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Predicting the invasion dynamics of anoles (and other lizards) using ecological niche modeling

Abstract

Ecological niche models are commonly used to predict areas of environmental suitability for non-native species. Depending on these models to enact appropriate management plans assumes that they are accurate, however most niche model studies do not provide appropriate validation. South Florida hosts the world's largest and 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 dispersal, abundance, and physiology in established non-native populations. Using Maxent, we developed niche models for 30 non-native lizard species established within Miami-Dade County, FL, including all 8 established non-native *Anolis* species, using native range data to project suitability in the invaded range. We then compared projections to data available on distribution, as well as empirically collected data on abundance and physiology (upper and lower thermal tolerances). Maxent performed well in predicting general invasion patterns of non-native species across geographic space, however performed poorly in predicting the relative invasion success of each species. Additionally, comparisons between predicted and observed thermal tolerances showed that most of the models overpredicted the range of suitable thermal habitat for each species. Overall, the niche models accurately predicted geographic hotspots for these species to occur but could not predict relative invasion success of each species individually. These results suggest that other factors, such as time since introduction, dispersal ability, biotic interactions, adaptation, and source populations may also influence the relative success of non-native species after they become established.

Introduction

Given widespread human-induced global change, one pertinent result is a significant increase in the dispersal and establishment of non-native species (Hoffman et al., 2010, Hobbs et al. 2013, Helmus et al. 2014). Non-native species can often impact native species negatively, meaning they may pose an important conservation risk. It is important for conservation practitioners to know where non-native species will spread to once they have established to effectively mitigate potential, or observed, negative impacts on native species. Ecological niche models (ENMs) are important tools in predicting the range dynamics and dispersal patterns of invasive species (Ficetola et al. 2007; Jeschke and Strayer 2008; Rödder et al. 2008). However, the accuracy of these predictive models is rarely tested, which has profound effects on how well the models are to be trusted when making conservation and management decisions.

Climate matching between native and invasive ranges has been observed to have a strong influence on establishment success of non-native species (Bomford et al. 2009; van Wilgen et al. 2009) and is shown to be one of the most important predictors of species distributions (Thullier et al. 2004; Algar et al. 2013). However, there are many other factors that can also influence invasion dynamics besides the climatic niche. For example, biotic interactions (Araújo and Luoto 2007), dispersal limitation (Algar et al. 2013), life history traits (Allen et al. 2017), topographic heterogeneity (Liu et al., 2014), and propagule pressure (van Wilgen and Richardson, 2012; Strubbe et al., 2015) may all be substantially influential. There is thus an insistent need for studies that validate niche model predictions, which can most thoroughly be achieved by contrasting model predictions with independently collected field data from the same geographic areas being projected to. However, due to logistic constraints, few studies have carried out this approach (Costa et al. 2010; Searcy and Shaffer, 2014; West et al. 2016), and even fewer on systems with multiple non-native species. Here we present one of the most extensive field validations of the ability of ENMs to predict the dispersal and range dynamics of invasive species by utilizing the world's largest community of non-native lizards, which is found in Miami, Florida. Our objective was to test ENM accuracy in predicting both where these non-native lizards are most likely to occur across geographic space and their relative success within a given geographic area. This was accomplished by comparing mean habitat suitability predicted by the ENMs built for the 30 non-native lizard species established in Miami-Dade County to field data determining observed geographic spread and patterns of relative abundance. We also examined the validity of the niche model predictions by comparing the predicted thermal limits to observed physiological thermal limits measured for non-native lizards residing in South Florida.

Methods

All niche modeling was performed using Maxent (Phillips et al. 2006), one of the most popular ENM algorithms due to its strong predictive abilities compared to other ENMs (Elith et al. 2006), especially in cases with low sample size (Pearson et al. 2007; Wisz et al. 2008), and which has been documented as a useful tool when predicting into novel climatic conditions such as those in non-native ranges (Elith et al. 2010, Strubbe et al. 2015). Maxent is a presence-only method, which uses species' occurrence data and environmental variables at those occurrences to predict the species distribution across environmental and geographic space. We built niche models for each of the 30 non-native lizard species established in Miami-Dade County, and for one native species, *Anolis carolinensis*, building the models with native range data and projecting them into Florida. All models were implemented using the 'DISMO' package (Hijmans et al. 2017) in R version 3.3.2 (R Core Team 2017). We obtained native range localities for each species from the Global Biodiversity Information Facility (https://www.gbif.org) and VertNet databases (https://www.vertnet.org) and removed outliers (geo-referencing errors or invasive range localities) by making comparisons to native range maps. The climate variables used were the 19 Bioclim variables at ~1-km^2 resolution downloaded from the WorldClim database (Hijmans et al. 2005), which represent different combinations of temperature and precipitation that are biologically important and most often used in Maxent modeling (Booth et al. 2014). For inquiries on detailed modeling methods contact the corresponding author (Caitlin C. Mothes).

