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GEOGRAPHIC RISK ASSESSMENT REVEALS SPATIAL VARIATION IN INVASION POTENTIAL OF EXOTIC REPTILES IN AN INVASIVE SPECIES HOTSPOT

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***Abstract.*—Invasive species are among the primary threats to biodiversity and risk assessment is one problem-solving approach that can prioritize and guide efforts to reduce the negative consequences of invasion. We used a niche-modeling framework to conduct a geographic risk assessment of exotic reptiles in the state of Florida, USA, a region with the highest density of invasive herpetofaunal species in the world. We then compared model predictions with observed records of exotic species across the state. We compiled georeferenced native occurrence locations of exotic reptile species found in Florida and used maximum entropy modeling with global-scale environmental data as inputs. The predicted number of species with suitable habitat was variable across the state and by management units, and it generally decreased with increasing latitude. These predictions were supported by observed richness of exotic species in the lower latitude and the known problem of exotic reptiles in southern Florida. Overall, minimum temperature made the greatest contributions in model predictions, but the level of each variable's contributions varied by species. The overall omission rate with the test data was small, but it was largely variable by species when we used the occurrence locations in Florida. Our use of a niche-modeling for geographic risk assessment of an assemblage of exotic reptile species can be applied cost-effectively to identify areas most susceptible to invasion. The observed large geographic variability in number of potential exotic reptiles suggests that local-scale environmental data can be employed to enhance management applications.**

Key Words.—alien species; biological invasions; climate; land cover type; maximum entropy modeling; species distribution model

INTRODUCTION

The United States is the greatest importer of exotic (nonnative) animals in the world, with more than 1 billion live animals entering the country from 2005 through 2008 (U.S. Government Accountability Office. 2010. Live Animal Imports. Available from http://www.gao.gov/new.items/d119.pdf [Accessed 24 August 2010]). Although there are a number of pathways for the introduction of exotic species (Carlton et al. 2003), escapees from the pet trade can increase propagule pressure and facilitate the establishment of invasive species. Invasive species are a subset of exotic species that sustain self-replacing populations, produce fertile offspring, become widespread, and may cause harm to humans, ecosystems, or the economy (Invasive Species Advisory Committee. 2006. Available from http://www.invasivespeciesinfo.gov/docs/council/isacdef.pdf [Accessed 13 January 2011]; Smith et al. 2009; Richardson et al. 2011). Because of the enormous economic, social, and ecological impacts of invasive species (Blackburn et al. 2008; Smith et al. 2009) and because removal of invasive species can be expensive and labor-intensive once they are established, management agencies seek effective approaches for early detection and removal of exotic species to prevent establishment of invasive species (Colunga-Garcia et al. 2010). Risk assessments, either taxonomic (Kolar and Lodge 2002; Bomford et al. 2009; Fujisaki et al. 2010) or geographic (Peterson and Vieglais 2001; Andersen et al. 2004b), provide one such management tool, by identifying species with a high risk of invasion success and the areas most likely to be populated by invasive species (Andersen et al. 2004a; Davis 2006).

Species distribution models or ecological niche models are frequently used to predict the potential range of exotic species (Welk et al. 2002; Peterson and Vieglais 2001; Andersen et al. 2004b) to assess invasion potential (e.g., their ability to spread over long distances; Richardson et al. 2011). A general approach is to parameterize models based on the native and successfully established range of species and project the defined environmental correlates into the adventive range (Welk et al. 2002; Richardson and Thuiller 2007; Ibanez et al. 2009). Although there are limitations to using species distribution models to forecast invasion risk, the approach has been used to successfully predict invasion risk in areas subsequently shown to have been invaded by target species (Arriaga et al. 2004; Ficetola et al. 2007; Urban et al. 2007). To understand the mechanism of species range shifts in the face of global-scale ecological changes, various methods have been developed that allow predictions using presence-only data, thereby expanding the use of existing-species occurrence data (Elith et al. 2011). Among environmental variables, climate variables (e.g., temperature and precipitation) are often seen as primary driving factors. Models are further refined with additional environmental variables such as land cover type (Pearson et al. 2004; Bradley and Mustard 2006; Ficetola et al. 2007).

