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Evaluating ecological niche model accuracy in predicting biotic invasions using South Florida's exotic lizard community

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Abstract

Aim: Predicting environmentally suitable areas for non-native species is an important step in managing biotic invasions, and ecological niche models are commonly used to accomplish this task. Depending on these models to enact appropriate management plans assumes their accuracy, but most niche model studies do not provide validation for their model outputs. South Florida hosts the world's most globally diverse non-native lizard community, providing a unique opportunity to evaluate the predictive ability of niche models by comparing model predictions to observed patterns of distribution, abundance and physiology in established non-native populations.

Location: Florida, USA.

Taxon: Lizards.

Methods: Using Maxent, we developed niche models for all 29 non-native lizard species with established populations in Miami-Dade County, Florida, using native range data to predict habitat suitability in the invaded range. We then used independently collected field data on abundance, geographical spread and thermal tolerances of the non-native populations to evaluate Maxent's ability to make predictions in both geographical and environmental space in the non-native range.

Results: Maxent performed well in predicting across geographical space where these non-native lizards were most likely to occur, but within a given geographical extent was unable to predict which individual species would be the most abundant or widespread. Comparisons with physiological data also revealed an imperfect fit, but without any consistent biases.

Main conclusions: We performed one of the most extensive field validations of Maxent's ability to predict where invasions are likely to occur, and our results support its continued use in this role. However, the program was unable to predict the relative abundance and geographical spread of established species, indicating limited utility for identifying which invasive species will be the greatest management concern. These results underscore the importance of other factors, such as time since introduction, dispersal ability and biotic interactions in determining the relative success of non-native species post-establishment.

KEYWORDS
biological invasions, climate suitability, ecological niche model, lizards, Maxent, model validation, non-native species, thermal tolerance

1 | INTRODUCTION

The global redistribution of biodiversity in the Anthropocene is intensifying the threat invasive species pose to native ecosystems (Hobbs, Higgs, & Hall, 2013; Hoffman et al., 2010). Methods that aim to identify regions at risk of invasions, as well as likely future distributions of non-native species once established, are incredibly valuable for conservation biologists and practitioners. Ecological niche models (ENMs) have revolutionized the fields of ecology, biogeography and conservation biology by utilizing occurrence localities and associated environmental data to map a species' niche in both geographical and environmental space. Therefore, one of the most important applications of ENMs lies in their ability to predict the success and distribution of biotic invasions (Ficetola, Thuiller, & Miaud, 2007; Jeschke & Strayer, 2008). However, the accuracy of these predictions is rarely tested, which has profound effects on how well the models are trusted when making conservation and management decisions. A study validating ENM predictions of the establishment and spread of species across a non-native region using independently derived field data could provide guidance on which model predictions are most accurate.

Maxent (Phillips, Anderson, & Schapire, 2006) is one of the most widely used ENM algorithms, outperforming other ENMs, especially with limited data availability (Elith et al., 2006). A presence-only method that demonstrates strong predictive abilities with as few as 15 known localities (Pearson, Raxworthy, Nakamura, & Peterson, 2007), Maxent can be applied to a broad range of species. It performs well at predicting known occurrences (Elith et al., 2006), outperforms other models at all sample sizes (Wisz et al., 2008), and makes predictions consistent with mechanistic models (Kearney, Wintle, & Porter, 2010). Maxent is also a useful tool for projecting into novel environmental conditions, such as those in non-native ranges or climate change scenarios (Elith, Kearney, & Phillips, 2010; Strubbe, Beauchard, & Matthysen, 2015). However, despite being widely adopted throughout the fields of ecology and evolution, there is continued debate regarding the accuracy of these model predictions (Araújo & Peterson, 2012).

More studies are needed that evaluate the predictive power of Maxent models and determine: (a) which model outputs provide accurate predictions and (b) under what set of conditions (of either the underlying data or the model building procedure) this predictive power is maximized. A common model validation method is to partition the locality dataset into training and test sections to build and evaluate the model, respectively (Fielding & Bell, 1997). However, this approach inflates model performance as training and test locality data were likely collected with the same sampling biases and are thus spatially correlated. Geographical rather than random data partitions can overcome this bias (Radosavljevic & Anderson, 2014), but assume niche homogeneity across partitions, which may not be true when local adaptation is present. These methods are also only applicable when evaluating model performance in the range from which the original locality

data were collected, and we cannot assume the same level of accuracy applies when the model is projected onto environmental conditions that are distant in either space (non-native range) or time (climate change scenarios). It is therefore most accurate to validate predictions with independently collected field data from the same geographical areas being projected to. Few studies, however, have carried out this approach (e.g. Costa, Nogueira, Machado, & Colli, 2010; Searcy & Shaffer, 2014; West, Kumar, Brown, Stohlgren, & Brombreg, 2016).

