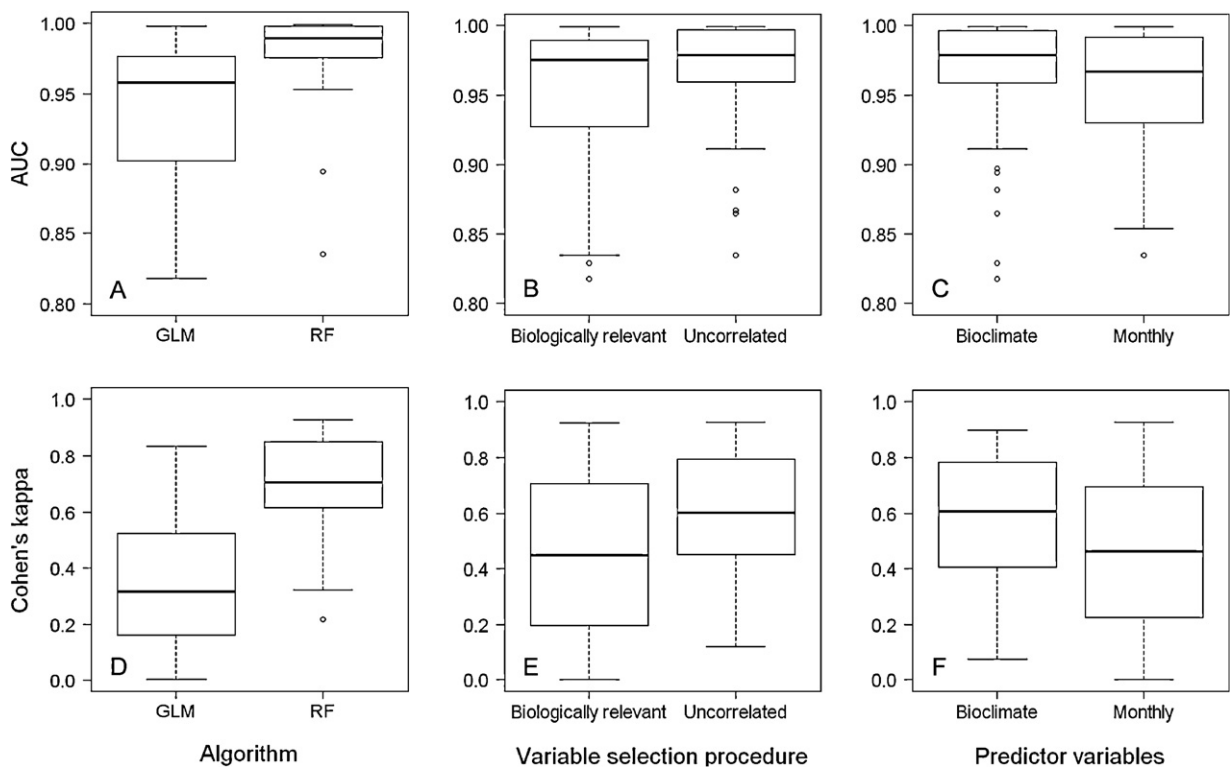
Fig. 1. Box and whisker plots showing differences in two metrics of model performance (the area under the receiver–operator characteristic curve, AUC, and Cohen's kappa) between random forest (RF) and generalized linear model (GLM) algorithms (panels A and D), two model selection approaches (using uncorrelated and biologically relevant variables, panels B and E), and two types of climate variables, bioclimate and monthly (panels C and F).

Table 2
Model performance (Cohen's kappa ('Kappa') and the area under the receiver–operator characteristic curve, AUC) between models for twelve species using bioclimate and monthly climate variables, two algorithms (random forest and generalized linear models, GLM), and two approaches to model selection (using uncorrelated predictor variables and a set of user-defined variables thought to be biologically relevant for the modeled species).