The state of Florida, USA, with its subtropical and tropical climates and high human population, provides a unique opportunity to optimize a geographic invasion risk assessment because the sheer number of exotic species that are established, that have failed to establish, and whose fate is unknown (Meshaka et al. 2004; Krysko et al. 2011; Meshaka 2011) allows for efficient validation of model predictions. Furthermore, Florida has been a living laboratory of invasion for decades and several general trends regarding invasion patterns in Florida are apparent. For example, exotic species richness decreases with increasing latitude in Florida (Smith 2006), in contrast to the trend for native species, which show greatest richness in the northern portion of the state (Means and Simberloff 1987). However, covariation among multiple abiotic gradients (e.g., temperature, altitude, and precipitation) and latitude in Florida obscure the primary determinants of the apparent latitudinal gradient in exotic species richness (Means and Simberloff 1987; Krysko et al. 2010). Geographic variation in propagule pressure, such as frequency of introduction, also obscures the cause of this pattern. It is not clear how the number of exotic species that can potentially establish vary spatially and how these variations are affected by environmental factors. The primary objective of this study is to examine geographic variability in the predicted index of suitable conditions and number of species that may potentially establish throughout the state of Florida by applying a species distribution model to an assemblage of exotic reptile species. We also validate model predictions using records of observed locations of exotic reptiles in Florida.

MATERIALS AND METHODS

Study site.—Much of the state of Florida is an approximately 600-km-long peninsula that comprises 151,939 km^2 of land area as a part of the coastal plain in the southeastern United States. Most of the area lies in the subtropical climate zone, which is characterized by hot, humid summers and mild, wet winters (Henry et al. 1994). The southernmost area of the state is generally considered a part of the tropical savanna region with highly concentrated precipitation in warmer months. Mean minimum temperature of the coldest month ranges from 3.3 ºC to 18.3 ºC from north to south (Henry et al. 1994). There is a little variation in mean maximum temperature during the summer from north to south, ranging from 31.7 ºC to 33.3 ºC, but there is a noticeable difference between coastal and interior areas (Henry et al. 1994). The landscape of the state is a mosaic of agricultural, natural, and urban habitats. There are a number of protected areas, such as state and national parks, a national preserve, and national wildlife refuges, in which a variety of native fauna is found. Due to the climatic and geographic virtues, the state is highly susceptible to biological invasions.

Data collection.—Using various sources (described in Fujisaki et al. 2010), we compiled a list of exotic reptiles in Florida that have successfully established. This preliminary list included 51 established species (one crocodilian, 42 lizards, four snakes, and four turtles) and 24 introduced (observed) species, which are exotic species that have been found in Florida and failed to become established or whose status are unknown (12 lizards, five snakes, and seven turtles). Details on the introduction history of these species are available in Krysko et al. (2011). Although additional species have been observed and are potentially established, we included only species for which we could verify the source of information (e.g., museum collection or published literature) at the time of our data collection.

We obtained coordinates of observed locations of species in their native and naturalized range outside of Florida where species have been established for a long term from Global Biodiversity Information Facility (GBIF), a public online database (GBIF data portal. Available from http://data.gbif.org [Accessed 2 April 2010]). We removed erroneous data for which the descriptive location and geographical location (coordinate) did not match. Although use of information outside of the native range could have enhanced distributional predictions (Jiménez-Valverde et al. 2011), we used only known native and naturalized occurrence data for this study because we were not able to identify whether those occurrence locations in GBIF were from individuals that were successfully established. To ensure that models were trained on data only from the native range of a species, we cross-checked occurrence locations with the native and naturalized range of each species outside of Florida, based on the literature, and we removed observations that fell outside of that range. We also obtained occurrence data of exotic animals in Florida from both the Division of Herpetology, Florida Museum of Natural History, University of Florida (UF-

Herpetology), and the Florida Fish and Wildlife Conservation Commission (FWC), and used only accurately georeferenced locations.

Global climate and geophysical data.—We obtained raster data of 19 current bioclimate variables that represent the years 1950–2000 and altitude from the Worldclim database (Available from http://www.worldclim.org [Accessed 26 August 2010]; Hijmans et al. 2005). We used Moderate Resolution Imaging Spectroradiometer (MODIS)/Terra Land Cover Type 2007 data with the International Geosphere-Biosphere Programme (IGBP) vegetation classification scheme, which differentiates 16 classes of land cover (Friedl et al. 2002). We reprojected the raw MODIS data with the MODIS reprojection tool and then resampled the raster data to match the 30 arc-second grid of the climate and altitude data using nearest-neighbor assignments. All land cover classes except for snow and ice are present in Florida. We aggregated the original classes into eight representative classes: forest, shrubland, grasslands, cropland, urban and built-up, barren or sparsely vegetated, wetland, and fresh water.

