



Comparing species distribution models constructed with different subsets of environmental predictors

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ABSTRACT

Aim To assess the usefulness of combining climate predictors with additional types of environmental predictors in species distribution models for range-restricted species, using common correlative species distribution modelling approaches.

Location Florida, USA

Methods We used five different algorithms to create distribution models for 14 vertebrate species, using seven different predictor sets: two with bioclimate predictors only, and five ‘combination’ models using bioclimate predictors plus ‘additional’ predictors from groups representing: human influence, land cover, extreme weather or noise (spatially random data). We use a linear mixed-model approach to analyse the effects of predictor set and algorithm on model accuracy, variable importance scores and spatial predictions.

Results Regardless of modelling algorithm, no one predictor set produced significantly more accurate models than all others, though models including human influence predictors were the only ones with significantly higher accuracy than climate-only models. Climate predictors had consistently higher variable importance scores than additional predictors in combination models, though there was variation related to predictor type and algorithm. While spatial predictions varied moderately between predictor sets, discrepancies were significantly greater between modelling algorithms than between predictor sets. Furthermore, there were no differences in the level of agreement between binary ‘presence–absence’ maps and independent species range maps related to the predictor set used.

Main conclusions Our results indicate that additional predictors have relatively minor effects on the accuracy of climate-based species distribution models and minor to moderate effects on spatial predictions. We suggest that implementing species distribution models with only climate predictors may provide an effective and efficient approach for initial assessments of environmental suitability.

Keywords

Bioclimate, extreme weather, Florida, human influence, land cover, species distribution modelling.

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INTRODUCTION

Describing and predicting species distributions are fundamental pursuits in biogeography, ecology and conservation

biology. Correlative species distribution (or ‘environmental niche’) models are commonly used predictive tools which quantify relationships between geo-referenced species occurrences and measurements of environmental variables

(Dormann *et al.*, 2012). A common challenge encountered in species distribution modelling (SDM) is the selection of environmental variables to use as predictors (Araújo & Guisan, 2006). While methods have been developed to assist in predictor selection (e.g. Ashcroft *et al.*, 2011), there remains no consensus on which predictors should be included in SDMs. A common suggestion is to select predictors with direct and proximal effect on species distribution and ecology (Austin, 2002, 2007), resulting in biologically informative and generalizable SDMs (Newbold, 2010). However, in many cases, it may be impractical to include many types of predictors due to data unavailability, time and/or resource limitations, or incomplete ecological knowledge.

One subset of SDMs includes only climate predictors (here, we use the term 'climate-only SDMs'), as climate is a dominant driver of species distributions (Pearson & Dawson, 2003), and recent climate change has become a widely acknowledged global change factor (Lebreton, 2011). Data collection and processing for climate-only SDMs require relatively little effort, and models can be easily extrapolated into new time periods using projections from global and regional climate models. Because of the potential usefulness of their outputs, (i.e. predictive suitability maps) climate-only SDMs have been identified as important tools for guiding future conservation efforts (Elith & Leathwick, 2009).

Although climate predictors are often used in correlative SDMs, some studies have criticized climate-only SDMs based on the lack of evidence for climatic range determination in species distributions (Bahn & McGill, 2007; Beale *et al.*, 2008). Climate-only SDMs may also be considered incomplete representations of complex environmental systems (Araújo & Peterson, 2012), because many other factors may affect species distributions (Heikkinen *et al.*, 2006). In response to those criticisms, modellers often include additional, non-climate predictors alongside climate in correlative SDMs (Austin & Van Niel, 2011).

In this study, we examine the effect of additional predictors in SDMs, by creating models with both 'climate-only' and 'combination' (climate + additional) predictor sets for 14 range-restricted vertebrate species. We created groups of additional predictors describing human influence, land cover and extreme weather [referring to meteorological events occurring over short time frames (1–7 days)]. As these additional predictor groups contain information on general landscape characteristics, we expect them to be useful for describing the ranges of multiple vertebrate species, though the particular predictor(s) within the group may vary by species. Furthermore, all contain dynamic predictors (they change over time), making them of interest for global change studies. We chose not to include predictors describing topographic variation or soils; discussions on these predictors in SDMs can be found elsewhere (Hof *et al.*, 2012; Stanton *et al.*, 2012).

Land cover and human influence are commonly believed to influence species ranges, and have been often included in SDMs (e.g. Pearson *et al.*, 2004; Blach-Overgaard *et al.*, 2010; Junker *et al.*, 2012). Extreme weather/climate has also been

recognized to impact species ranges, particularly at the margins (Seabrook *et al.*, 2014), and strong storms can have substantial effects on species persistence or abundance in a given area (Parmesan *et al.*, 2000). For example, hurricanes (in 1935 and 1960) and subsequent habitat changes are thought to be responsible for the extirpation of the Cape Sable seaside sparrow from its eponymous range (Bass & Kushlan, 1982), and contribute to increased extinction risk for coastal Florida scrub jay populations (Breininger *et al.*, 1999). However, extreme weather predictors are not commonly included in SDMs, potentially due to difficulty in data acquisition, or dismissed because extreme weather patterns may be expected to co-vary with climate (Zimmermann *et al.*, 2009).

Although many studies combine climate with additional predictors in SDMs, fewer include explicit comparisons of climate-only vs. combination models. These studies have generally focused on explanatory power of climate vs. additional predictors and model accuracy differences. For example, Blach-Overgaard *et al.* (2010) combined climate with both land cover and human influence predictors for SDMs of palms in Africa, and compared accuracy among models parameterized with different sets of predictors. Barbet-Massin *et al.* (2011), Luoto *et al.* (2007) and Thuiller *et al.* (2004) examined explanatory power of land cover predictors in SDMs and/or their effect on model accuracy. Zimmermann *et al.* (2009) and Bateman *et al.* (2012) both tested the usefulness of extreme climate and/or weather data in SDMs. With the exception of Bateman *et al.*, each of these studies analysed models for multiple species, but only Barbet-Massin *et al.* used more than a single modelling process. Furthermore, direct comparisons of model prediction maps from different predictor sets were not included in their analyses.

