A Distribution Model for the Green Iguana, *Iguana iguana* (Linnaeus, 1758) (Reptilia: Iguanidae), in Puerto Rico[1]

Carlos Andrés Rodríguez Gómez[2], Rafael L. Joglar[3], Mariano Solórzano[4], and William A. Gould[4]

Abstract: In Puerto Rico, the Green Iguana, *Iguana iguana*, is considered an introduced and invasive species responsible for annual losses estimated in millions of dollars to local governmental and private sectors. The purpose of this study was to use GAP analyses to generate habitat distribution models for Green Iguanas in Puerto Rico. The two models had 79.7% and 88.4% predictability, respectively. The second model, which included road corridors as a habitat widely known to be used by iguanas for dispersal, basking, and mating displays, might have overestimated the Green Iguana's distribution. The use of one model over the other should be evaluated on a case-by-case basis, depending on habitat type. These habitat modeling and mapping efforts should be repeated periodically as new distributional records are obtained and the land-cover changes to provide land managers an updated distribution of this species in the islands.

Keywords: Green Iguana, distribution, invasive species, land cover, PRGAP analysis

Introduction

Seldomly are there simple solutions that provide for the control of invasive species, more so now in our globalized economy. Global anthropogenic activities have led to the creation of novel environments and introductions of alien species that interact with native species, thus creating novel ecosystems (Lugo et al. 2012). Understanding Invasive Alien Species (IAS) requires research at multiple scales and the efficient dissemination of data (Strayer 2012). Modeling and mapping the geographic distributions of IAS and habitat suitability has important implications for their management (Corsi et al. 2000, Brotons et al. 2004, Bolongie 2008). Projecting species distributions is crucial for the eradication or control of IAS, particularly if they are invading critical areas of conservation, infrastructural, and agricultural importance (Gassó et al. 2012). Furthermore, using key environmental factors for the target species to model its distributions can lead researchers and land managers to a better understanding of how

---

[1] Submitted on January 22, 2020. Accepted on February 20, 2020, Last revisions received on February 24, 2020.

[2] Para La Naturaleza, a Unit of the Puerto Rico Conservation Trust, PO Box 9023554, San Juan, Puerto Rico 00902-3554. Corresponding author; e-mail: ca.rodriguezgomez@gmail.com ; ca.rodriguezgomez@yahoo.es .

[3] Department of Biology, University of Puerto Rico, PO Box 23360, San Juan, Puerto Rico 00931-3360. E-mail: rjoglar@gmail.com .

[4] USDA Forest Service, International Institute of Tropical Forestry, Río Piedras, Puerto Rico 00926-1119. Emails: mariano.solorzano@gmail.com, william.a.gould@usda.gov .

DOI: 10.9784/LEB7(4) RodriguezGomez**.01**
Electronically available on February 25, 2020. Mailed on February 25, 2020.

underlying environmental factors at the local and landscape levels influence distribution and dispersal into new regions (McPherson and Jetz 2007). With such knowledge, managers are better able to determine where an invasive species could disperse and to dedicate resources toward eradication of populations that have not become established (Townsend and Vieglais 2001, Gibson et al. 2004, Gassó et al. 2012)

The genus *Iguana* is widely distributed in subtropical and tropical America. Two species are currently recognized. The Lesser Antillean Iguana, *Iguana delicatissima* Laurenti, 1768 (Reptilia: Iguanidae) is confined to the Lesser Antilles, whereas the Green Iguana, *Iguana iguana* (Linnaeus, 1758), has the widest distribution of all American iguanians (Etheridge 1982), with a native range extending from Mexico to Paraguay and Brazil and into some of the Lesser Antilles (Buckley et al. 2016, Henderson and Powell 2009, Savage 2002, and Rivero 1998). Genetic studies of green iguanas have demonstrated that it is a complex of at least two species, with evidence of cryptic lineages (Bock and McCracken 1988, Stephen et al. 2013, Vuillaume et al. 2015, Breuil et al. 2019). The latter also has been widely introduced, with accidental or intentional release responsible for populations in the Antilles, including Puerto Rico, Dominican Republic, Grand Cayman, southern Florida, and even some Pacific islands (Falcón et al. 2013). In Puerto Rico, Green Iguana populations have expanded to the point that they have become a nuisance, costing millions of dollars in damage to infrastructure and agriculture (López-Torres et al. 2011, Falcón et al. 2012).