Model and analysis.—We used the maximum entropy (MaxEnt) algorithm (Phillips et al. 2006; Elith et al. 2011), which (1) efficiently handles interactions between response and predictors (Elith et al. 2006, 2011); (2) produces robust predictions even with a small amount of presence-only data (Elith et al. 2006; Hernandez et al. 2006; Guisan et al. 2007); and (3) is simple to apply and provide associated diagnostic results in readily examinable forms (Phillips et al. 2006), making this method particularly useful in predicting distribution of multiple species. Because we were interested in the potential distribution of assemblages of exotic reptiles and anticipated that only a small number of occurrence records in the native range would be available for some of our target species, these traits of MaxEnt were important. A large number of studies have used MaxEnt to predict potential distribution of exotic species (e.g., Elith et al. 2006; Jimenez-Valverde et al. 2011).

MaxEnt is a machine-learning method for species distribution modeling that uses presence data and background absence data (Phillips et al. 2006) to define a spatially explicit probability distribution of the environmental suitability for a particular species. Following Phillips et al. (2009), we used a target-group background approach that introduces similar biases in the background data and the presence data, such as uneven detection rate and propagule pressure in natural and populated areas. We used the lowest-presence threshold (Pearson et al. 2007) with MaxEnt 3.3.3k, which uses the lowest value of the predicted index (larger values indicate greater suitability) of suitable conditions at locations of species presence as a threshold value. MaxEnt assesses variable contribution during the model optimization process, with improvement made by changes in coefficients associated with each variable converted to percent to quantify the contribution of each variable to the overall model. Another measure of variable importance is permutation importance, which is determined by randomly permuting the values of each variable at training points and measuring the decline in AUC (Area Under the Curve; Phillips. 2014. A brief tutorial on Maxent. Available at from http://www.cs.princeton.edu/~schapire/maxent/tutorial/tutorial.doc [Accessed 20 November 2014]).

Because obtaining reliable variable importance requires the input of uncorrelated variables, we calculated bivariate correlation between the variables and derived a set of uncorrelated variables (r < 0.5). These variables are minimum temperature of coldest month, precipitation of wettest month, precipitation of driest month, precipitation seasonality, altitude, and land cover type. With eight reclassified land cover types, there were 13 predictor variables (eight categorical + five continuous variables). Hernandez et al. (2006) compared modeling algorithms and reported that MaxEnt was the most capable in prediction with occurrence locations as small as 5, 10, and 25. Considering available number of occurrence locations and including representative number of species, we set the minimum number of native occurrence locations to 130 so that there were at least 10 locations for each predictor.

We assessed the predictive performance of the model for each species using the area under the receiver operating characteristic curve (AUC), a threshold-independent measure of model performance that measures the degree to which predicted probabilities at random occupied points exceed those at random background points (Fielding and Bell 1997). We employed 10-fold cross-validation and we randomly split each subset of the native occurrence location data into training and testing subsets, using about 90% of the presence data to train models and the remaining 10% as test cases to calculate AUC. A large difference between training and test AUC values indicates overfitting (Radosavljevic and Anderson 2014). MaxEnt models can restrict predictions to areas where environmental conditions are within those observed in the native range by bounding environmental variables in a process called clamping. It also produces Multivariate Environmental Similarity Surface (MESS) to provide information on whether the environmental variables of the predicted area are within the range of the training data.

To understand regional differences in number of species with above-the-threshold index, we compared number of species with suitable habitat for each group of established and introduced species among 10 regions of the FWC Upland Invasive Plant Working Groups. The

TABLE 1. Summary of AUC and omission rate for training, test, and validation (occurrence in Florida) in MaxEnt prediction of 14 exotic reptiles in Florida.

Species	n	Training AUC	Test AUC	Presence area	Test omission	n Validation	Validation omission
Agama agama	156	0.98	0.97	0.18	0.01	19	1.00
Ameiva ameiva	177	0.95	0.93	0.23	0.03	4	0.50
Anolis chlorocyanus	193	0.96	0.96	0.16	0.01	1	0.00
Anolis cybotes	512	0.95	0.95	0.20	0.00	--	--
Basiliscus vittatus	203	0.96	0.94	0.28	0.01	11	0.27
Calotes versicolor	304	0.96	0.95	0.40	0.01	--	--
Eutropis multifasciata	167	0.95	0.92	0.31	0.02	--	--
Gehya mutilata	350	0.94	0.93	0.55	0.00	--	--
Gekko gecko	144	0.94	0.91	0.31	0.02	5	0.80
Hemidactylus frenatus	442	0.93	0.92	0.90	0.00	1	0.00
Hemidactylus turcicus	973	0.86	0.85	0.72	0.00	8	0.00
Phrynosoma cornutum	615	0.95	0.95	0.96	0.00	--	--
Stellagama stellio	286	0.97	0.97	0.54	0.00	--	--
Tarentola mauritanica	2,536	0.93	0.93	0.50	0.00	--	--