Species	Uncorrelated predictor variables							
	Random forest				GLM			
	Bioclimate		Monthly		Bioclimate		Monthly	
	Kappa	AUC	Kappa	AUC	Kappa	AUC	Kappa	AUC
Mammals								
Florida Panther	0.869 ± 0.041	0.986 ± 0.017	0.836 ± 0.049	0.992 ± 0.011	0.575 ± 0.079	0.959 ± 0.029	0.456 ± 0.064	0.978 ± 0.007
Birds								
Florida Grasshopper Sparrow	0.744 ± 0.140	0.998 ± 0.009	0.704 ± 0.128	0.992 ± 0.024	0.557 ± 0.096	0.997 ± 0.002	0.284 ± 0.125	0.963 ± 0.042
Florida Scrub Jay	0.882 ± 0.030	0.999 ± 0.001	0.895 ± 0.029	0.999 ± 0.001	0.834 ± 0.031	0.998 ± 0.001	0.538 ± 0.047	0.976 ± 0.005
Piping Plover	0.681 ± 0.025	0.963 ± 0.004	0.676 ± 0.026	0.966 ± 0.005	0.529 ± 0.022	0.911 ± 0.008	0.297 ± 0.024	0.835 ± 0.011
Wood Stork	0.759 ± 0.017	0.963 ± 0.004	0.419 ± 0.017	0.705 ± 0.018	0.480 ± 0.017	0.882 ± 0.007	0.121 ± 0.011	0.626 ± 0.014
Audubon Crested Caracara	0.900 ± 0.031	0.999 ± 0.000	0.890 ± 0.030	0.999 ± 0.000	0.830 ± 0.041	0.997 ± 0.001	0.446 ± 0.060	0.968 ± 0.007
Snail Kite	0.837 ± 0.045	0.999 ± 0.001	0.928 ± 0.037	0.999 ± 0.004	0.675 ± 0.077	0.997 ± 0.002	0.127 ± 0.074	0.867 ± 0.034
Whooping Crane	0.600 ± 0.058	0.980 ± 0.011	0.597 ± 0.058	0.983 ± 0.009	0.171 ± 0.111	0.944 ± 0.009	0.233 ± 0.027	0.930 ± 0.010
Red-cockaded Woodpecker	0.696 ± 0.028	0.980 ± 0.005	0.684 ± 0.025	0.979 ± 0.004	0.604 ± 0.027	0.973 ± 0.003	0.518 ± 0.025	0.960 ± 0.004
Amphibians and reptiles								
American Crocodile	0.466 ± 0.059	0.953 ± 0.021	0.467 ± 0.063	0.976 ± 0.010	0.315 ± 0.059	0.865 ± 0.039	0.225 ± 0.035	0.941 ± 0.012
Sand Skink	0.618 ± 0.174	0.998 ± 0.002	0.611 ± 0.156	0.999 ± 0.002	0.275 ± 0.112	0.994 ± 0.003	0.369 ± 0.166	0.995 ± 0.003
Eastern Indigo Snake	0.836 ± 0.026	0.996 ± 0.001	0.841 ± 0.025	0.996 ± 0.001	0.611 ± 0.033	0.971 ± 0.013	0.569 ± 0.033	0.965 ± 0.008