In this study, we performed an extensive field validation of Maxent's ability to predict biotic invasions by utilizing the world's largest community of non-native lizards, which is found in Miami, Florida. Our objective was to test Maxent's accuracy at predicting: (a) where these non-native lizards are most likely to occur across geographical space, and (b) their relative success within a given geographical area. This was accomplished by comparing Maxent's predicted habitat suitability for all 29 non-native lizard species established in Miami-Dade County to multiple datasets representing observed geographical spread and relative abundance. We also collected physiological data on thermal limits for 10 of these non-native species to evaluate Maxent's response curves, which are an output that plots suitability against each individual environmental variable used in the model (Phillips, 2010). These response curves define the *n*-dimensional hypervolume of the niche model in environmental space, which is then projected into geographical space. Most model validations exclusively focus on the geographical projections, and very few have analysed the individual response curves on which they are based (e.g. Buermann et al., 2008; Convertino et al., 2012; Searcy & Shaffer, 2016; Williams, Belbin, Austin, Stein, & Ferrier, 2012).

2 | MATERIALS AND METHODS

2.1 | Niche Modelling in Maxent

We produced ecological niche models for 29 non-native lizard species established in Miami-Dade County, and for one native species, *Anolis carolinensis*. For each species, we used native range data obtained from the Global Biodiversity Information Facility (https://www.gbif.org) and VertNet databases (https://www.vertnet.org) to project habitat suitability into the invaded range (Florida). We removed outliers (geo-referencing errors or invasive range localities) by making comparisons to native range maps. The number of native range localities per species ranged from 17 to 1283, with an average of 436.

Models were built using Maxent, a presence-only algorithm that compares known presences to background points drawn from a predefined geographical extent. It is important for this geographical extent to represent the area the target species would be capable of colonizing if the habitat were suitable (Anderson & Raza, 2010). To generate these biologically realistic geographical extents, we created unique buffer distances for each species that approximate their dispersal limitation on an evolutionary time-scale (this is a

generalization of the method used in Searcy & Shaffer, 2014). To do this, we calculated the distance between the two most spatially segregated clusters of native range localities for each species, because over its evolutionary history a species must have either occurred continuously across, or dispersed across, this distance and would presumably still occur in the intervening area if the habitat was suitable. To perform this calculation, we used the 'cluster' package (Maechler, Rousseeuw, Struyf, Hubert, & Hornik, 2017) in R 3.3.2 (R Core Team 2017). The buffer distance was then half of this calculated inter-cluster distance, as this is the minimum distance that ensures all habitat along the straight line between the two clusters is included in the geographical extent. The geographical extent for each species was thus all the known native range localities surrounded by this buffer distance.

The default in Maxent is for the background points to be randomly selected from within the geographical extent. This approach, however, fails to account for sampling bias, as background points may be chosen from areas that are suitable but less accessible, and thus void of locality data. To account for sampling bias, we used target group background points (Phillips et al., 2009) rather than random ones, using all other squamates as our target group. This ensures that all background points were visited by squamate researchers, who thus had a reasonable probability of recording the target species if it were present. For our models, the average number of background points was 3530, ranging from 27 to 28196.

Climate is one of the most important predictors of species distributions (Algar, Mahler, Glor, & Losos, 2013; Thuiller, Araújo, & Lavorel, 2004), and climate matching between native and invasive ranges has a strong influence on establishment success (Bomford, Kraus, Barry, & Lawrence, 2009; van Wilgen, Roura-Pascual, & Richardson, 2009). Thus, most studies using Maxent to predict invasive ranges use climate data (e.g. Filz, Bohr, & Lötters, 2018; Jovanović et al., 2018; Suzuki-Ohno et al., 2017). To evaluate this common use of Maxent, we built our models using the 19 Bioclim variables at ~1-km^2 resolution (downloaded from WorldClim; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). These are the environmental variables most often used in niche modelling (Booth, Nix, Busby, & Hutchinson, 2014), and one of the only global environmental datasets covering both native and invasive ranges for these organisms.