As our focus was on SDM use in an applied conservation context, we modelled distributions of 14 terrestrial vertebrate species or subspecies (six birds, four mammals and four reptiles) occurring only in the state of Florida, USA, and with various protection statuses (Table 1). Since we lack data on future conditions for additional predictors, we built and evaluated SDMs for a contemporary timeframe (~1980–2010). Using seven different predictor sets (two climate-only, five combination) and five different modelling algorithms, we used metrics describing model accuracy, variable importance and spatial predictions to evaluate the influence of additional predictors in correlative SDMs. Our results help inform the selection of predictors for practical SDM applications, particularly for projects in which a common modelling framework is applied for a group of species.

METHODS

Distributional data

Occurrence records for study species were gathered from online databases, the Florida natural history museum and literature sources. We selected only occurrences collected after the year 1975, to reduce temporal discrepancies between

Table 1 Fourteen study species for which models were created in this study, indicating federal/state protection statuses, presences (number of grid cells occupied), and original source of range maps.

Species	Status	Presences	Range map source
Cape Sable seaside sparrow (<i>Ammodramus maritimus mirabilis</i>)	E*	41	IUCN (2013)§
Florida grasshopper sparrow (<i>Ammodramus savannarum floridanus</i>)	E*	32	Shriver & Vickery (1999)
Florida scrub jay (<i>Aphelocoma coerulescens</i>)	T*	880	IUCN (2013)
Florida burrowing owl (<i>Athene cunicularia floridana</i>)	SSC†	253	IUCN (2013)§
Bluetail mole skink (<i>Eumeces egregius lividus</i>)	T*	16	Martin (1998)
Everglades mink (<i>Neovison vison evergladensis</i>)	T†	21	Humphrey & Setzer (1989)
Sand skink (<i>Neoseps reynoldsi</i>)	T*	15	IUCN (2013)
Florida mouse (<i>Podomys floridanus</i>)	SSC†	100	IUCN (2013)
Audubon's crested caracara, Florida population (<i>Polyborus plancus audubonii</i>)	T*	589	IUCN (2013)§
Florida panther (<i>Puma concolor coryi</i>)	E*	824	IUCN (2013)§
Florida worm lizard (<i>Rhineura floridana</i>)	‡	95	IUCN (2013)
Everglade snail kite (<i>Rostrhamus sociabilis plumbeus</i>)	E*	296	IUCN (2013)§
Florida scrub lizard (<i>Sceloporus woodi</i>)	UR*	50	IUCN (2013)
Florida black bear (<i>Ursus americanus floridanus</i>)	T†	80	IUCN (2013)§

Status key (E, Endangered; T, Threatened; SSC, Species of Special Concern; UR, Under Review.)

*Federal (US) listing.

†State (Florida) listing.

‡Not listed.

§Subspecies range was interpreted from species-level IUCN range map.

occurrences and environmental data. We included one occurrence per 0.04 decimal-degree grid cell (hereafter referred to as 4-km, the spatial resolution we applied to all predictors in this study; cell area = ~16 km²). Number of occupied cells varied widely amongst species (range = 15–880, median = 88; Table 1). We also gathered data on the species' geographic ranges, which we used for comparison with modelling outputs (explained below). When possible, range maps were gathered from the International Union for Conservation of Nature (IUCN, 2013); see Table 1 for all range map sources. All range maps were converted to a binary presence–absence format at the 4-km resolution.

Environmental data

Bioclimate

Monthly temperature (minimum and maximum) and total precipitation gridded datasets at a 4-km resolution were downloaded from the PRISM database (PRISM Climate Group, 2012), and averaged for the 30-year period 1981–2010. From these data, we created an initial set of 19 bioclimate predictors, using the *dismo* package (Hijmans *et al.*, 2013) in R (R Core Team, 2013). From this group of 19 we selected *a priori* eight standard bioclimate predictors commonly used in SDMs, describing annual averages, seasonality and highest/lowest monthly values of temperature and precipitation (Table 2; Williams *et al.*, 2003; Barbet-Massin *et al.*, 2011; and Jiménez-Valverde *et al.*, 2011 use similar sets). Because some of the eight standard predictors were highly

correlated (see Table S1a in the supporting information), we decided to test an uncorrelated set of eight bioclimate predictors (all pairwise correlation coefficients (r) < |0.8|) as an alternative. We found that models using the standard predictors had similar or slightly better performance than models using the uncorrelated set for most species, and as recent work suggests that it may be advantageous to include multiple correlated climate variables in SDMs (Braunisch *et al.*, 2013), we decided to use the standard bioclimate predictors for subsequent modelling. Pairwise correlations between all study predictors were subsequently calculated (Table S1).

Human influence

Predictors describing human influence were derived from data sources utilized by the Human Influence Index (Sanderson *et al.*, 2002). Four of the predictors are distance-based (each cell's mean distance from the nearest coastline, navigable waterway, major road or railroad), while the others depict night-time light brightness and human population density (Table 2). Sanderson *et al.* (2002) also incorporated agricultural and urban areas into their HII, but since these were distinct predictors in the land cover set, we excluded them from the human influence predictor group.

Land cover

The University of Maryland's (UMD) global land cover classification at a one-kilometre resolution (Hansen *et al.*, 2000) was used to create land cover predictors. The UMD

Table 2 Environmental predictors used in the current study. The eight random predictors are not listed, all of which range from 0–1.