Species	Biologically relevant predictor variables							
	Random forest				GLM			
	Bioclimate		Monthly		Bioclimate		Monthly	
	Kappa	AUC	Kappa	AUC	Kappa	AUC	Kappa	AUC
Mammals								
Florida Panther	0.862 ± 0.049	0.985 ± 0.017	0.807 ± 0.050	0.985 ± 0.016	0.355 ± 0.031	0.979 ± 0.006	0.151 ± 0.012	0.957 ± 0.006
Birds								
Florida Grasshopper Sparrow	0.708 ± 0.122	0.996 ± 0.015	0.705 ± 0.157	0.990 ± 0.026	0.076 ± 0.007	0.976 ± 0.004	0.002 ± 0.007	0.911 ± 0.007
Florida Scrub Jay	0.881 ± 0.030	0.999 ± 0.001	0.881 ± 0.030	0.999 ± 0.001	0.661 ± 0.037	0.990 ± 0.002	0.105 ± 0.005	0.952 ± 0.004
Piping Plover	0.639 ± 0.025	0.959 ± 0.006	0.647 ± 0.025	0.961 ± 0.006	0.323 ± 0.021	0.829 ± 0.012	0.333 ± 0.022	0.854 ± 0.010
Wood Stork	0.740 ± 0.017	0.954 ± 0.006	0.219 ± 0.011	0.835 ± 0.010	0.595 ± 0.020	0.897 ± 0.008	0.169 ± 0.008	0.663 ± 0.007
Audubon Crested Caracara	0.898 ± 0.034	0.999 ± 0.001	0.890 ± 0.029	0.999 ± 0.000	0.430 ± 0.032	0.979 ± 0.003	0.225 ± 0.013	0.937 ± 0.004
Snail Kite	0.808 ± 0.053	0.993 ± 0.010	0.925 ± 0.045	0.995 ± 0.010	0.303 ± 0.027	0.976 ± 0.003	0.021 ± 0.002	0.761 ± 0.030
Whooping Crane	0.581 ± 0.042	0.978 ± 0.010	0.589 ± 0.042	0.981 ± 0.009	0.156 ± 0.056	0.924 ± 0.009	0.175 ± 0.011	0.907 ± 0.006
Red-cockaded Woodpecker	0.676 ± 0.028	0.977 ± 0.005	0.673 ± 0.026	0.975 ± 0.005	0.513 ± 0.023	0.963 ± 0.003	0.438 ± 0.023	0.947 ± 0.004
Amphibians and reptiles								
American Crocodile	0.324 ± 0.057	0.894 ± 0.036	0.645 ± 0.075	0.956 ± 0.026	0.103 ± 0.036	0.818 ± 0.035	0.118 ± 0.013	0.897 ± 0.019
Sand Skink	0.460 ± 0.117	0.989 ± 0.039	0.385 ± 0.183	0.998 ± 0.004	0.079 ± 0.006	0.977 ± 0.004	0.078 ± 0.009	0.976 ± 0.004
Eastern Indigo Snake	0.817 ± 0.027	0.994 ± 0.004	0.828 ± 0.026	0.994 ± 0.003	0.384 ± 0.027	0.961 ± 0.004	0.282 ± 0.018	0.930 ± 0.004

stork fledglings emerge at the end of the dry season when prey are concentrated in drying pools, Ramo and Busto, 1992; reproductive activity of Florida sand skinks is associated with precipitation regimes, Ashton and Telfor, 2006), we also selected variables representing these seasonal precipitation extremes. For this 'biologically relevant' subset of variables we included January (dry season) and July (wet season) temperature and precipitation as monthly variables and precipitation during the coolest quarter, precipitation during the warmest quarter and temperature during the coolest and warmest quarters as bioclimate variables.

Presence data for focal species were obtained from online databases, the primary literature and field observations. We used a modification of the target group approach (Phillips et al., 2009) to define the geographic domain for modeling. Whereas a strict interpretation of the target group approach uses georeferenced presence data for closely related species sampled using similar methods as the focal species (Phillips et al., 2009), we obtained presence data for target group species from a single online database (www.gbif.org), drew the 100% minimum convex polygon circumscribing those target group occurrences, and randomly sampled 10,000 'pseudo-absences' (Chefaoui and Lobo, 2008) from within the polygon defined by the target group occurrences. We defined the target group area for the Florida panther (*Puma concolor coryi*) as the

composite range of all New World felids. The target group for the Florida grasshopper sparrow (*Ammodramus savannarum floridanus*) was defined as the range of full species *Ammodramus savannarum* (which ranges from Canada through Central America to northern South America), for the Florida scrub jay (*Aphelocoma coerulescens*) as the composite range of all *Aphelocoma* spp., for the piping plover (*Charadrius melodus*) as the composite range of all New World species of the genus *Charadrius*, for the wood stork (*Mycteria americana*) as the composite range of New World storks (family Ciconiidae), for the Audubon crested caracara (*Caracara plancus audubonii*) as the combined range of the northern and southern caracara (*Caracara cheriway* and *Caracara plancus*), for the Everglades snail kite (*Rostrhamus sociabilis plumbeus*) as all New World species of the subfamily Milvinae, for the whooping crane (*Grus americana*) 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 (*Picoides borealis*) 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 (*Crocodylus acutus*) was defined as the composite range of all New World crocodilians, for the Florida sand skink (*Neoseps reynoldsi*) as North American species of the *Eumeces + Neoseps* clade from a recent skink phylogeny (Brandley et al., 2005), and for the eastern indigo

snake (*Drymarchon corais couperi*) 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.