To prevent potential overfitting of the models, Maxent has a built-in regularization procedure that balances model fit and complexity. The default values for the regularization parameters have been chosen to provide the best average fit across a wide range of species (Phillips & Dudík, 2008). However, for any given species, they may over or underfit the data, so we used model selection to identify the optimal regularization multiplier for each species (Warren & Seifert, 2011). We created two models for each species, one model using the default feature settings and the other with user-defined features, choosing linear, quadratic and product (LQP) features, which are expected to generate smoother response curves (Phillips & Dudík, 2008). For each model, we tested 25 regularization multipliers ranging from 0 to 1 in

increments of 0.2 and integers 1–20. We then chose the best multiplier based on AIC$_c$ and used that value when constructing each final model. We ran the models using 10-fold cross validation to calculate the average area under the Receiver Operating Characteristic curve (AUC) of all runs. AUC is a measure of Maxent's ability to accurately order occurrence and background points along a scale of suitable to unsuitable climatic habitat and is commonly used as an indicator of model performance (Elith et al., 2006).

After completing the models, we wanted to test whether inaccuracies in the original occurrence data might have skewed the results. To do this, we deleted all occurrence points that had a geographical uncertainty ≥1000 m. We used this filtered dataset to create new models for each species as described above. All models were implemented using the 'dismo' package (Hijmans, Phillips, Leathwick, & Elith, 2017) in R.

2.2 | Comparing predicted habitat suitability to survey data

We first assessed Maxent's ability to predict across the invasive range where non-native lizards are most likely to occur. To do this, we averaged the predicted habitat suitability for all 29 species and then calculated the mean of this variable within each of Florida's 67 counties. We then calculated the total number of records for these 29 species in each county (using the GBIF data) and used multiple linear regression to determine whether mean predicted habitat suitability could predict this measure of non-native lizard abundance, using county area as a covariate.

We then compiled multiple datasets that represent relative invasion success (abundance and geographical spread) of Miami-Dade County's 29 established exotic lizard species. These datasets consist of: (a) herpetofaunal field surveys conducted in 30 parks spread throughout Miami-Dade County from March to May 2017 (S. L. Clements, pers. comm.) recording both total abundance and number of park presences for each non-native lizard species, (b) the number of Florida counties each species has been recorded in (Krysko, Enge, et al., 2011), (c) the number of known localities in both Florida and Miami-Dade County where each species occurs based on the GBIF database, and (d) the Krysko, Burgess, et al. (2011) dataset, which assigns each species a ranking from 1 to 5 based on how abundant and widespread its established populations are in Florida.

We again used multiple linear regression to evaluate how well Maxent models predict each of these measures of relative spread and abundance. These tests assess Maxent's ability to predict relative invasion success within a given geographical extent. For the survey data and the number of GBIF localities in Miami-Dade County, the predictor variable was mean habitat suitability predicted by Maxent across Miami-Dade County. For the other success metrics, we used mean predicted habitat suitability across all of Florida as the predictor. For all analyses, we used the year each species was introduced to Florida as a covariate to account for how long they have had to reproduce and spread.

2.3 | Comparing response curves to physiological data

We also tested the accuracy of Maxent's response curves using thermal tolerance data measured from 10 species caught in the Miami area (Table 1). These data were collected between Fall 2016 and Spring 2018, utilizing non-lethal methods (as in Gunderson & Leal, 2012) to measure critical thermal maximum (CT_{max}) and minimum (CT_{min}). These thermal limits were measured as the temperature at which an individual lost the ability to right itself, as such an impairment would be lethal if sustained in the wild (Huey & Stevenson, 1979).

Individuals were first acclimated to room temperature, with starting body temperature averaging 25.6°C for both tests. To calculate CT_{max}, individuals were placed in a large cardboard box with a 150 W incandescent lightbulb suspended 1 m above the lizard. To prevent individuals from taking shelter from the heat lamp, a noose was tied around the lizard's waist and staked to the bottom of the box. The noose was made long enough to allow individuals some movement to lower stress levels. A thermocouple thermometer was placed in the cloaca and secured with a small piece of surgical tape to monitor the rise in body temperature. Once the body temperature reached 36°C, we flipped the individual on its back at 1°C increments, pinching the thigh of the lizard to induce a righting response. When the individual was no longer able to right itself, the body temperature was recorded as that individual's CT_{max}. Similar methods were used to calculate CT_{min} by placing individuals in a plastic container within a large cooler of ice to gradually decrease body temperature, and flipping them on their backs starting at 14°C.