We used a wide array of datasets to evaluate the observed relative abundance and geographic spread of Miami-Dade County's 30 established exotic lizard species. One dataset consisted of herpetofaunal field surveys conducted by members of the Searcy Lab in 30 parks spread throughout Miami-Dade County (S. L. Clements, unpublished data). A second dataset we used was the number of Florida counties each species has been recorded in (Krysko, Enge, et al., 2011). Third, we used the GBIF database to calculate the number of known localities in both Florida and Miami-Dade County for each species. Finally, we used the Krysko, Burgess, et al. (2011) dataset, which assigns each species a ranking from 1-5 based on how abundant and widespread its established populations are in Florida. We then used multiple linear regression to analyze how well Maxent models predicted each of these observed measures of relative invasion spread and abundance. For the surveys conducted by the Searcy lab and the number of GBIF localities in Miami-Dade County, the predictor variable we considered was mean habitat suitability predicted by Maxent across Miami-Dade County. For the other success metrics, we considered mean habitat suitability across all of Florida as the predictor. For all analyses, the year in which each species was first introduced to Florida was used as a covariate, since current abundance/incidence of each species will be a combination of its ability to invade and the amount of time it has had to do so. All these analyses assess Maxent's ability to predict relative invasion success within a given geographic extent (either Miami-Dade County or all of Florida). To assess Maxent's ability to predict hotspots for non-native lizard invasion across the state, we averaged the predicted habitat suitability across Florida for all 30 non-native lizard species, and then calculated the mean predicted suitability for each of Florida's 67 counties. We then calculated the total number of records for these 30 species in each county (using the GBIF data) and created a linear model relating the number of records to the mean predicted suitability, using county area as a covariate.

As another method of testing the accuracy of the niche models, we measured the thermal limits of individuals caught in the Miami area to compare with the model's response curves, which plot predicted suitability against each individual environmental variable. We used response curves for Bioclim variable Bio5 (maximum temperature of the warmest month) to determine the predicted maximum thermal limit and Bio6 (minimum temperature of the coldest month) to determine the predicted minimum thermal limit. We considered the predicted thermal limit as the temperature at which the response curve reached its minimum suitability value, and then compared this temperature to the 95% confidence interval of the observed thermal limit and recorded whether the predicted limit fell above, below, or within the 95% CI of the observed limit.

Individuals were collected from ten species, with an average sample size of eight individuals per species. The majority of the lizards were captured at Fairchild Tropical Botanic Gardens in Miami FL, while *Ameiva ameiva* were captured at Evelyn Greer Park (Pinecrest FL) and *Anolis chlorocyanus* and *A. cybotes* were collected in Parkland FL. The physiological traits measured were critical thermal maximum (CT_{max}) and critical thermal minimum (CT_{min}). These thermal limits were measured as the temperature at which an individual lost the ability to right itself, signifying ecological death as such an impairment would be lethal if sustained in the wild (Huey and Stevenson 1979). Thermal tolerance data was collected between Fall 2016 and Spring 2018, utilizing non-lethal methods (as in Gunderson and Leal 2012). 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 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 Tupperware within a larger cooler of ice to gradually decrease body temperature, and flipping them on their backs starting at 14° C.

Results

Averaging the predicted habitat suitability across all 30 models projected onto Florida, we see a strong correlation between the predicted distribution of these non-native lizards and their observed abundance (Habitat suitability: $P < 0.001$; County area: $P < 0.001$; $R^2 = 0.60$; Figure 1). However, when looking at relative invasion success within a given geographic extent, Maxent does a poor job predicting which non-native species are most abundant or widespread. We used mean predicted habitat suitability for each species to rank the predicted invasion success in both Florida and Miami-Dade County. We compared these predicted values to actual invasion success based on four different datasets. 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 = 0.76; Year of introduction: P = 0.04) or number of parks in which a species occurred (Habitat suitability: P = 0.77; Year of introduction: P = 0.06).