regions of the working groups are as follows: east central, Mosquito Coast, northeast, Panhandle, southeast, southwest, Sun Coast, Treasure Coast, west central, and Withlacoochee. They are also serving as contact points for reporting invasive animals. Using only accurately georeferenced and non-duplicated occurrence locations in Florida provided by FWC, we calculated the omission rate, that is, the number of observed locations that occurred in the area where the predicted probability was below the threshold divided by total number of occurrence locations.

RESULTS

Among all established and introduced reptile species in Florida, we applied the MaxEnt model to predict the index of suitable conditions for 14 species, excluding species for which we did not find a sufficient number of native occurrence locations (Table 1, Appendix 1). The available number of native occurrence locations was highly variable; for the species we modeled, the mean number of native range occurrences after removing duplicate locations was 504.1 (SD = 628.5) and ranged from 144 to 2,536 locations (Table 1). The predicted index was then converted to potential species presence or absence based on the lowest-presence threshold. Overall performance of models for the 14 species was high (mean test AUC = 0.93 ± 0.03 SD, range = 0.85–0.97; Table 1), indicating that, on average, predicted index of suitable conditions at observed locations was greater than the background points (AUC > 0.5 indicates better discrimination than the background points). Visual inspection of response curves and the absence of a large difference between test and training AUC (training AUC minus test AUC < 0.03) did not indicate a problem of overfitting.

By examining differences in predicted values with and without clamping, we confirmed that clamping did not alter the predicted values (i.e., our results were not strongly affected by prediction into environmental space not represented in species native ranges). The MESS indicated that one or some predictor variables in a small portion of Florida along the coast are out of the training data for one species, *Stellagama stellio*; and, thus, a caution is required to interpret the prediction in the area for this species (Appendix 1). Although this species has been observed in Florida, only two known specimens have been collected and its establishment has not been evidenced.

Both predicted index of suitable conditions and number of species above the threshold probability were highly variable across the state (Fig. 1, Appendix 1). The predicted number of species increased in the lower latitude, and the regional summary showed distinct differences between northern and southern regions (Fig. 2); for example, 11 species were above the threshold index in the southern part of the state (Fig. 1). However, this trend was not necessarily consistent for all species. This inverse trend held for most of the species (11 species; Spearman's ρ: -0.94 to -0.74, $P < 0.001$ for all); but for three species (*Hemidactylus turicus*, *Stellagama stellio*, and *Tarentola mauritanica*), the index increased with increasing latitude (Spearman's ρ: 0.83–0.91, $P < 0.001$ for all three species).

Among predictor variables, on average, minimum temperature made the largest contribution to the prediction (42.8%), followed by precipitation of wettest month (20.4%), precipitation seasonality (14.6%), precipitation of driest month (9.1%), land cover type (7.6%), and altitude (5.5%). This order was consistent for the permutation importance, except that the land cover type had the smallest percent (Table 2). For 14 assessed species, there were 181 unduplicated observed