These observed thermal limits were then compared to Maxent's response curves for Bio5 (maximum temperature of the warmest month) and Bio6 (minimum temperature of the coldest month). We considered the predicted thermal limit as the temperature at which the response curve crossed the MaxSS suitability threshold (Vale, Tarroso, & Brito, 2014). For *Hemidactylus mabouia*, the response

TABLE 1 Sample size, mean and standard deviation for each thermal limit measured from individuals collected in South Florida

Species	CT_{max} (°C)		CT_{min} (°C)	
	N	Mean [SD]	N	Mean [SD]
Agama agama	6	45.10 [1.01]	6	9.77 [0.94]
Ameiva ameiva	6	44.67 [1.29]	5	12.24 [1.05]
Anolis carolinensis	11	42.96 [0.98]	12	9.75 [1.49]
Anolis chlorocyanus	6	39.12 [0.84]	6	9.18 [0.54]
Anolis cristatellus	10	39.10 [0.91]	10	8.04 [0.94]
Anolis cybotes	8	38.76 [1.55]	8	9.54 [1.49]
Anolis distichus	10	39.76 [0.98]	11	9.60 [1.70]
Anolis sagrei	10	42.13 [1.23]	11	9.05 [1.01]
Basiliscus vittatus	11	41.43 [1.79]	10	11.29 [1.02]
Hemidactylus mabouia	6	40.38 [1.98]	6	8.57 [1.24]

curves did not reach the threshold value, thus we considered the predicted limit the value at which the curve hit minimum suitability. This predicted thermal limit was then compared to the interval over which 95% of individual lizards reach their observed thermal limit, and we recorded whether the predicted limit fell above, below or within this 95% range.

3 | RESULTS

3.1 | Climatic habitat suitability

Averaging across all 29 species, we saw a strong correlation between the predicted and observed distributions of these non-native lizards (Habitat suitability: p = 1e-10; County area: p = 8.8e-08; R^2 = 0.70; Figure 1). However, when looking at relative invasion success within a given geographical extent, Maxent was less accurate in predicting which non-native species would be the most abundant or widespread. For the Miami-Dade park survey data, we did not find any relationship between mean predicted suitability in Miami-Dade County and either total abundances (Habitat suitability: p = 0.23; Year of introduction: p = 0.007; Figure 2b) or number of parks in which a species occurred (Habitat suitability: p = 0.11; Year of introduction: p = 0.01, Figure 2a). At the statewide scale, the number of counties each species has been recorded in was not related to the mean predicted habitat suitability across Florida (Habitat suitability: p = 0.79; Year of introduction: p = 0.001). Using the localities from GBIF, we did not find any relationship between mean predicted habitat suitability and number of recorded localities in either Miami-Dade County (Habitat suitability: p = 0.39, Year of introduction: p = 0.01; Figure 2c) or Florida (Habitat suitability: p = 0.91, Year of introduction: p = 3.2e-04; Figure 2d). We also did not find any correlation with mean predicted habitat suitability across Florida and the Krysko, Burgess, et al. (2011) establishment rankings (Habitat suitability: p = 0.85; Year of introduction: p = 0.01). All of these results were qualitatively identical whether using default or LQP feature classes and whether using all or filtered localities. The reported statistics are based on LQP features and all localities.