At the statewide scale, the number of counties each species has been recorded in was not related to the ranking of mean predicted suitability in Florida (Habitat suitability: P = 0.62; Year of introduction: P = 0.001). Using the museum records from GBIF, we did not find any relationship between mean predicted habitat suitability and number of recorded localities in either Florida (Habitat suitability: P = 0.7, Year of introduction: P = 0.001) or Miami-Dade County (Habitat suitability: P = 0.97, Year of introduction: P = 0.005). Using the establishment rankings from Krysko et al. (2011) we also did not find any correlation with mean predicted habitat suitability across Florida (Habitat suitability: P = 0.71; Year of introduction: P = 0.03).

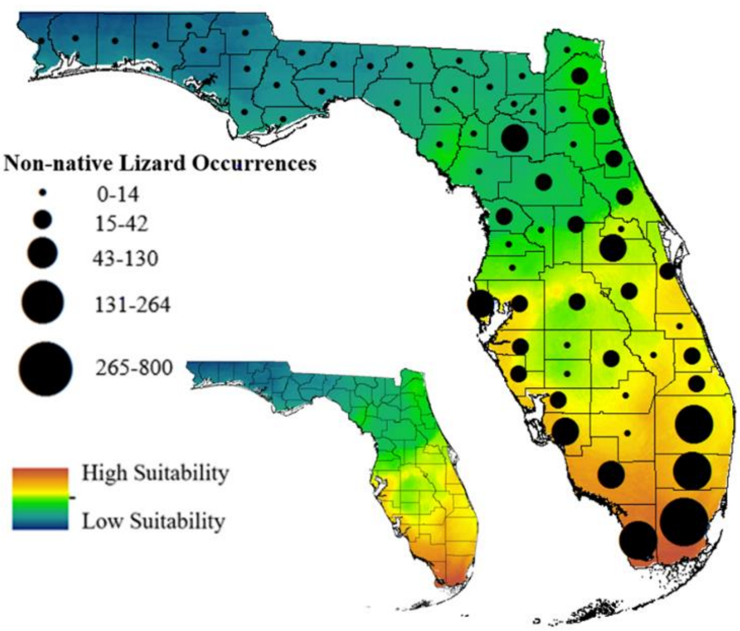

Figure 1. Predicted habitat suitability averaged across all 30 non-native lizard species established in Miami-Dade County. Black circles represent the number of recorded non-native lizard localities within each Florida county.

We summarized the relationship between the predicted and observed thermal limits into four categories (Table 1). Namely, predicted thermal limits either fell below, within, or above the 95% CI of the observed thermal limit based on the physiological data, 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). Looking at the relationship between observed and predicted CT_{max} based on the response curves for Bio5, we see that for the majority (7 out of 10 species), the relationship could not be determined because Bio5 did not play a role in generating the niche model for that species. This suggests that few of the lizard species we modeled are up against their maximum thermal limit. For the comparison between observed and predicted CT_{min}, the majority (6 out of 10 species) showed the predicted thermal limit below the observed thermal limit. This means that Maxent is predicting suitable regions with temperatures colder than these non-native lizards can persist in based on their physiology, unless they find some other means of dealing with these colder climates (see Discussion).

Table 1. Summary of the relationship between Maxent's predicted thermal limits and the observed thermal limits based on the measured physiological data.

Relationship of Predicted to Observed Thermal Limits	CT_{min}	CT_{max}
Below	6	2
Match	0	1
Above	1	0
N/A*	3	7
Total Species	10	10

*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).

What about the anoles?

Figure 2 shows the predicted habitat suitability maps for eight *Anolis* species established within south Florida. The *Anolis* species with the highest predicted suitability across Florida was the Hispaniolan big-headed anole (*Anolis cybotes*), followed closely by the Cuban brown anole (*A. sagrei*), and the lowest was the Hispaniolan green anole (*A. chlorocyanus*). When predicting within only Miami-Dade County, the Hispaniolan bark anole (*A. distichus)* had the highest predicted environmental suitability, followed closely by *A. sagrei*, with *A. chlorocyanus* again showing the lowest predicted suitability. As with the entire non-native lizard community, we did not find any relationships between the observed and predicted invasion success when looking at just the *Anolis* group. When conducting analyses, we removed the Cuban green anole (*A. porcatus*) due to the difficulty in differentiating the species correctly from the American green anole (*A. carolinensis*; Camposano 2011). For the thermal tolerances, we collected data on five out of the eight non-native anoles, and the native *A. carolinensis* (along with four other non-native species; Table 2). When we compared our observed critical thermal minimum to the predicted minimum temperatures, models for *A. cybotes* and *A. sagrei* did not detect minimum temperature as an important variable in determining their distributions. However, *A. cristatellus* had an observed thermal minimum that was below the predicted limit, and *A. carolinensis*, *A. chlorocyanus*, and *A. distichus* all had observed thermal minimums that were above the predicted limit. Maximum temperature was not a significant contributor in predicting the species distribution for any species, with the exception of *A. carolinensis* which had an observed CT_{max} that was warmer than the predicted maximum temperature.