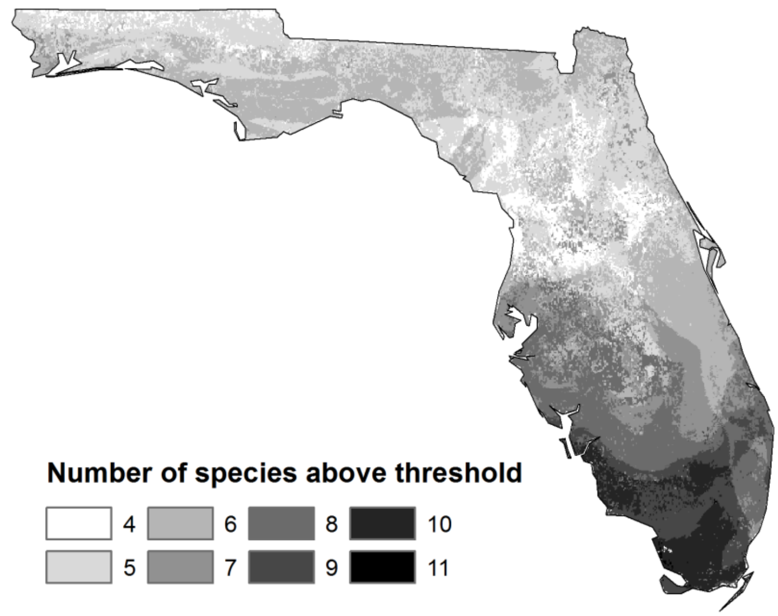

FIGURE 1. Predicted total number of species whose index that the environmental conditions are suitable is above minimum training threshold based on 14 exotic reptiles in Florida using MaxEnt.

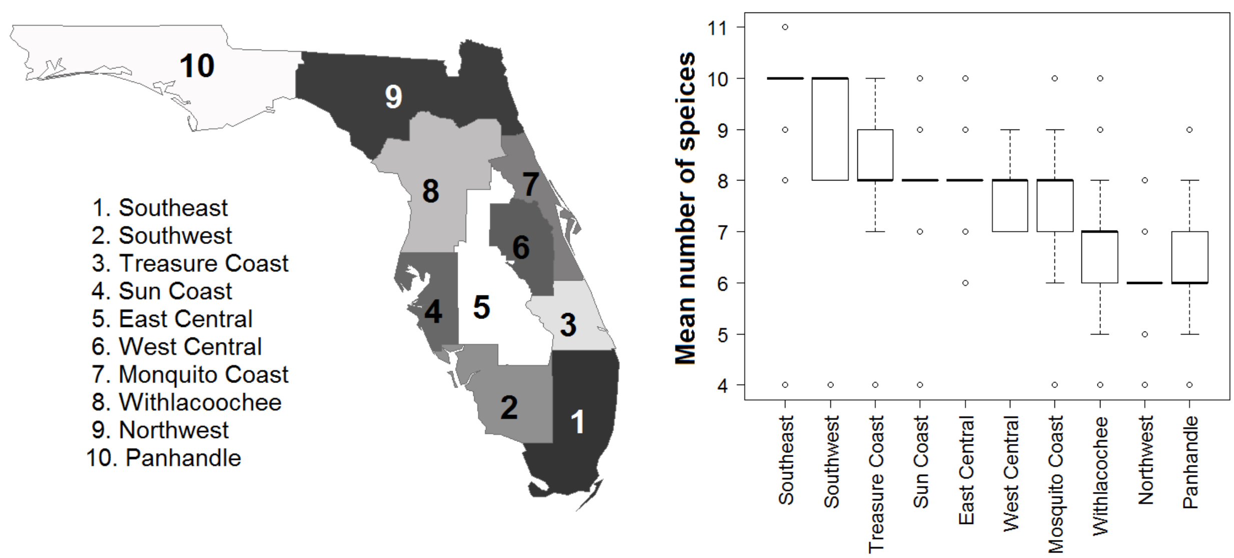

FIGURE 2. A map of 10 Florida regions (left) as defined by the Florida Fish and Wildlife Conservation Committee Upland Invasive Plant Working Group, and box plots (right) of MaxEnt-predicted median probability and number of species above minimum training thresholds in each region. For the box plot, the thick horizontal lines are the medians, the boxes encompass the 1st to 3rd quartiles, and the open circles are outliers.

locations that were accurately georeferenced in Florida. When the test data were used, the overall omission rate was low, ranging from 0 to 0.03 (Table 1). But when the observed location data in Florida were used, the omission rate was highly variable by species, from 0 (no omission) to 1.0 (all omitted; Table 1).

DISCUSSION

Florida is generally thought to be highly susceptible to reptile invasions, but our results showed great variability in the predicted number of exotic reptile species for which conditions are suitable across the state. In general, the predicted number of species was higher in

TABLE 2. Summary of variable contribution and permutation importance of each environmental variables used in MaxEnt prediction for 14 exotic reptiles in Florida. The six environmental variables are: minimum temperature of coldest month, precipitation of wettest month, precipitation seasonality, precipitation of driest month, altitude, and land cover type (forest, shrubland, grasslands, cropland, urban and built-up, barren or sparsely vegetated, wetland, and water).