Understanding IAS at regional and local scales is of extreme importance in our globalized world (Meyerson and Mooney 2007). Nevertheless, few studies have projected Green Iguana distributions at either local or regional levels, only Falcón et al. (2012 and 2013) have considered current and potential distributions of Green Iguanas outside their native range. Falcón et al. (2012) evaluated the risk of spread of Green Iguanas in the Greater Caribbean Basin using the maximum entropy niche-modeling algorithm (MaxEnt) to predict the potential distribution using temperature and precipitation as predictor variables. This model had a high predictive capability, predicting suitable habitats for iguanas in southern and central coastal Florida and throughout the Caribbean Basin. Falcón et al. (2013), using the same methodology, predicted a high climatic suitability for Green Iguanas on many Pacific Islands, including those where the species has already become established.

To date, a model predicting current and potential distribution of Green Iguanas in Puerto Rico has not been developed. Falcón et al. (2012) predicted highly suitable areas for the species, especially along the coast, but their model was based on temperature and precipitation data alone and did not consider confirmed sightings. A model that considers crucial habitats for Green Iguanas based on behavior, daily and seasonal needs, and confirmed geo-referenced sightings is lacking. To meet the need of a more robust distribution model for Green Iguanas, we employed the methodologies of the Puerto Rico Gap Analysis

Project (PRGAP) (Gould et al. 2008) to generate a distribution model for Green Iguanas in Puerto Rico, using crucial habitats based the extensive literature regarding the species' natural history and presence data gathered in the field.

Methods

Presence Data for Iguana iguana. We gathered 173 data points in 48 of 78 municipalities in Puerto Rico from 16 December 2010 through 1 February 2011 and on 25 July 2011, using a Garmin 76CSx to mark and store the coordinates for localities where Green Iguanas were present. We traveled by car along the major roads in both the highlands and lowlands of Puerto Rico and, because iguanas are known to frequent riparian habitats, we focused on rivers, artificial lakes, lagoons, estuaries, mangrove forests, and protected areas. When a Green Iguana was observed (alive or road-killed), we stopped and thoroughly searched for more individuals in the area. If we were near a sighted individual, we marked its position as a confirmed point. If the iguana was farther away, we marked the point where we were and recorded an approximate distance and direction to the individual. Later, using Google Earth 2011, aided by the general direction and distance recorded in the field, we entered a new point marked as confirmed presence.

PRGAP Hexagon map: Iguana iguana presence. The PRGAP analysis project uses a grid of hexagons (Figure 1) with an area of 24 km^2 (Gould et al. 2008). Confirmed hexagons were based on points gathered in 2011. With the aid of Facebook, we created an event called "I have Green Iguanas in my community" with the purpose of confirming which communities close to areas already confirmed, had Green Iguanas and which did not, in the process confirming the presence of Green Iguanas in 30 municipalities. In addition, we called seven mayoral offices and municipal government agencies in Aguada, Aguas Buenas, Arroyo, Añasco, Barceloneta, Cataño, and Río Grande, which were not exhaustively visited in our field trips, asking if they knew of any trouble with Green Iguanas. Hexagons categorized as having a probable Green Iguana presence were classified using our knowledge of the species' habitat preferences and requirements.

Variables used to build the model. Variables selected to build the Green Iguana distribution model for Puerto Rico were based on Savage (2002), who noted that these lizards prefer riparian vegetation and gallery forests preferably near water to elevations as high as 500 m above sea level. From the literature (Bock et al 1998, Rand et al. 1989) and our experience in the field, we know that Green Iguanas, especially females, can migrate as far as three kilometers to find suitable nesting sites during the egg-laying season.