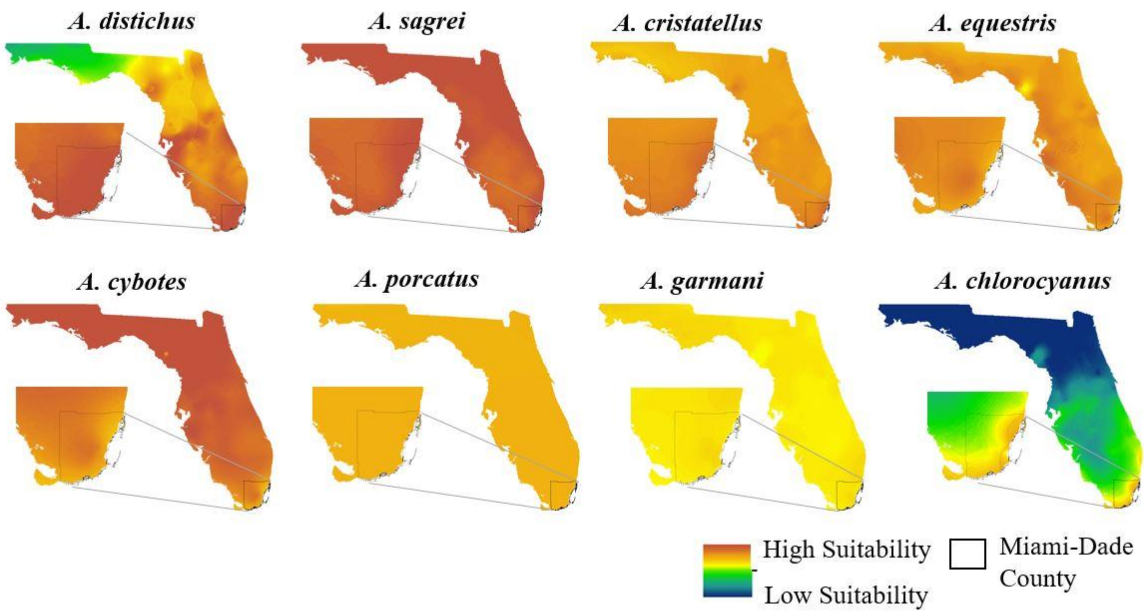

Figure 2. Maxent's predicted habitat suitability for all established non-native *Anolis* species in Florida.

Our results show that the niche models performed quite well at predicting the hotspots across Florida where non-native lizards are most likely to occur (Figure 1). However, within this non-native lizard community the models were not able to predict relative invasion success of individual species in terms of their total abundance or geographic spread. Overall, Maxent accurately predicted regions of suitable climate supporting establishment of these lizards, but other factors not included in niche model calculations may be impacting a species' ability to multiply and spread after colonization. Previous studies have 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 et al. 2013; Liu et al., 2014).

While none of our metrics of invasion success across the entire group of non-native lizards exhibited a correlation with predicted habitat suitability, almost all of them showed a strong relationship with year of introduction. This indicates that a species' observed invasion success is largely determined by the amount of time it has had to establish, reproduce, and disperse, such that species introduced longer ago will generally be both more abundant and 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 et al. 2009). This may provide evidence that priority effects are particularly important in the establishment of non-native species, and the subsequent development of community structure and organization. Further research on the general importance of priority effects in the assembly patterns of *Anolis* communities would be valuable (see Stroud 2018).

Table 2. Sample size, mean, and 95% confidence intervals for each thermal limit measured from individuals collected in South Florida.