Environmental predictor	Code	Unit	Range (min–max)	Primary data source
Bioclimate (1981–2010)				
Annual mean temperature	bc1	°C	18.5–25.5	PRISM Climate Group (2012)
Temperature seasonality (standard deviation of monthly means × 100)	bc4	°C	309.5–673.9	PRISM Climate Group (2012)
Maximum temperature of the warmest month	bc5	°C	31.4–34.2	PRISM Climate Group (2012)
Minimum temperature of the coldest month	bc6	°C	2.3–17.7	PRISM Climate Group (2012)
Annual precipitation	bc12	mm	989.1–1728.0	PRISM Climate Group (2012)
Precipitation of wettest month	bc13	mm	139.1–268.6	PRISM Climate Group (2012)
Precipitation of driest month	bc14	mm	36.8–111.0	PRISM Climate Group (2012)
Precipitation seasonality (coefficient of variation of monthly means)	bc15	n.a.	17.0–73.6	PRISM Climate Group (2012)
Human influence (~1990–2000)				
Distance from coastline	d_coast	km	0–119.8	National Imagery & Mapping Agency (NIMA) (1997)
Distance from navigable water	d_nav_wtr	km	0–94.5	National Imagery & Mapping Agency (NIMA) (1997)
Distance from major roads	d_roads	km	0–33.5	National Imagery & Mapping Agency (NIMA) (1997)
Distance from railroads	d_railrds	km	0–156.2	National Imagery & Mapping Agency (NIMA) (1997)
Anthropogenic night-time lights	n_lights	Average light intensity	0–63	Elvidge <i>et al.</i> (1997)
Population density	pop_dens	persons/km ²	0–4130.5	Center for International Earth Science Information Network (CIESIN)/Columbia University, & Centro Internacional de Agricultura Tropical (CIAT) (2005)
Land cover (~1992–1993)				
Water	lc_water	Proportion of cell area	0–1	Hansen <i>et al.</i> (2000)
Forest	lc_forest	Proportion of cell area	0–1	Hansen <i>et al.</i> (2000)
Woodland	lc_wood	Proportion of cell area	0–1	Hansen <i>et al.</i> (2000)
Shrubland	lc_shrub	Proportion of cell area	0–0.9	Hansen <i>et al.</i> (2000)
Grassland	lc_grass	Proportion of cell area	0–1	Hansen <i>et al.</i> (2000)
Cropland	lc_crop	Proportion of cell area	0–1	Hansen <i>et al.</i> (2000)
Bare ground	lc_bare	Proportion of cell area	0–0.1	Hansen <i>et al.</i> (2000)
Urban	lc_urban	Proportion of cell area	0–1	Hansen <i>et al.</i> (2000)
Extreme weather (1981–2010)				
Daily extreme maximum temperature, 1-year return*	tmx_1y	°C	34.0–38.1	NOAA (2012)
Daily extreme minimum temperature, 1-year return*	tmn_1y	°C	–8.7–8.1	NOAA (2012)
Mean annual maximum diurnal temperature range	dmx	°C	22.9–45.7	NOAA (2012)
1-day maximum precipitation event, 1-year return*	pr1d1y	mm	60.5–119.3	NOAA (2012)
7-day maximum precipitation event, 1-year return*	pr7d1y	mm	124.8–210.4	NOAA (2012)
Mean annual number of precipitation days ≥50 mm	pr50yr	# days	3.1–8.8	NOAA (2012)
Tropical storms (within 40 km)†	ts_40	# storms	5–25	Knapp <i>et al.</i> (2009)
Hurricanes (within 40 km)†	hc_40	# storms	0–16	Knapp <i>et al.</i> (2009)

*‘One-year return’ indicates an extreme value for an event that is expected to be met/exceeded once a year, on average.

†The count for total storms covers the period 1900–2010.

classification is derived from satellite data from 1992 to 1993 and divides land cover into 14 classes, which we reduced to eight by combining covers for forest, woodland and shrubland into single classes (Table 2). To create continuous variables from the land cover categories, we aggregated data within 4-km cells (encompassing 16 UMD cells), calculating the proportion of each land cover category in the cell.

Extreme weather

Measures of extreme weather were derived from daily temperature and precipitation records for weather stations in the US National Weather Service's Cooperative Observer Program (National Oceanic & Atmospheric Administration (NOAA), 2012). We gathered data for stations with < 10% missing data for the period 1981–2010, for Florida and extreme southern Alabama and Georgia. Using daily records of maximum temperature, minimum temperature and precipitation, we calculated six measures describing extreme temperature and precipitation events for each station (Table 2). Values for these metrics were spatially interpolated to a 4-km resolution for the state of Florida, using an ordinary kriging technique in ArcGIS Desktop 10.0 (ESRI, 2011). Geo-referenced tracks of hurricanes and tropical storms (storms with winds > 64 knots and > 34 knots respectively) impacting Florida were extracted from the International Best Track Archive for Climate Stewardship (IBTrACS) dataset (Knapp *et al.*, 2009), and a 40-km buffer (i.e. 10 cells) was created around each track to represent a zone of (greatest) storm influence. Because of the long-term impacts of tropical storms and their relative infrequency, we extracted storm tracks for a longer time period than for other predictors (1900–2010).

Random predictors

We created eight predictors with random spatial signatures (noise) and values ranging from 0–1 using the 'Create Random Raster' tool in ArcGIS. Since species distributions are not geographically random, we expect contribution from noisy predictors may reduce accuracy of the models, though high-performance algorithms should minimize this contribution. Incorporating random predictors in SDMs provides (1) a test of an algorithm's ability to mask the influence of additional noisy predictors, and (2) a reference point with which to compare other combination models.

Species distribution modelling

Modelling parameters

We used five algorithms to build SDMs – two regression methods: generalized linear models (GLM) and multivariate adaptive regression splines (MARS), and three machine-learning methods: generalized boosting method (GBM), random forests (RF) and maximum entropy (Maxent). All algorithms were implemented using the *biomod2* package

(Thuiller *et al.*, 2013) in R. Detailed descriptions of the GLM, MARS, GBM and RF algorithms can be found in Marmion *et al.* (2009a), and in Phillips *et al.* (2006) for Maxent. All five algorithms require a presence–absence (PA) dataset to build models. Using suggestions from Barbet-Massin *et al.* (2012) as a guide, we generated 'pseudo-absences' in 10% of unoccupied cells for each species (range = 829–916).