We evaluated CEM performance using two metrics: the area under the receiver–operator characteristic curve, AUC, which measures the tendency for a random occupied grid cell to have a higher suitability than a random background cell (Manel et al., 2001; Fielding and Bell, 1997), and Cohen's kappa (hereafter 'kappa'), a measure of agreement between predicted and observed presence/absence that corrects for agreement resulting from chance (Manel et al., 2001; Fielding and Bell, 1997). Metrics were calculated from a cross-validation procedure based on a 75–25% training-testing split of the occurrence data. Because kappa is a threshold-dependent metric, we determined the threshold for converting the probabilistic values returned from models to presence/absence by identifying the threshold at which kappa was maximized (Freeman and Moisen, 2008). To identify that threshold, we ran five replicate model runs using random partitions of the species occurrence data for each 0.01 unit change in threshold between 0.01 and 0.99 and calculated kappa for each randomization. We calculated the average kappa for each unit change in the threshold to identify the threshold at which kappa was maximized. We then used that threshold to calculate kappa for each model.

We tested for significant differences in performance as a function of algorithm (RF or GLM), variable type (bioclimate or monthly), model selection procedure (uncorrelated or biological relevant) and their interaction using a generalized linear mixed-effects model (Bolker et al., 2008) specifying a binomial distribution with a logit link. Algorithm, variable and model selection factors were tested as fixed effects, whereas species was treated as a random effect. The significance of fixed effects and their interaction was tested as the likelihood ratio between the full model and a model with the effect being tested removed.

We evaluated the consistency of spatial predictions between CEMs constructed with bioclimate and monthly variables using a spatial correlation statistic (Syphard and Franklin, 2009). The spatial correlation is calculated by pairing the cell-based observations in one map with the corresponding cells from a second map, and calculating Pearson's correlation (r) across all pairs of cells in the two maps. We tested for significant differences in the consistency of spatial predictions between CEMs constructed using bioclimate and monthly variables between algorithms, model selection procedure, and their interaction using a generalized linear mixed effects model as described for AUC and kappa above. All analyses were run in R (R Development Core Team, 2005) using the base package, randomForest and lme4 libraries.

3. Results

Generalized linear mixed effects models describing effects of variable type, model selection procedure and algorithm on AUC did not differ with or without interaction terms ($\chi^2 = 0.058$, df = 4, $P = 0.999$), so the significance of independent variables was tested against a full model without interaction terms. Models without the effects of the variable being tested were never significantly different from the full model ($\chi^2 = 1.256$, df = 1, $P = 0.262$, $\chi^2 = 0.067$, df = 1, $P = 0.796$, and $\chi^2 = 0.406$, df = 1, $P = 0.524$ for models without the effect of algorithm, model selection procedure and predictor variable type, respectively), and inspection of boxplots revealed minimal differences in AUC between factor levels (Fig. 1A–C).
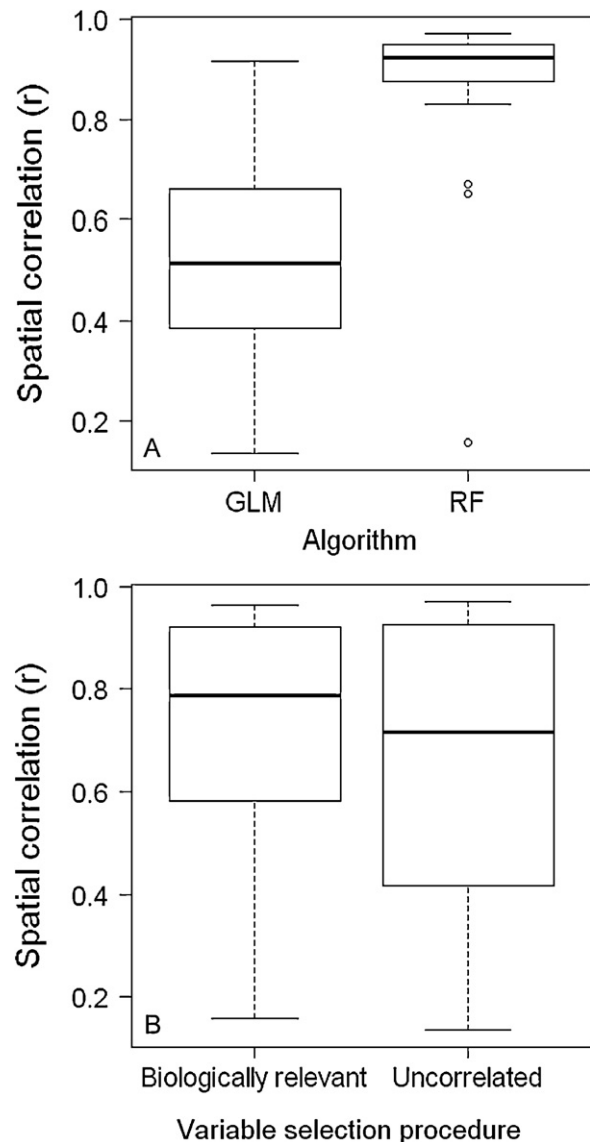