3.2 | Response curves and thermal limits

To analyse the Maxent response curves, we summarized the relationship between the predicted and observed thermal limits into four categories (Table 2). Namely, predicted thermal limits either fell below, within, or above the interval where 95% of observed thermal limit occur, or were classified as "NA" if the variable did not contribute to the niche model of the species in question (i.e. the response curve was flat). Results were similar using either default or LQP features. For CT_{max}, 8 out of 10 and 10 out of 10 species had flat response curves, using default and LQP features, respectively. This suggests that few of these lizard species are up against their maximum thermal limit. For CT_{min}, both feature types showed one species with predicted thermal limit below
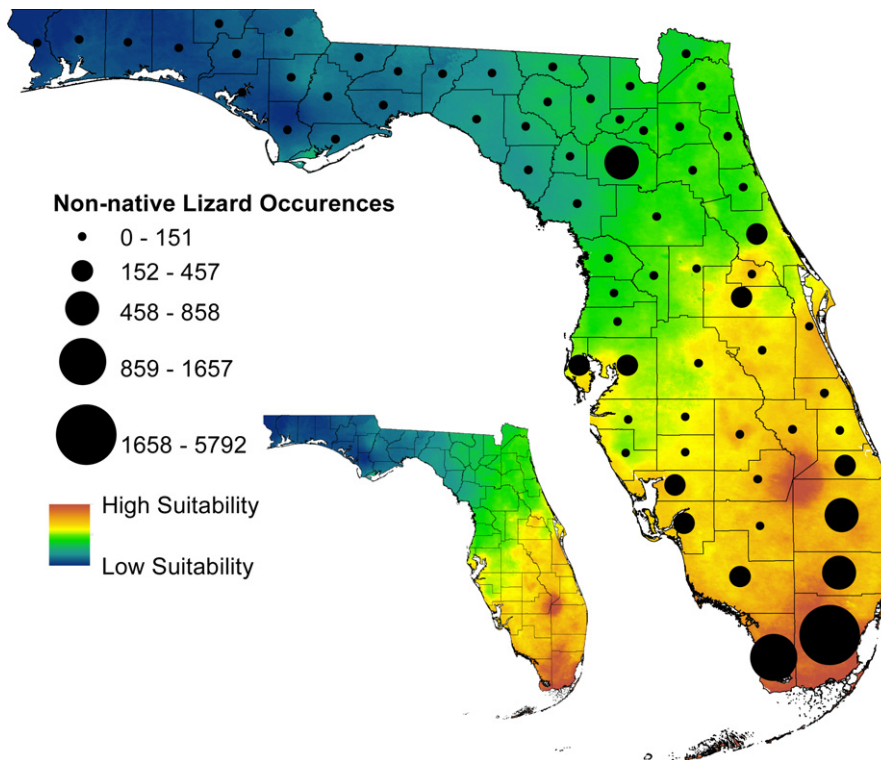
FIGURE 1 Predicted habitat suitability averaged across all 29 non-native lizard species established in Miami-Dade County. Black circles represent the number of recorded non-native lizard localities within each Florida county. There was a strong positive correlation between the predicted and observed distributions of these non-native lizards (p = 1e-10)

the observed limit, two species with predicted limits above the observed limit, and two species with matching observed and predicted limits. The mean difference between observed and predicted thermal limits was 3.8°C and 4.0°C for default and LQP features, respectively.

3.3 | AUC

By creating Maxent models for a diverse species pool, we were able to test for relationships between model performance (AUC) and area of the geographical extent, buffer distance and number of localities. We found that geographical extent had the strongest relationship with AUC, (R^2 = 0.57, p = 2.5e-06; Figure 3) and was positively correlated. Buffer distance also had a significant, but slightly weaker, positive correlation with AUC (R^2 = 0.5, p = 1.9e-05), while we found no relationship between AUC and number of localities (R^2 = 0.009, p = 0.63).

4 | DISCUSSION

4.1 | Discrepancies in suitability predictions

Our results show that Maxent performed well at predicting where non-native lizards were most likely to occur. However, within a given geographical extent (either Miami-Dade County or Florida as a whole), Maxent was not able to predict relative invasion success in terms of abundance or geographical spread between the different non-native lizard species.

These results suggest that while Maxent performs well at the task it was primarily created for (predicting habitat suitability across

geographical space), it may not be able to accurately predict relative invasion success across species. Overall, Maxent accurately predicted regions of suitable climate supporting non-native lizard establishment, but other factors not included in niche model calculations may be impacting each species' ability to spread after colonization. Previous studies also found that ecological niche models are accurate in predicting establishment success (Bomford et al., 2009; van Wilgen et al., 2009), but not subsequent spread (Gallardo, zu Ermgassen, & Aldridge, 2013; Liu et al., 2014). Other factors that may impact invasion success post-establishment include biotic interactions and dispersal capability. There are numerous examples of interspecific interactions (Short & Petren, 2012; Townsend & Krysko, 2003) and unequal dispersal capability (Kolbe et al., 2016) impacting the invasion success of lizards in Florida.