Modelling process

Our modelling process consisted of three general steps, using all five algorithms. The following process describes the methodology for one species. In the first step (predictor ranking), we created models with each predictor group (bioclimate, human influence, extreme weather, land cover and random) separately, in order to identify the most important predictors in each set. To do this, we created models for five PA dataset repetitions (where new pseudo-absences were generated in each repetition) using 100% of the PA data. Using *biomod2*'s algorithm-independent variable importance metric (Thuiller *et al.*, 2009; explained in the *Variable importance* section below), we calculated each predictor's median importance value, for each algorithm across the five PA runs. The average of these values was calculated and used to rank the predictors within each group. In the second step (cross-validation), we created models using eleven different predictor sets: (i) all eight bioclimate predictors (coded bio.8), (ii–vi) the top four most important predictors from each original predictor group (coded bio.4 (bioclimate), hi.4 (human influence), lc.4 (land cover), ex.4 (extreme weather) and r.4 (random)), (vii–x): four combination models using the four most important bioclimate predictors and the four most important predictors from the additional sets (coded bio.hi, bio.lc, bio.ex and bio.r), and (xi) one combination model using the four most important bioclimate predictors plus the four most important predictors from all non-random predictor groups (coded bio.all). Sets ii–xi used the rankings from step one to determine top four predictors. A total of 250 models for each predictor set were run (five algorithms × 50 replications), using one PA dataset and random 75/25 percent training/testing dataset partitions. From these models, we generated statistics describing model accuracy, variable importance and thresholds for suitability maps (described below). In the final step (prediction), we created one model for each predictor set and algorithm combination from step two, using the full PA dataset. These models were used to create one suitability map for each predictor set and algorithm combination.

Model evaluation

Accuracy metrics

Two metrics were calculated to assess accuracy across the 50 replications in the cross-validation step: (1) area under the receiver operating characteristic (ROC) curve (AUC), and (2) the true skill statistic (TSS). The ROC curve plots

sensitivity as a function of commission error (1—specificity), and AUC measures the area beneath this curve, providing a single-value, threshold independent metric of model's ability to discriminate presences and pseudo-absences (Fielding & Bell, 1997). The TSS metric quantifies a model's ability to correctly classify presences and absences (calculated as sensitivity + specificity — 1) for a defined threshold, and has been shown to be independent of species' prevalence (Allouche *et al.*, 2006).

Variable importance

For each cross-validation run, we computed an estimate of variable importance (VI) for all predictors. Briefly, VI is calculated as the correlation coefficient (r) between initial model predictions and model predictions made when the variable in question is randomly permuted — the higher the correlation, the less importance the variable is given (Thuiller *et al.*, 2009). We normalized importance scores for all predictors by calculating the proportion of each predictor's importance relative to the sum of all predictor's importance scores in each model (so that total VI was equal to one), and averaged scores across 50 cross-validation runs. In the five 8-predictor models, we summed the importance scores of non-bio.4 predictors (SUM_{VI}), in order to test for differences in SUM_{VI} related to predictor type and algorithm.

Comparison of predictive suitability maps

To analyse similarity of suitability maps (from the prediction step) regarding predictor set or algorithm, we calculated the spatial correlation between map combinations. Using the continuous probability map output for each model, we calculated pairwise correlation coefficients (r) between maps for each species from different predictor sets (using the same algorithm) and from different algorithms (using the same predictor set).

To further evaluate suitability map predictions, we converted all suitability maps ($n = 30$ for each species) to binary presence-absence (Jiménez-Valverde & Lobo, 2007). We selected thresholds using the ROC plot-based approach (Liu *et al.*, 2005), and averaged thresholds across the 50 cross-validation runs. All values at or above the threshold were considered suitable area in species' final prediction maps. To determine the effect of predictor set and algorithm on suitable area predictions, we calculated the number of cells above the threshold for each map (N_{cells}). We also measured the similarity between mapped suitable area and range maps for each species (Table 1). Similarity was quantified using Cohen's kappa (hereafter kappa), which uses data from a confusion matrix to measure agreement between classes (in this case, presence-absence; Fielding & Bell, 1997). We recognize that range maps can be broad generalizations of species distributions, though they function here only as independent benchmarks for comparing spatial predictions of suitability maps; as such, kappa should not be interpreted as a performance measure.

Model and algorithm comparisons

We used linear mixed-effects (LME) models to fit model metrics (assessing accuracy, variable importance and suitability map predictions, as described in the previous sections) as a function of the predictor set, the algorithm, and their two-way interaction (predictor set * algorithm). Species was included as a random effect. Significance of fixed effects was tested as the likelihood ratio between the full model and a model with the effect tested removed. When the interaction fixed effect was not significant, we tested for pairwise differences between levels within the significant fixed effect(s), by performing post-hoc multiple comparisons tests using Tukey's contrasts on the LME model including only significant fixed effects. The R packages *lme4* (Bates *et al.*, 2013) and *multcomp* (Hothorn *et al.*, 2008) were used to perform LME analyses.

RESULTS

Model accuracy

Prior to analysing our primary question (differences between climate-only and combination SDMs), we tested the validity of the assumption that climate-only models should be considered as a base for comparison, by comparing the accuracy of all 4-predictor models from each predictor group (bio.4, hi.4, lc.4, ex.4 and r.4) in the cross-validation step. This preliminary investigation confirmed that bio.4 models out-performed models from all other sets, with ex.4 the closest in accuracy (Fig. S1). As such, all subsequent analyses focus only on the group of seven climate-only and combination models (bio.4, bio.8, bio.hi, bio.ex, bio.lc, bio.r and bio.all).