Fig. 2. Box and whisker plots showing differences in spatial correlations (r) between prediction maps using bioclimate and monthly climate variables. Prediction maps were compared using two modeling algorithms, random forest (RF) and generalized linear models (GLM; panel A), and two approaches to variable selection, using uncorrelated and biologically relevant variables (panel B).

As with AUC, generalized linear mixed effects models describing effects of variable type, model selection procedure and algorithm on kappa did not differ with or without interaction terms ($\chi^2 = 1.211$, df = 4, $P = 0.876$), so the significance of independent variables was tested against a full model without interaction terms. However, compared to the full model, the model without the effect of algorithm (GLM or RF) was significantly different ($\chi^2 = 13.148$, df = 1, $P < 0.001$), whereas models without the effect of model selection procedure (uncorrelated or biologically relevant selection) and predictor type (monthly or bioclimate) were not significantly different from the full model ($\chi^2 = 1.430$, df = 1, $P = 0.232$ and $\chi^2 = 1.078$, df = 1, $P = 0.299$ for models without model selection procedure and predictor type, respectively). Kappa was greater, on average, for models constructed using the RF algorithm compared with GLM models (Fig. 1D), whereas variable selection procedure and predictor type have no significant effect on kappa (Fig. 1E and F).

There was no difference between generalized linear mixed effects models with or without an interaction term when describing