The ability of Maxent to predict relative invasion success may also be hampered by this non-native lizard community not yet being in equilibrium. Previous studies have demonstrated that predicted habitat suitability from ENMs serves more as an upper bound for abundance than as a simple linear predictor (Acevedo et al., 2017; Russell et al., 2015; VanDerWal, Shoo, Johnson & Williams, 2009). The relationship between predicted habitat suitability and abundance in these species may therefore be weakened by the fact that none of these lizards have yet attained their maximum abundance. The fact that this community is not yet in equilibrium is further indicated by the fact that while none of our metrics of invasion success exhibited a correlation with predicted habitat suitability, all six of them showed a strong relationship with year of introduction. This indicates that a species' observed invasion success is largely determined by the time it has had to reproduce and disperse, such that species introduced longer ago will generally be both more abundant and
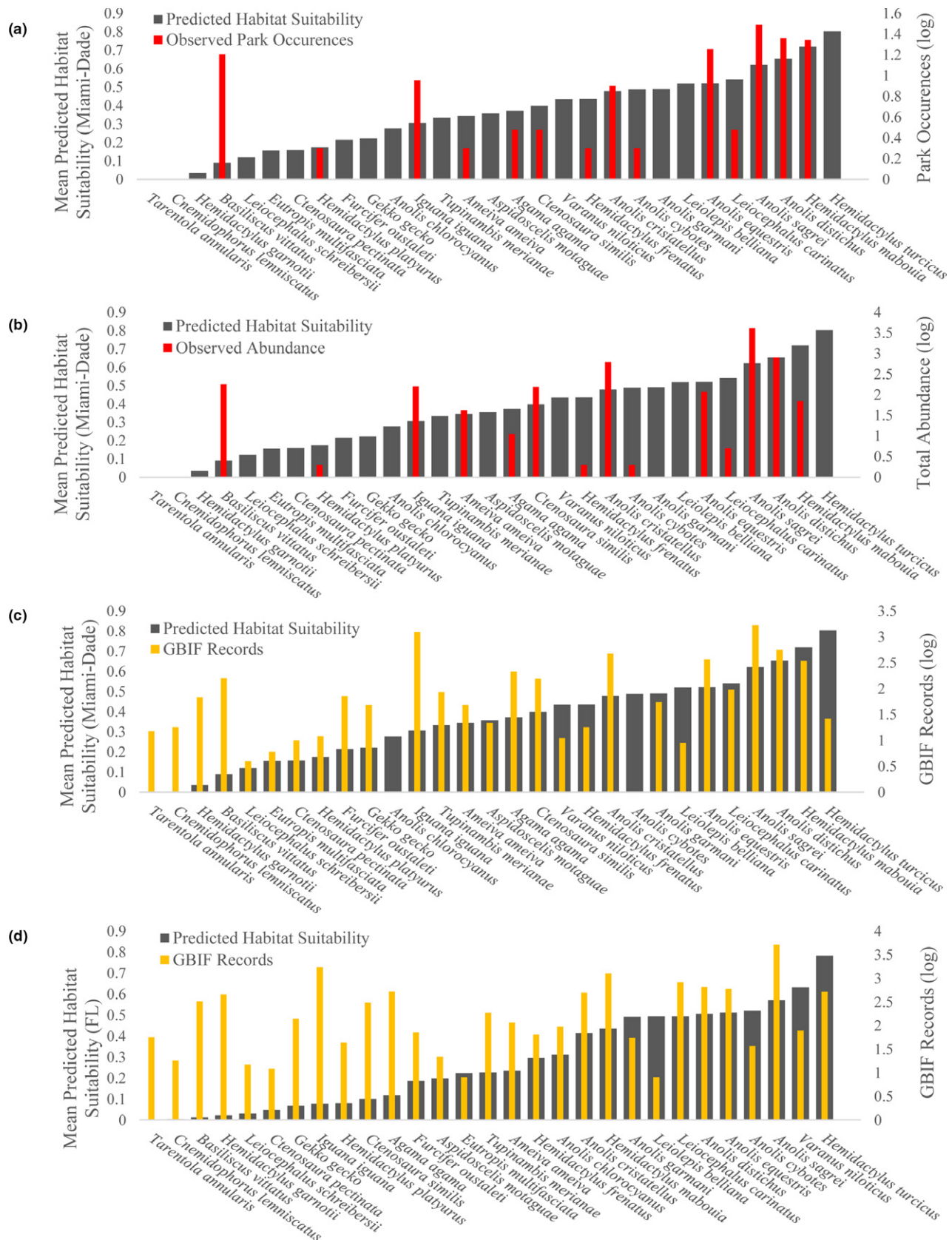
FIGURE 2 Maxent's ranking of predicted invasion success in Miami-Dade County for all 29 species (based on mean predicted habitat suitability) compared to observed: a) number of park presences, b) total abundance and c) number of GBIF records. Maxent's ranking of predicted invasion success for all of Florida is shown in d) compared to total number of GBIF records across the state. Although not shown above, all statistical models included year of introduction as a covariate