Among all species and predictor sets, most SDMs performed well, with overall means of 0.901 for AUC (range: 0.590–0.997), and 0.744 for TSS (range: 0.248–0.984; we list the accuracy of the best-performing algorithm and the mean of all algorithms for all species and predictor set combinations in Table S2). For both AUC and TSS, LME models revealed significant main effects of predictor set (AUC: $\chi^2 = 35.889$, d.f. = 6, $P < 0.001$; TSS: $\chi^2 = 28.281$, d.f. = 6, $P < 0.001$) and algorithm (AUC: $\chi^2 = 191.72$, d.f. = 4, $P < 0.001$; TSS: $\chi^2 = 162.42$, d.f. = 4, $P < 0.001$), but not their interaction. Post-hoc multiple pairwise comparisons tests indicated that bio.hi models had significantly higher accuracy than bio.4 and bio.8 (AUC: both $P < 0.01$). The group [bio.hi, bio.ex, and bio.all] had higher accuracy than bio.r (AUC and TSS: all $P < 0.01$); and bio.lc out-performed bio.r for AUC ($P < 0.01$); Fig. 1(a,b). Despite significant differences in accuracy, the magnitude of differences was small, with only 0.022 AUC points (and 0.034 TSS points) separating highest (bio.hi) and lowest (bio.r) mean accuracy measures. Among algorithms, all pairwise comparisons of accuracy were significantly different for both AUC and TSS ($P < 0.01$), with the exception of Maxent:GBM. Random forests models had the highest mean accuracy (mean AUC:

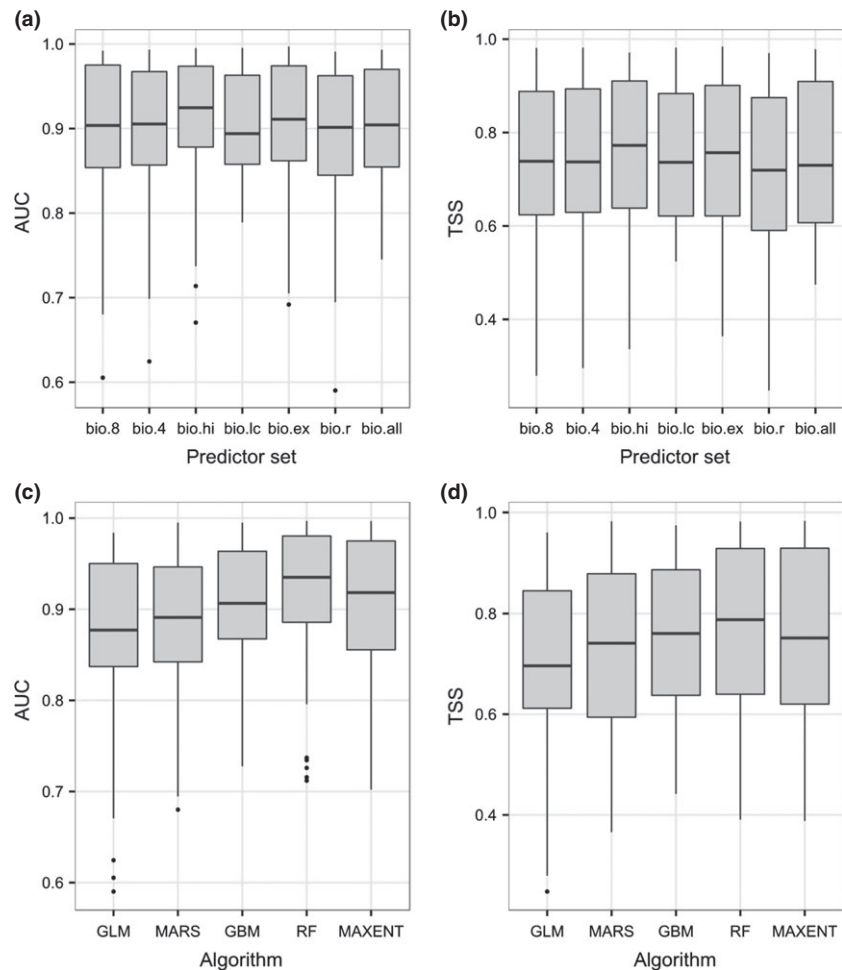


Figure 1 Box-whisker plots illustrating the effects on model accuracy (AUC and TSS) related to predictor set (a,b) and modelling algorithm (c,d). Horizontal lines indicate median values.

0.924; TSS: 0.777), followed by Maxent, GBM, MARS and GLM (mean AUC: 0.875; TSS: 0.702; Fig. 1c–d).

Variable importance

Using our predictor ranking procedure, predictors were chosen at different frequencies for inclusion in four-predictor sets for the 14 species (range: 0–13; Table S3 reports individual predictor selection and importance measurements). In eight-predictor models, mean sum of non-bio.4 importance (SUM_{VI}) was low (mean = 0.226, SD = 0.182). In the six-eight-predictor models, SUM_{VI} was highest in bio.ex and bio.all models; models using the bio.lc and bio.r sets had low contribution from additional predictors. The interaction of predictor set and algorithm was significant in the LME model for SUM_{VI} ($\chi^2 = 28.448$, d.f. = 16, $P < 0.05$); as such we present all simple effects in Fig. 2.

Predictive suitability maps

Mean spatial correlation (across five modelling algorithms) between bio.4 maps and all other sets revealed that maps created with bio.r predictors were the most similar (mean

$r = 0.919$, SD = 0.082), followed by bio.8, bio.lc, bio.ex, bio.all and bio.hi ($r = 0.832$, SD = 0.119). A two-tailed t -test showed that spatial correlation was lower ($P < 0.001$) within predictor sets (i.e. across five modelling algorithms; mean $r = 0.791$, SD = 0.123) than within modelling algorithms (i.e. across seven predictor sets; mean $r = 0.852$, SD = 0.115). Representative suitability maps using all seven predictor sets for the Sand skink (*Neoseps reynoldsi*) are included in Fig. 3, and Table S4 lists spatial correlations for suitability maps for all combinations of predictor sets for each modelling algorithm.