	Variable contribution (%)				Permutation importance (%)			
Variables	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
Min. temperature	42.76	21.28	9.97	83.58	46.82	20.15	9.32	78.43
Precipitation wettest	20.35	18.83	1.10	67.63	19.51	23.36	0.62	83.14
Precipitation season	14.56	15.27	2.56	56.68	13.45	13.60	1.48	46.88
Precipitation driest	9.18	9.38	0.59	35.59	13.37	8.48	0.97	29.80
Land cover	7.51	11.91	0.15	47.34	1.54	1.32	0.01	4.72
Altitude	5.64	7.09	0.26	24.29	5.30	5.54	0.50	20.91

lower latitudes, underscoring the problems of exotic reptiles in southern Florida, such as the growth of large exotic snake populations in Everglades National Park and the Florida Keys (Snow et al. 2007). In Florida, thermal clines follow a latitudinal gradient, so this observed trend is essentially characterized by climatic factors. In fact, minimum temperature is the dominant factor contributing to MaxEnt predictions, contributing about 42% to predicted probability of suitable conditions. Because of the high correlation between minimum and maximum temperatures, we included only minimum temperature in our prediction; however, for many reptile species, both minimum and maximum temperature have an important influence on physiology and behavior, such as survival and reproduction, and may be determining factors for species distribution (Mazzotti et al. 2011). Because many exotic reptiles in the animal trade are of a tropical and subtropical origin, their native ranges are typically characterized by warm temperatures. Susceptibility of exotic lizards and snakes to cool temperatures was evidenced by the die-off of Burmese Pythons (*Python bivittatus*) in the Everglades region and Green Iguanas (*Iguana iguana*) in southern Florida during a prolonged cold period in January 2010 (Avery et al. 2010; Mazzotti et al. 2011). Previous taxonomic risk assessments also suggested that successful establishment in an exotic range requires that temperatures match those of the native range (Bomford et al. 2009; Fujisaki et al. 2010).

Although climatic factors (temperature and precipitation) made an overall larger contribution in MaxEnt predictions than nonclimatic factors (land cover type and altitude), the level of contributions largely varies by species. Land cover type contributed only 0.16% for *Phrynosoma cornutum*, but the contribution of this variable was 47% for *Stellagama stellio*. This result corroborates a previous study that reported improved model prediction when land cover was included in the predicted variables (Tingley and Herman 2009). Similarly, contribution of altitude showed a large range, from 0.26% (*Eutropis multifasciata*) to 24% (*Phrynosoma cornutum*). This suggests the importance of including these variables despite their relatively small average contribution. With these findings, we note that although our approach to summarizing invasion risk of a target group is useful in elucidating the overall trend, invasion risks vary by species even among the reptile group. In this study, where we examined each variable's contribution separately, a model selection approach could be useful in seeking the best set of explanatory variables (Warren et al. 2011). We also found that MESS values indicated a high uncertainty of invasion risk along the coast by one species (*Stellagama stellio*), which is frequently present in rocky areas in Mediterranean, arid, and semi-arid regions (IUCN, International Union for Conservation of Nature. 2012. The IUCN Red List of Threatened Species. Version 2014.3. Available from www.iucnredlist.org [Accessed 5 January 2015]).

In the face of a growing number of exotic species, numerous efforts have been made to address problematic exotics in Florida, including early detection and removal. One example is the formation of partnerships of federal, state, and local government agencies, tribes, nonprofit organizations, and individuals in 17 geographically stratified areas called Cooperative Invasive Species Management Areas (CISMA). In addition to early detection and removal, CISMA activities include documentation and data management such as maintaining reporting systems, accurately identifying species, ascertaining the introduction pathway and status of establishment, and georeferencing observed locations. Information about species observations and the status of each specimen (whether successfully established or not) obtained by these efforts is valuable, especially with the availability of a tool such as MaxEnt, which allows us to readily produce the predictions and diagnostic outputs. In this study, we used only occurrence locations in native and naturalized ranges where species has been established for a long term outside of Florida for predictions because of uncertainty about the status of observed specimens outside of these ranges in the GBIF database. Information on the status of observed specimens allows us to use the occurrence data in the state for training and formal validation. Notably, the occurrence data in Florida that we used to calculate the omission rate did not indicate the establishment status of each specimen. Whereas lower omission rates with test data (subset of native occurrence locations) than with the validation data we observed was general when the independent validation data set is used (Hijimans 2012; Syfert et al. 2013), this unknown status of the individuals in the validation data possibly contributed to a large omission rate of some species.