TABLE 2 Summary of the relationship between Maxent's predicted thermal limits and observed thermal limits based on physiological measurements

Relationship of predicted to observed thermal limits	Default features		LQP features	
	CT$_{min}$	CT$_{max}$	CT$_{min}$	CT$_{max}$
Below	1	2	1	0
Match	2	0	2	0
Above	2	0	2	0
N/A[a]	5	8	5	10
Total species	10	10	10	10

[a]No constraints based on this variable are included in the species' niche model, and thus the response curve is flat (i.e. there is no indication of the species being up against this thermal limit).
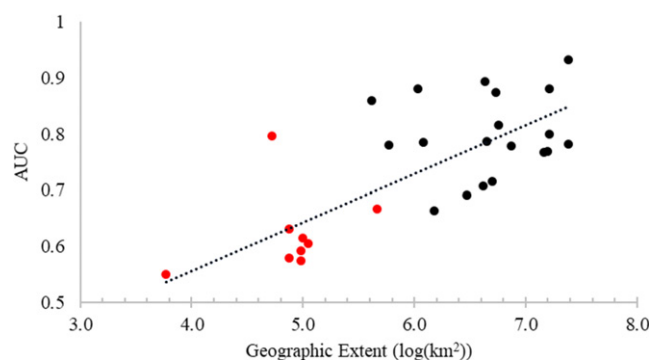

FIGURE 3 As the geographical extent increases in area, the AUC for the respective model also increases, indicating improved model performance ($R^2 = 0.57$, $p < 0.001$). Red points represent species that are native only to islands. An AUC value equal to 0.5 represents a model that is no better than random. AUC values are usually interpreted as follows: 0.5–0.7 model is not performing well, 0.7–0.9 model has reasonable performance, >0.9 model has high performance (Peterson et al., 2011)

more widespread. This agrees with other studies that have identified time since introduction as a main driver of invasion success among both coastal marine invertebrates (Byers et al., 2015) and woody trees (Pyšek, Křivánek, & Jarošík, 2009). If each species' approach to its equilibrium distribution in the non-native range was truly linear, then including year of introduction as a covariate would have sufficiently accounted for the community's current non-equilibrium state. However, range expansion away from an introduction site has been repeatedly shown to manifest non-linear dynamics (Sakai et al., 2001).

4.2 | Response curve accuracy is case-dependent

The response curves represent Maxent's predictions in environmental space, and few studies have tested their accuracy. Previous studies that compared response curves to frequency histograms representing how much of a species' range falls along each section of an environmental gradient found strong matches (Buermann et al., 2008; Williams et al., 2012). This, however, only indicates that

response curves can capture the realized niche, whereas projecting niche models into novel environmental conditions in either time (climate change predictions) or space (invasive ranges) requires knowledge of the fundamental niche. Studies comparing response curves to independent data sources not based on the species range have found examples of close matches, but also instances of wide disagreement (Convertino et al., 2012; Searcy & Shaffer, 2016).