The GIS layers used for this project were provided by the GIS lab of the United States Forest Service, International Institute of Tropical Forestry (USFS-IITF). The first layer was the PRGAP land cover map, from which we selected only 50 of 70 land cover types thought to be crucial for Green Iguana survival (Table 1).

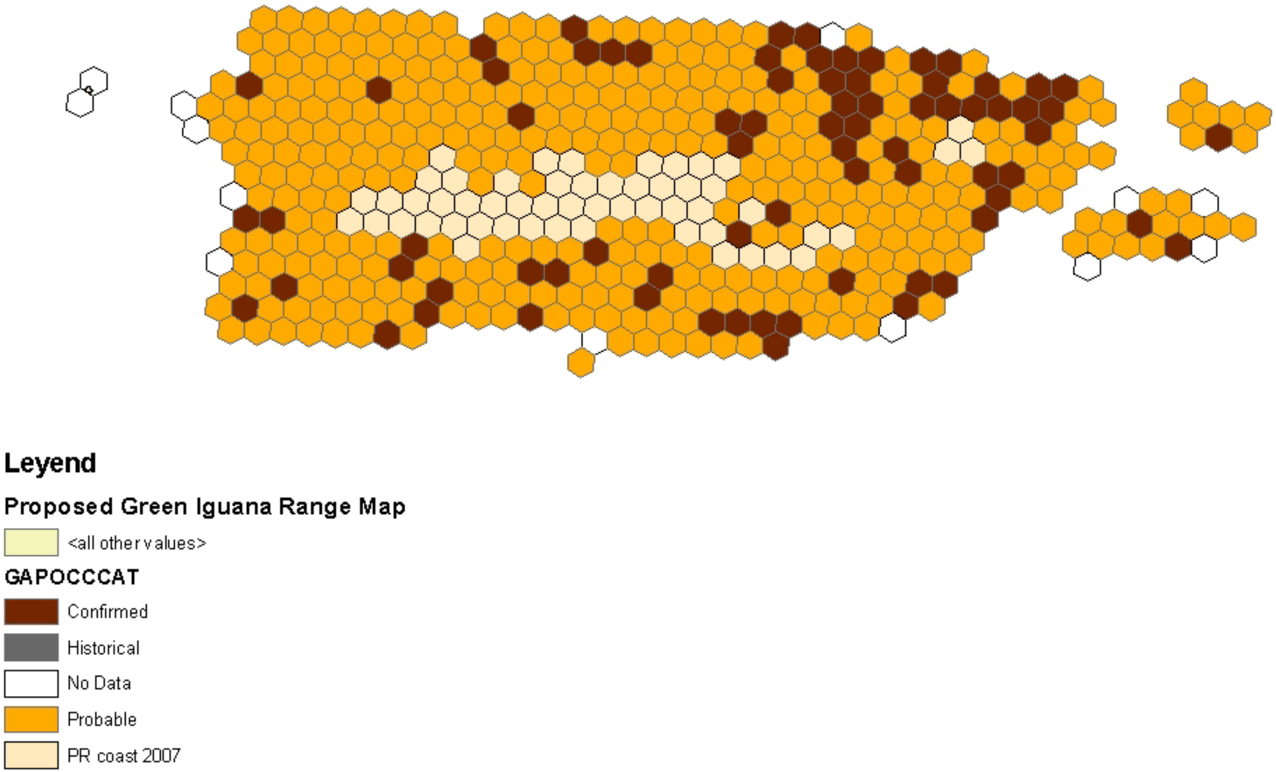

Figure 1. Green Iguana distribution displayed on a map of Puerto Rico with 24-km^2 hexagon grid. This map shows confirmed, and probable hexagons based on points gathered in the field and expert opinion for the Green Iguana. Hexagons with probable Green Iguana presence are colored yellow. Hexagons with confirmed iguana presence are colored brown.

Table 1. Habitat types from the land cover map of the PRGAP analysis. These habitat types were selected considering the daily and seasonal needs of Green Iguanas in Puerto Rico.