Use of occurrence locations outside of the native range of a species is a way to improve the model in accounting for the adaptability of species to establish outside of environmental conditions in their native range. The threshold method is another factor that could affect the omission rate. We used minimum training value because of small number of occurrence data for several species. This method is considered appropriate to guide fieldwork to identify unknown distribution or undiscovered species (Pearson et al. 2007). But there are a number of methods and another commonly used method is to balance sensitivity and specificity, such as maximum sum of sensitivity and specificity (Liu et al. 2013).

The geographic assessments we conducted here can extend the knowledge gained through previous risk assessments by identifying specific geographic areas that are highly vulnerable to invasions by particular species or groups of species. Our results could be further refined by using finer-scale data of land cover type, which can vary within a small management unit. Finer-scale predictions of habitat suitability would allow planning of location-specific management activities such as monitoring and inventories, even within smaller management units such as natural areas (e.g., national parks and preserves, state parks) and agricultural areas. Also, some studies accounted for life history traits and human factors, which tend to correlate to invasion success, in predicting establishment success of alien reptiles (Fujisaki et al. 2010; Mahoney et al. 2015). In the present study, we only considered environmental factors, but these factors are also important in the invasion process and thus including these variables may improve the predictions. Finally, the choice of modelling algorithm is one of the primary determinants of overall model performance (Dormann et al. 2008). Choice of the model may depend on the applications and data sets. Sound advice and cautions as well as limitations of MaxEnt are found in many articles including Phillips (2008), Rodda et al. (2011), and Kriticos et al. (2013).

Since we created our list of target species, additional exotic herpetofaunal species have been introduced and become established in Florida (Kenneth L. Krysko, pers. obs.). Some institutions in Florida, such as UF-Herpetology, have been working toward accurately georeferencing occurrence locations in the state and make the data available online (https://www.flmnh.ufl.edu/herpetology/) or shared with other online databases such as GBIF and HerpNet (http://www.herpnet.org). Such data could be useful to further improve our predictions. Further, numerous imported exotic reptile species have not yet been observed in the wild but could be introduced through various pathways. Previous taxonomic risk assessments of exotic species have proposed various algorithms to predict potentially invasive species and have discussed their utility in invasive species management (Hayes and Barry 2008). Such assessments have been a part of the Australian national screening protocol for plants (Pheloung et al. 1999; Keller et al. 2007) and have been recommended for introduction as a part of invasive management practice in the United States (Lodge et al. 2006). Geographic assessments such as ours can be used to develop cost-effective management strategies by depicting spatial variability in habitat suitability for established, introduced, and imported species over wide geographic areas with variable environmental conditions.