Linear mixed-effects models indicated that predictor set ($\chi^2 = 50.65$, d.f. = 6, $P < 0.001$) and algorithm ($\chi^2 = 146.3$, d.f. = 4, $P < 0.001$), but not their interaction, had significant effects on suitable area predictions (N_{cells} ; see Fig. S2 for N_{cells} plots for each species.). Maps created with bio.r had significantly higher N_{cells} than all other combination models (all $P < 0.01$) in pairwise comparisons. Climate-only models (bio.4 and bio.8) had higher N_{cells} values than bio.all (both $P < 0.01$), as well as bio.lc and bio.hi (for bio.4 only; both $P < 0.01$). Modelling algorithm had a strong influence on N_{cells} , with all pairwise comparisons significantly different ($P < 0.001$) with the exception of the three combinations

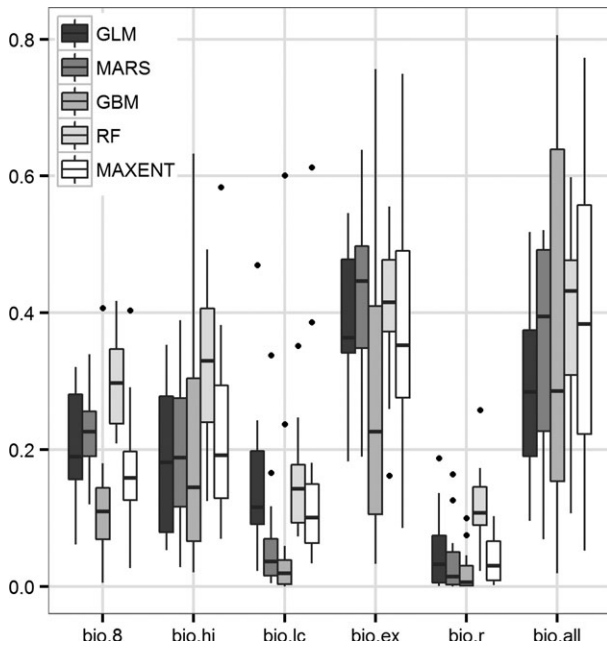


Figure 2 Box-whisker plots illustrating the sum of non-bio.4 variable importance (SUM_{VI}) for all simple effects (predictor set \times modelling algorithm combinations). Horizontal lines indicate median values.

involving GBM, MARS and Maxent. Representative presence-absence maps for the Florida scrub jay (*Aphelocoma coerulescens*) are included in Fig. 4.

As measured by the kappa statistic, overlap between mapped suitable area and range maps varied little among predictor sets; mean kappa ranged from 0.374 (bio.lc) to

0.388 (bio.ex), values considered ‘fair’ agreement (Landis & Koch, 1977). The LME model for kappa revealed algorithm as the only significant main effect ($\chi^2 = 41.591$, d.f. = 4, $P < 0.001$), with mean kappa ranging from 0.359 (RF) to 0.406 (GLM). Kappa values from both RF and MARS prediction maps were significantly lower than those from GLM, GBM and Maxent ($P < 0.01$); Fig. S3.

DISCUSSION

We found that additional predictors in combination SDMs had relatively minor effects on model accuracy, with minor to moderate effects on the area of range predictions (N_{cells}). Suitability map discrepancies were higher among algorithms than predictor sets, and comparisons of presence-absence maps from different predictor sets with species range maps showed no significant differences in agreement. Additional predictors also had lower importance scores than climate predictors in combination models. Our results suggest that climate predictors have a strong influence on combination SDM accuracy and suitability predictions.

Our results indicated minor effects of additional predictors beyond the bio.4 set (the most important bioclimate predictors), whether they represented patterns of bioclimate, human influence, land cover, extreme weather or no pattern at all (random). The group [bio.4, bio.8, and bio.r] did not differ significantly from one another in any of our analyses, suggesting that the most important bioclimate predictors (i.e. bio.4) primarily shaped the patterns in all three models. Combination models [bio.hi, bio.ex, bio.lc and bio.all] provided improvements in accuracy (AUC and TSS) and refined predictions (lower N_{cells}) relative to the model