	CT_{max} (°C)		CT_{min} (°C)	
Species	**N**	**Mean [95% CI]**	**N**	**Mean [95% CI]**
Agama agama	6	45.10 [44.29, 45.91]	6	9.77 [9.01, 10.52]
Ameiva ameiva	6	44.67 [43.64, 45.69]	5	12.24 [11.34, 13.16]
Anolis carolinensis	11	42.96 [42.38, 43.54]	12	9.75 [8.90, 10.60]
Anolis chlorcyanus	6	39.12 [38.45, 39.79]	6	9.18 [8.75, 9.62]
Anolis cristatellus	10	39.10 [38.53, 39.67]	10	8.04 [7.45, 8.62]
Anolis cybotes	8	38.76 [37.69, 39.84]	8	9.54 [8.50, 10.57]
Anolis distichus	10	39.76 [39.15, 40.38]	11	9.60 [8.60, 10.6]
Anolis sagrei	10	42.13 [41.37, 42.89]	11	9.05 [8.46, 9.64]
Basiliscus vittatus	11	41.43 [40.37, 42.49]	10	11.29 [10.66, 11.92]
Hemidactylus mabouia	6	40.38 [38.79, 41.97]	6	8.57 [7.57, 9.56]

What determines invasion success? And other insights from* Anolis *lizards

When we investigate patterns among only non-native *Anolis* in Florida, we can gain important insights into additional factors that may be impacting the invasion success of these lizards post-establishment. One factor may be biotic interactions. Many studies have shown how interspecific interactions between native/non-native and non-native/non-native *Anolis* species has impacted the community structure of these lizards in the non-native range (Losos et al. 1993; Losos 2009; Stuart et al. 2014; Kolbe et al. 2016). Therefore, these negative relationships at the micro-scale may reflect patterns observed at the macro-scale.

The capability of these species to disperse through Miami's urban landscape may also impact how abundant and widespread they are in this non-native range. The native habitat in the Miami area is highly fragmented (reduced to <2% of its original extent; Bradley and Martin 2012) and dominated by an urban matrix, providing novel challenges that many of these species may not have dealt with in their native ranges. For example, *A. cristatellus* is largely constrained to forest habitat and appears incapable of unaided dispersal across open habitats and impervious urban surfaces, causing it to have a low dispersal rate compared to other non-native *Anolis* species (Kolbe et al., 2016).

Adaption to the non-native range is another aspect of invasion success that is not accounted for in Maxent models. One might expect that rapid adaptation may be unlikely in non-native populations due to bottleneck effects and subsequent low genetic diversity, but a study of the eight non-native *Anolis* species in Miami showed that the majority of them come from multiple source populations, suggesting this is a common trend for non-native lizards (Kolbe et al., 2007). Subsequent admixture between these source populations increases genetic diversity and the possibility for rapid phenotypic shifts, such as the rapid shift in thermal tolerance observed in *A. cristatellus* (Leal and Gunderson 2012; Kolbe et al. 2012). There is also evidence of adaptation to the non-native range in *A. sagrei*, which shows significant physiological variation along the latitudinal gradient of Florida, with the northernmost populations experiencing and subsequentially tolerating colder temperatures (i.e. exhibiting a lower critical thermal minima; Kolbe et al. 2014).

Another factor that may affect comparisons between the empirical data and the niche models is the source populations that these non-native lizards originated from. We generated our Maxent models based on the entire native range, but the source populations may constitute only a small subset of that range. If there is local adaption to climate, then these source populations will not encompass the total climatic tolerance found in the native range and will determine how individuals respond to the habitat of the non-native region. For example, *A. cristatellus* has two populations in Miami-Dade County that originated from climatically different areas of Puerto Rico, and therefore have shown differential responses to Florida climate (Kolbe et al. 2012). Many of these species' native range populations are distributed across a variety of altitudes and temperatures, but the source populations may be primarily coastal, low altitude populations, and therefore may not be representative of the entire range of populations used to train the model. This may explain why the majority of our response curve comparisons showed the niche models predicting that species could persist at colder temperatures than indicated by the observed physiological traits of the non-native populations.

Conclusions

The niche models performed well at their originally intended function: predicting the distribution of species across geographic space. The predictive ability of ENMs has been repeatedly supported across native ranges (Elith et al., 2006; Costa et al., 2010; Searcy & Shaffer, 2014) and for individual non-native species (Ficetola et al., 2007), but this was the first time it had been documented across such a broad suite of non-native taxa (30 non-native lizard species, including 8 introduced *Anolis*). Where Maxent failed was its ability to predict relative invasion success within the pool of established species, which complicates its use in prioritizing management actions within this non-native community. Reasons for the discrepancies we see are likely due the confounding influences of length of time since introduction, interspecific variation in ecology and dispersal capability, interspecific interactions, and founder effects of non-native populations. 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 around the world (Hobbs et al., 2013).

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