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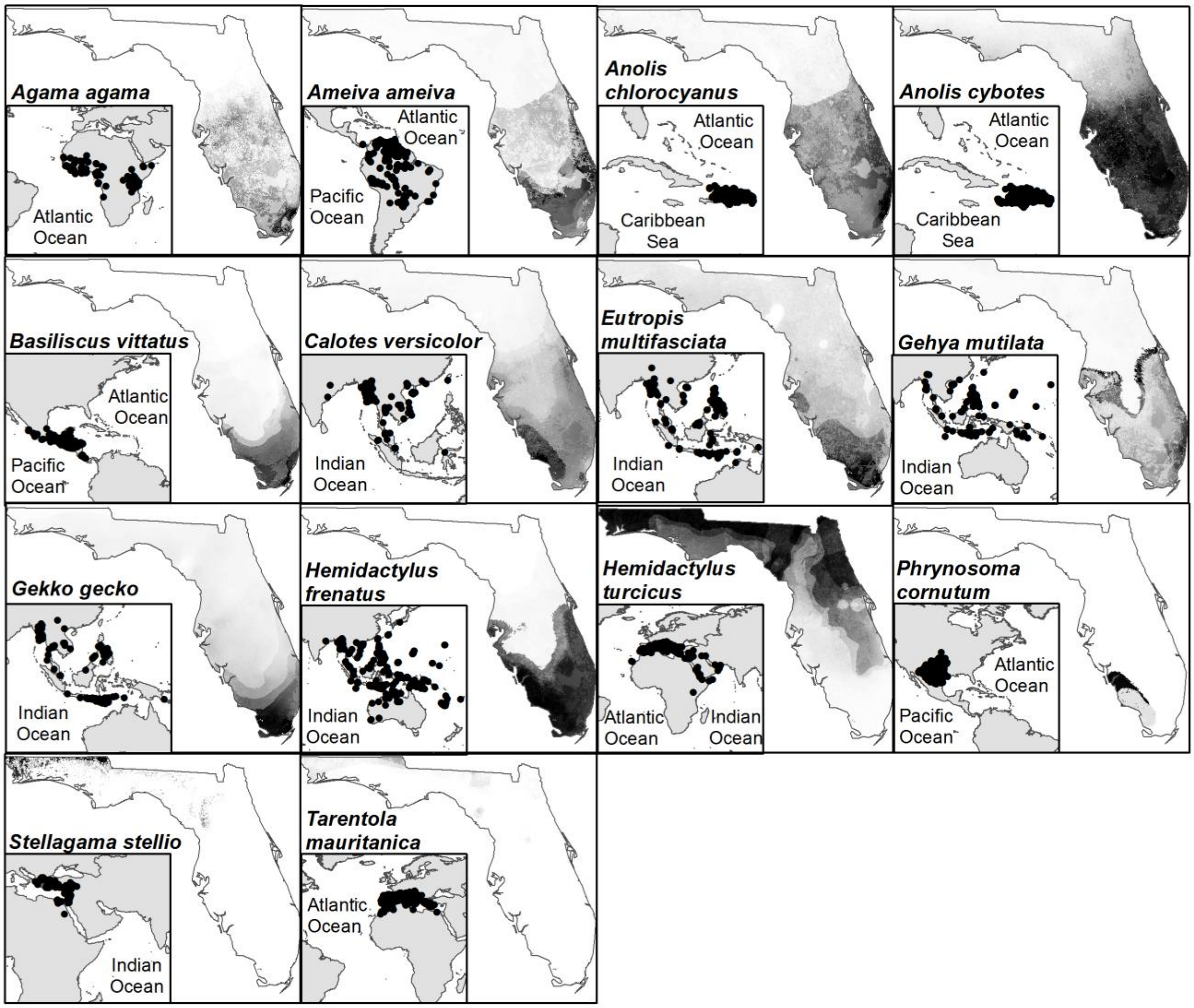
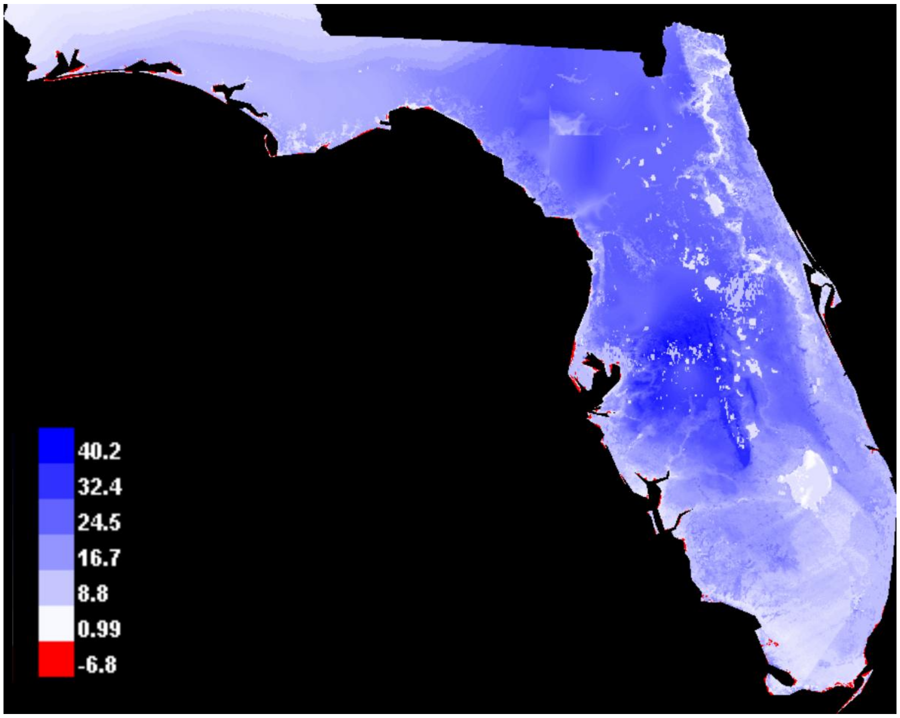


APPENDIX 1. Predicted index that habitat is suitable in Florida for 14 assessed species. Grayscale indicates low (light tone) to high (dark tone). Map in the inset boxes show occurrence locations in native, extended, and naturalized range where species are known to be established.



Appendix 2. Multivariate Environmental Similarity Surface (MESS) of *Stellagama stellio*. Predictions of the red areas require a caution because one or more predictor variables are out of the range of the training data.