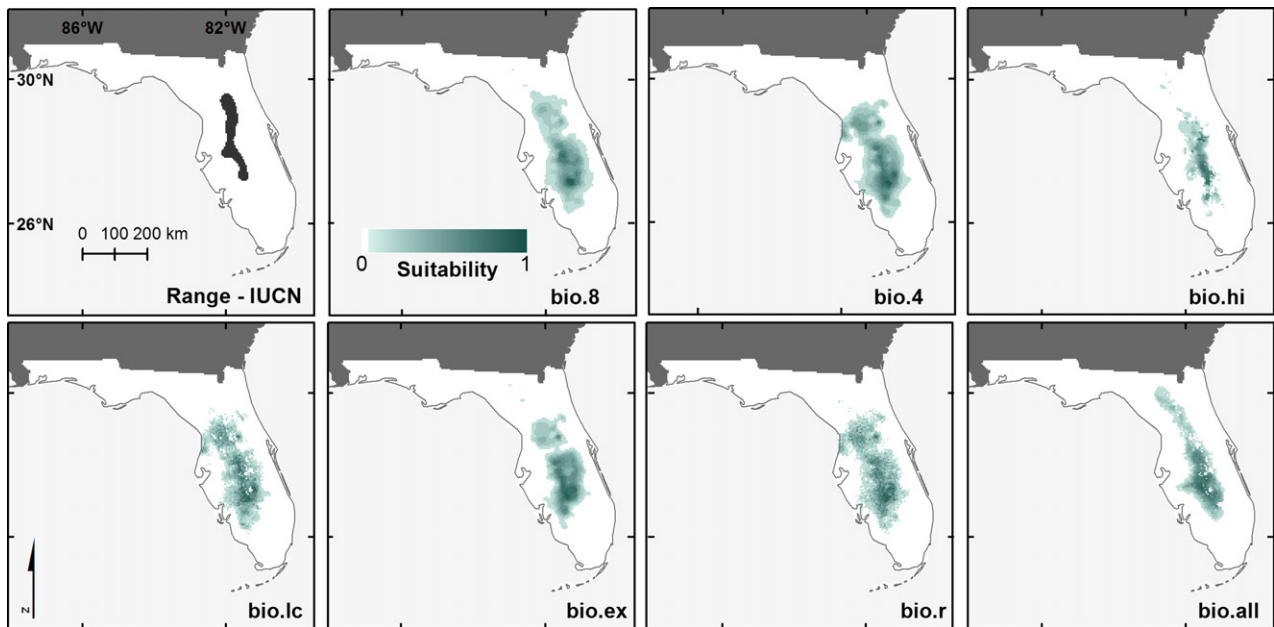


Figure 3 Species range map, and predicted environmental suitability maps for the Sand skink, *Neoseps reynoldsi*, using seven different predictor sets and the maximum entropy (Maxent) algorithm.

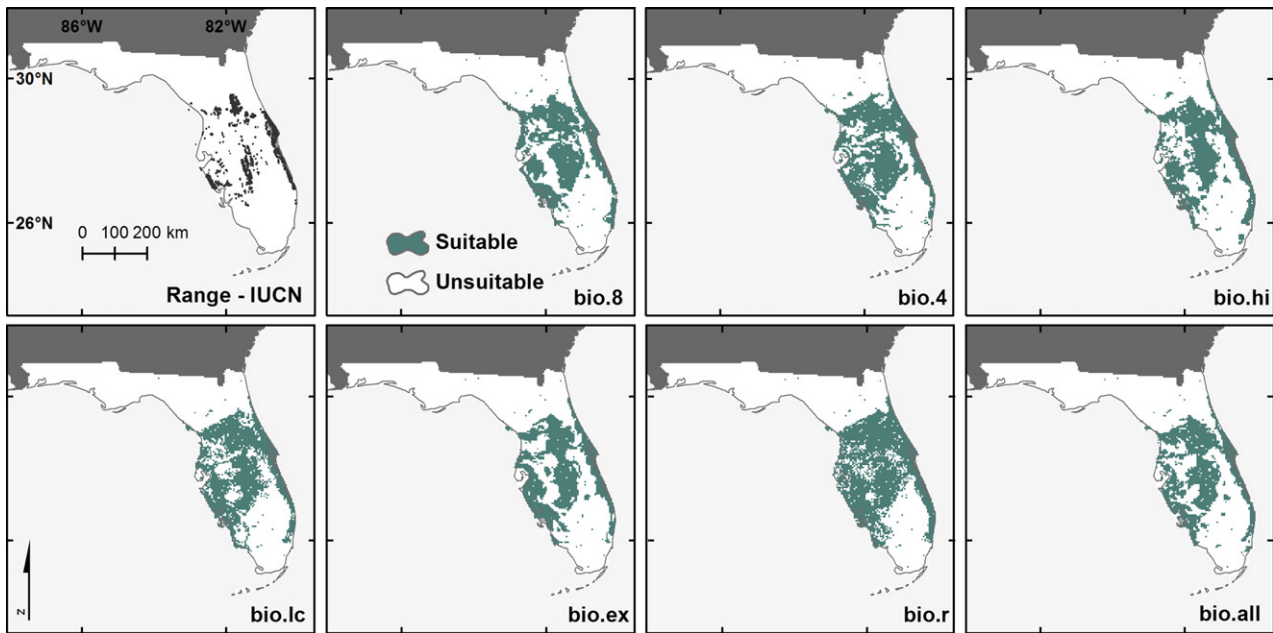


Figure 4 Species range map, and predicted presence–absence maps for the Florida scrub jay, *Aphelocoma coerulescens*, using seven different predictor sets and the random forests (RF) algorithm.

including random predictors (bio.r), but models including human influence predictors were the only ones with both higher accuracy and more refined predictions than climate-only models. While absolute differences in accuracy were minor, this result was generally consistent across species (Table S2). This result differed from that of Blach-Overgaaard *et al.* (2010), who found no significant differences in accuracy of climate-only models vs. those including climate, human influence and land cover predictors. Bio.ex models were the second-highest performing models on average (similar to bio.all), with slightly improved accuracy and refined predictions for most species over climate-only models. This result is consistent with Zimmermann *et al.* (2009), who noted that predictors representing extremes improved accuracy of SDMs by refining predictions at range margins. Accuracy of models including land cover was inconsistent across study species, ranging from slightly reducing accuracy to moderately improving it; we found no significant difference in accuracy between climate-only and climate + land cover models, in slight contrast to (small) significant differences noted by Barbet-Massin *et al.* (2011) and Luoto *et al.* (2007; at 10-km and 20-km resolutions only). Our result mirrors Thuiller *et al.* (2004), who found that including land cover with climate in SDMs for a large group of species in Europe did little to improve model accuracy overall, but generally provided improvement over climate-only models with the poorest predictions. This was evident for two species with the lowest-accuracy climate-only models in this study, the Florida burrowing owl (*Athene cunicularia floridana*) and Florida black bear (*Ursus americanus floridanus*); Table S2. In summary, our results are also consistent with studies finding SDMs with different parameterizations (e.g. differing algo-

rithms, predictor sets, spatial extents) can produce similar accuracy measurements but divergent predictions of suitability (Heikkinen *et al.*, 2006; Hernandez *et al.*, 2008; Domisch *et al.*, 2013).