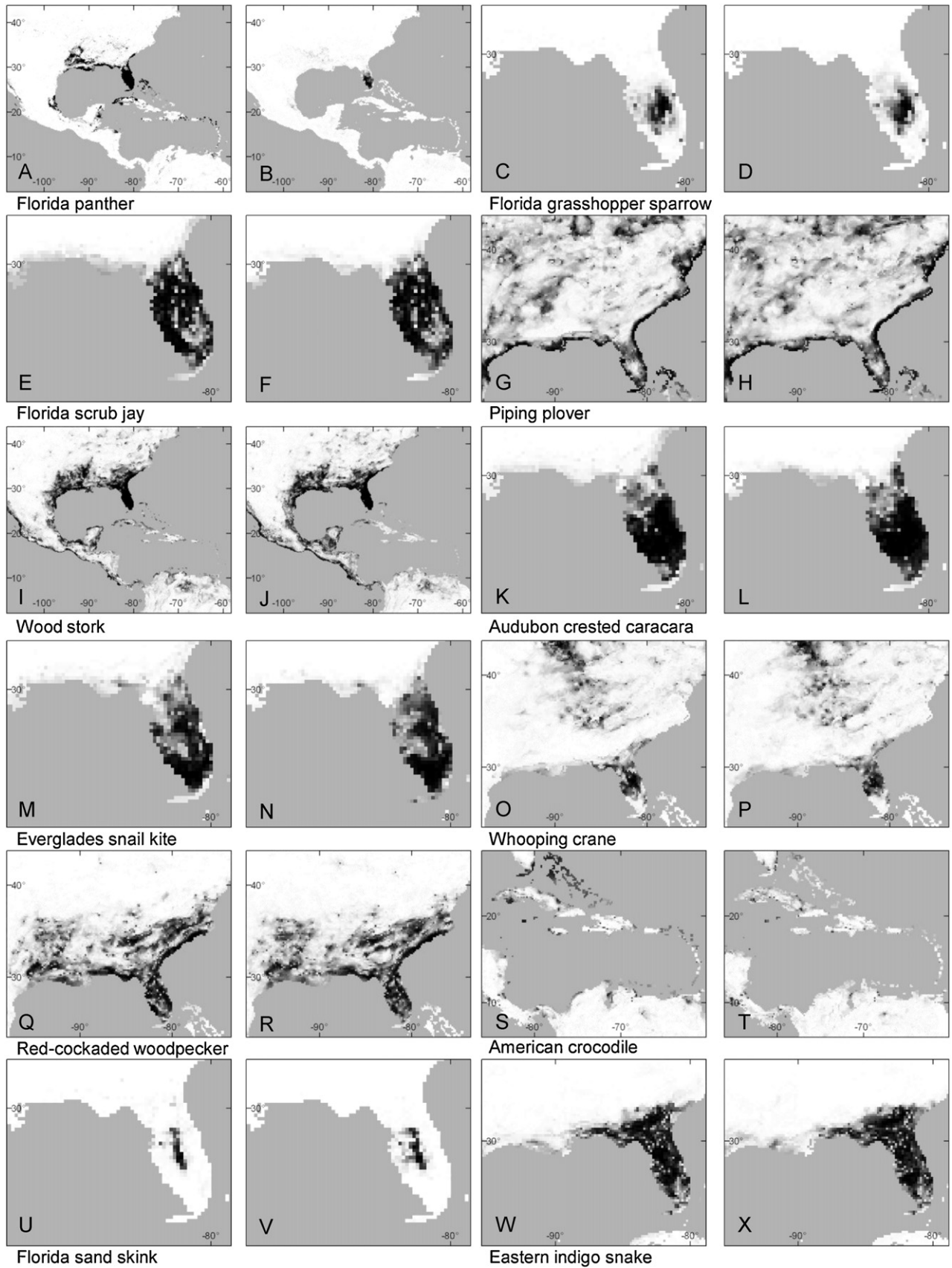
Fig. 3. Prediction maps from climate envelope models for twelve species of threatened and endangered vertebrates in the southeastern USA. Darker colors indicate areas of greater climate suitability. Only prediction maps constructed using the random forest algorithm with uncorrelated predictor variables are shown. The first map for each species shows predictions using bioclimate variables and the second map illustrates predictions using monthly climate variables.

Table 3
Spatial correlation (r) between models using bioclimate (BC) and monthly climate variables (M) for twelve species, two algorithms (random forest and generalized linear models, GLM), and two approaches to model selection (using uncorrelated predictor variables and a set of user-defined variables thought to be biologically relevant for the modeled species).

Species	Uncorrelated predictor variables		Biologically relevant predictor variables	
	Random Forest	GLM	Random Forest	GLM
Mammals				
Florida Panther	0.867	0.137	0.864	0.437
Birds				
Florida Grasshopper Sparrow	0.946	0.373	0.933	0.479
Florida Scrub Jay	0.968	0.530	0.964	0.608
Piping Plover	0.903	0.501	0.886	0.916
Wood Stork	0.882	0.556	0.831	0.673
Audubon Crested Caracara	0.953	0.226	0.941	0.451
Snail Kite	0.932	0.170	0.929	0.357
Whooping Crane	0.912	0.381	0.916	0.689
Red-cockaded Woodpecker	0.960	0.761	0.158	0.868
Amphibians and reptiles				
American Crocodile	0.671	0.392	0.652	0.559
Sand Skink	0.921	0.580	0.925	0.745
Eastern Indigo Snake	0.970	0.443	0.963	0.650
Average ± 1 SD	0.907 ± 0.081	0.421 ± 0.182	0.830 ± 0.228	0.619 ± 0.173