We found that Maxent's response curves were not a perfect fit with the observed physiological limits, but worked well for some species and did not show any consistent bias towards either over or under predicting thermal limits. For the species in which the predicted CT$_{min}$ was below the observed CT$_{min}$ (*H. mabouia*), the discrepancy is likely attributable to the source populations these non-native lizards came from. Source populations only constitute a small subset of a species' native range (Kolbe et al., 2007), and if there is local adaption to climate, then source populations will not encompass the total climatic tolerance found in the native range. In the case of *H. mabouia*, the native range spans coastal lowlands to Mt. Kilimanjaro. Therefore, while some *H. mabouia* populations persist in colder temperatures, if the source populations all came from warmer environments along the coast that would explain the observed CT$_{min}$ being higher than for the native range as a whole. For cases in which the predicted CT$_{min}$ was above the observed CT$_{min}$, it may be indicative of adaptation to the non-native range subsequent to invasion. This has already been documented in *A. sagrei*, which shows significant physiological variation along a latitudinal gradient in Florida, with the northernmost populations tolerating colder temperatures (Kolbe, Ehrenberger, Moniz, & Angilletta, 2014). Additionally, the spatial scale at which these interpolated climate variables are calculated (1 km^2) may explain the imperfect fit between model predictions and observed physiological tolerances. At a 1-km resolution and 30-year average, the temperature value of each pixel may not be representative of the microclimate experienced by these relatively small-bodied species that are actively thermoregulating (Sears & Angilletta, 2015). Our results could thus be improved using climate data at a finer spatial and temporal scale, but that data are not available at the global scale needed for this study.

4.3 | Geographical Extent Positively Influences AUC

Many studies have stressed how important geographical extent is in niche model performance, emphasizing that the best methods use areas that are not too small or too large, encompassing only the area accessible to the species over a relevant time-scale (Anderson & Raza, 2010; Barve et al., 2011). Following these recommendations, we found that size of the geographical extent had a strong positive influence on AUC. This agrees with previous findings that experimented with different background areas (Giovanelli, de Siqueira, Haddad, & Alexandrino, 2010; VanDerWal, Shoo, Graham, & Williams, 2009). However, it disagrees with studies that found a negative correlation between AUC and range size (Hernandez, Graham, Master, & Albert, 2006; Newbold et al., 2010). These two sets of studies were essentially testing different questions. The first set was

varying only the area from which background points were collected while holding the actual species ranges constant, while the second set was examining species with varying range sizes within a set region from which background points were collected. It is the ratio of these two quantities (range size:background extent) that determines accuracy based on AUC (Lobo, Jiménez-Valverde, & Real, 2008), with accuracy increasing as the ratio decreases. For example, many *Anolis* species confined to Caribbean islands may have their range limits set by dispersal barriers (e.g. saltwater) rather than by gradients in climatic conditions. If this is true and the entire island upon which the species is found constitutes suitable climatic habitat, Maxent will be unable to identify rules (constraints) that distinguish suitable from unsuitable habitat, as there is no unsuitable habitat within the region from which background points are being drawn. This will have important consequences for model accuracy (Figure 3), and illustrates the issue with having a large range size:background extent ratio.

In the past, it was common to set a single background extent for all the species being analysed, and thus species with larger ranges within this extent would have larger range size:background extent ratios and less accurate AUC (Hernandez et al., 2006; Newbold et al., 2010). We now recognize the importance of setting a realistic background extent for each species (Anderson & Raza, 2010; Barve et al., 2011), although there is no single accepted protocol for doing this. In general, we should expect species with larger ranges to also be assigned larger background extents. Our particular method for selecting the background extent apparently expanded the background extent more rapidly than the true range size and thus led to species at the large range size/geographical extent end of the spectrum having higher AUC than species at the small end of the spectrum. Whether this will be true of other methods that are developed to select realistic background extents remains to be seen.

5 | CONCLUSIONS

These results suggest that the most effective use of ecological niche models in invasion biology will be to predict where candidate invasive species are most likely to invade, and thus where monitoring efforts should be focused, rather than for identifying which individual taxa are the greatest threat. Maxent's ability to accurately predict species distributions has been repeatedly documented across native ranges (Costa et al., 2010; Elith et al., 2006; Searcy & Shaffer, 2014) and for individual non-native species (Ficetola et al., 2007), but never for such a broad suite of non-native taxa (29 non-native lizard species). Where Maxent failed was its ability to predict relative invasion success across the pool of established species, which complicates its use in prioritizing management actions within this non-native community. Reasons for the discrepancies were likely due to lags in invasive spread, varying dispersal capabilities, biotic interactions and local adaptation to either the native or invasive ranges. Future studies will need to investigate which of these factors best determine relative success within this diverse assemblage of non-native species,

as such novel ecosystems are expected to increase in frequency at a global scale (Hobbs et al., 2013). Additionally, there is continuing need for studies that validate niche model outputs using independently derived field data.

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BIOSKETCH

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