Examination of variable importance scores provides insight into the minor effects of additional predictors found in this study. While there was some variation among algorithms, SUM_{VI} scores generally indicated that climate predictors contributed more strongly to model predictions than additional predictors. Human influence predictors had generally moderate to low SUM_{VI}, with a large portion of the contribution from the ‘distance to coast’ predictor, which had the highest mean VI among all additional predictors selected for more than two species (Table S3). Among non-bio.4 predictor sets, bio.ex models easily had the highest SUM_{VI}, though this is likely influenced by collinearity with bioclimate predictors (Table S1a). Land cover predictor SUM_{VI} was surprisingly low, qualitatively similar to the random predictors for two algorithms, though there were several high-importance outliers (Fig. 2).

Though not the primary focus of this study, we did note some important differences between modelling algorithms. The high performance of machine-learning algorithms for SDMs is well-documented (Marmion *et al.*, 2009b), and these algorithms (random forests, Maxent and GBM) consistently outperformed regression-based methods (MARS and GLM). The high specificity of the random forests algorithm was also notable, with generally low N_{cells} predictions (Fig. S2). Spatial correlation between suitability maps revealed differential effects of algorithm (Table S4). Notably, the MARS algorithm produced the most dissimilar suitability maps between predictor sets (all $r < 0.859$), while the GBM maps

showed consistently high similarity (all $r > 0.880$), coinciding with low contribution of additional predictors in GBM combination models (Fig. 2).

Several important caveats in our study merit attention. Most importantly, our initial selection of predictors is not exhaustive, and our results should not be extrapolated to imply that only climate predictors are useful in SDMs. Our selection of predictors was limited to groups frequently included in SDMs or implicated in delimiting species ranges, and also for which reliable, accessible data were available. Also, we modelled rare and/or range-limited taxa, so our conclusions may not apply to common species. Distributions of rare species are often more accurately predicted by SDMs than common species (Bahn & McGill, 2007; Franklin *et al.*, 2009), which is reflected by the generally high accuracy of the models. Sampling biases may have affected the significance of anthropogenic-influenced predictors in this study. For example, model response curves for human influence predictors in the Florida worm lizard (*Rhineura floridana*) bio.hi model reveal positive associations with night-time lights and population density (Fig. S4a). While this could be related to certain habitat preferences, it may also be due to the cryptic nature of this species and/or sampling biases towards populated areas, an issue with many biodiversity datasets (Barbosa *et al.*, 2013). In contrast, the intensively sampled Florida panther (*Puma concolor coryi*) exhibited intuitive human-avoiding relationships with population density and distance from coast predictors (Fig. S4b). Also, it is possible that additional predictors tested here may have proved more useful at different scales and/or extents (Austin & Van Niel, 2011). For example, extreme weather predictors representing temperature events at the 4-km resolution cannot account for potentially significant microclimate influences due to local habitat and topography (Suggitt *et al.*, 2011). The importance of land cover information in SDMs can be scale-dependent (Luoto *et al.*, 2007), though this relationship is likely affected by the land cover data chosen (Gillingham *et al.*, 2012). It is possible that the one-km resolution land-cover dataset (or 4-km aggregated resolution) was too coarse to resolve specific habitat associations for species in this study. Fine-scale data on landscape characteristics (e.g. remotely sensed vegetation) have been demonstrated to be useful for SDMs at appropriate spatial resolutions (e.g. Lyet *et al.*, 2013; Shirley *et al.*, 2013). Likewise, the eight-class land cover classification used here may have been inadequate for species associated with rare or specific habitats/vegetation types, in which cases vegetation inventory datasets may be useful (e.g. Matthews *et al.*, 2011). Finally, in this study we did not project models into novel environments (e.g. under climate change), where different predictors may lead to more divergent model predictions (Braunisch *et al.*, 2013; Harris *et al.*, 2013). The issue of predictive SDM modelling with predictors lacking future scenarios is an important one, and needs further research (but see Stanton *et al.*, 2012).

For contemporary predictions of species distributions, we found that climate predictors have a strong effect on SDM accuracy and spatial predictions, and found little evidence

that additional predictors tested here are essential in correlative SDMs. Even so, our results do not suggest that it is detrimental to include additional predictors to climate-based SDMs, only that a parsimonious climate-only approach may be effective for multi-species SDM projects. We expect that novel methods for integrating climate with diverse environmental datasets – within the correlative SDM framework or in conjunction with other methods – will be useful for advancing predictive modelling of species ranges.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Boxplot comparing TSS for all 4-predictor models.

Figure S2 Point plots displaying suitable area predictions (N_{cells}) for individual species.

Figure S3 Box and whisker plot illustrating the effect of modelling algorithm on overlap between range maps and presence–absence maps, as measured by kappa.

Figure S4 Response plots for human influence predictors in random forests bio.hi models for the (a) Florida worm lizard and (b) Florida panther.

Table S1 Pairwise spatial correlation (Pearson's r) between all study predictors.

Table S2 Accuracy (AUC and TSS) of best-performing algorithm and mean for all algorithms for each species and predictor set combination.

Comparing SDMs with different environmental predictors

Table S3 Predictor selection frequency and mean variable importance scores.

Table S4 Pairwise mean (± 1 SD) spatial correlation between probabilistic suitability maps from the seven different predictor sets.

BIOSKETCH

The authors are interested in understanding the environmental factors that shape species distributions. They conduct long-term applied research on invasive species, threatened and endangered species, climate change and human dimensions of natural resource management, with particular emphasis on science support for Everglades restoration.

Author contributions: All authors conceived the idea; D.N.B, M.B., A.M.B., C.S. and J.I.W. collected the data; D.N.B. conducted the analysis and led the writing, and all authors provided comments and revisions to the manuscript.

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