the consistency of spatial correlations between models constructed from bioclimate or monthly variables ($\chi^2 = 1.024$, df = 1, $P = 0.312$), so the significance of fixed effects was tested against the model without an interaction term. The generalized linear mixed effects model without the effect of model selection procedure was not significantly different than the full model ($\chi^2 = 0.244$, df = 1, $P = 0.621$), whereas the model without the term for algorithm was significantly different from the full model ($\chi^2 = 7.226$, df = 1, $P = 0.007$). Thus, we found that spatial correlations between prediction maps constructed from bioclimate or monthly variables were relatively high when the RF algorithm was used, and lower when GLMs were used to create models (Fig. 2A). Spatial correlations between prediction maps constructed from bioclimate or monthly variables did not differ as a function of model selection procedure (e.g., whether uncorrelated or biologically relevant variables were used; Fig. 2B).

4. Discussion

There were no differences in performance between CEMs created with bioclimate variables compared with models constructed from monthly climate variables (Fig. 1C and F). Kappa was higher for CEMs constructed using the RF algorithm than when GLMs were used (Fig. 1D), but no other aspects of model performance varied significantly with algorithm, model selection procedure or predictor variables. Spatial correlations between models created with bioclimate and monthly variables were uniformly high when the RF algorithm was used for modeling (Fig. 2A), whereas there was more spatial variability between prediction maps made using GLMs. Our results suggest that, in general, when using a high performance algorithm (RF), choosing bioclimate or monthly variables for modeling does not significantly alter spatial predictions (Fig. 3).

Based on our analyses, there is no reason to suspect a priori that inclusion of bioclimate variables produces 'better' models than monthly variables. This result stands in contrast to another study that found bioclimate variables produced inferior predictions compared with monthly data inputs (Stankowski and Parker, 2010). That study used only generalized linear models to make predictions, whereas our results are based on the both GLMs and the RF algorithm. Random forests are becoming a popular method for climate envelope modeling (Cutler et al., 2007; Chapman, 2010), and we observed overall greater performance, and more consistent spatial predictions, with the RF algorithm compared to GLMs. In fact, the use of RF in our study eliminated much of the variation, on

average, in both model performance and spatial predictions among species and predictor variable treatments. Additional work investigating model consistency across types of predictor variables and algorithms will help continue to clarify sources of uncertainty in CEMs (Dormann et al., 2008).

Although we found no evidence that using either bioclimate or monthly variables significantly improved CEM performance or altered spatial predictions overall, it is likely that bioclimate variables may be a better choice when modeling species with large geographic ranges and contrasting seasonal regimes. A species that occurs both north and south of the equator, for example, may simultaneously experience summer and winter conditions in the same month. In that case, using bioclimate rather than monthly variables may more meaningfully describe the climate conditions experienced by the species. There was some evidence in our analyses that this may be the case for the wood stork, a species that occurs from northern Argentina to South Carolina. Whereas both AUC and kappa generally indicated very similar performance for CEMs constructed using the RF algorithm with uncorrelated bioclimate and monthly predictor variables (the first four columns in Table 1), the one exception was the wood stork, a species for which both metrics indicated that bioclimate models had greater performance compared to models constructed from monthly variables.

Despite the overall consistency of models created with the RF algorithm, we did observe a discrepancy in spatial predictions even when AUC performance was high for the American crocodile in our study (Tables 2 and 3). Because application of results from CEMs ultimately rests on the spatial predictions they make, good model performance is not sufficient to evaluate model utility. Our results suggest that judicious variable selection may be essential when model predictions will inform climate change adaptation for individual species, because good average performance does not guarantee robust results for all species. When alternative models show similar performance but make competing spatial predictions, it becomes especially important to consider the functional relationship between species occurrence and climate in order to select the 'best' model. Many have argued for more rigorous selection of predictor variables in CEMs (Austin, 2002; Araújo and Guisan, 2006; Austin and Van Niel, 2011), and our work suggests that although in many cases spatial predictions were similar even when different variables were included in models, some species show discrepant spatial predictions even when model performance is high; for those species, rigorous selection of predictor variables is particularly important.

Acknowledgements

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