Habitat Type Description	**Iguana needs (Daily[D], Seasonal [S], Transitional [T])**
Mature secondary lowland dry alluvial semi deciduous forest	D
Young secondary lowland dry alluvial semi deciduous forest	D
Lowland dry alluvial shrubland and woodland	D
Mature secondary lowland dry limestone evergreen forest	D
Mature secondary lowland dry limestone semi deciduous forest	D
Young secondary lowland dry limestone semi deciduous forest	D
Lowland dry limestone woodland and shrubland	D
Lowland dry limestone shrubland	D
Lowland dry cactus shrubland	D
Coastal dwarf woodland and shrubland	D
Lowland dry limestone cliffside semi deciduous forest	D
Lowland dry limestone cliffside shrubland and woodland	D
Mature secondary lowland dry non-calcareous semi deciduous forest	D
Young secondary lowland dry non-calcareous semi deciduous forest	D
Lowland dry non-calcareous shrubland and woodland	D
Abandoned dry forest plantation	D
Mature secondary lowland moist alluvial evergreen forest	D
Young secondary lowland moist alluvial evergreen forest	D
Lowland moist alluvial shrubland and woodland	D
Mature secondary moist limestone evergreen and semi deciduous forest	D
Young secondary moist limestone evergreen and semi deciduous forest	D
Moist limestone shrubland and woodland	D
Mature secondary lowland moist non-calcareous evergreen forest	D

Young secondary lowland moist non-calcareous evergreen forest	D
Lowland moist non-calcareous shrubland and woodland	D
Lowland moist abandoned and active coffee plantations	D
Mangrove forest and shrubland	D
Freshwater *Pterocarpus* swamp	D
Lowland dry riparian forest	D
Lowland dry riparian shrubland and woodland	D
Lowland moist riparian forest	D
Lowland moist riparian shrubland and woodland	D
Dry grasslands and pastures	S
Dry cactus grassland and shrubland	S
Fine to coarse sandy beaches, mixed sand and gravel beaches	S
Riparian and other natural barrens	S
Artificial barrens	S and T
Moist grasslands and pastures	T
Emergent herbaceous non-saline wetlands	T
Emergent herbaceous saline wetlands	T
Seasonally flooded herbaceous non-saline wetlands	T
Seasonally flooded herbaceous saline wetlands	T
Hay and row crops	T
Woody agriculture and plantations: Palm plantations	T
Rocky cliffs and shelves	T
Salt and mudflats	T
Salt production	T
Freshwater	T
Saltwater	T
Aquiculture	T

From our observations in the field and evidence from literature (e.g., Savage 2002, Meshaka et al. 2007, Krysko et al. 2007, López-Torres et al. 2011), daily needs for all Green Iguana age classes include: (1) perching sites for thermoregulation, displaying, and escape; (2) food items on the ground or in surrounding vegetation; and (3) water for drinking, thermoregulation, and escape. Seasonally, Green Iguanas require additional microhabitats, and they vary among age classes. During the mating season from December to early March (López-Torres et al. 2011), dominant males will compete and defend perch sites that are both conspicuous to other iguanas and meet as many of the daily needs, particularly those of females (Dugan 1982), as possible. During the nesting and egg-laying season, from February to May (López-Torres et al. 2011), females migrate as far as 3 km to find suitable nesting sites in Panama (Montgomery et al. 1973) and up to 1.5 km in Fajardo, Puerto Rico (Rodriguez-Gómez, personal observation). Transitional needs include the habitats that separate the essential daily and seasonal habitats.

Based on daily, seasonal, and transitional needs, we divided PRGAP land cover types into three corresponding categories (Table 1). The daily-needs category includes all lowland mature and secondary forests, woodlands, as well as shrublands on limestone, non-calcareous, alluvial soils, and all riparian forests, woodlands, and shrublands, mangroves, and *Pterocarpus* forests. The seasonal-needs category includes all fine-to-course sandy beaches, riparian, natural, and artificial barrens, as well as dry pastures. The transitional-needs category includes roads, bodies of water, barrens, mud and salt flats, wet and dry pastures, agricultural lands, as well as cliffs and shelves.

Another variable important in determining the distribution of Green Iguanas was the presence of bodies of water. Using a hydrology map modified at the USFS-IITF Lab, we identified all bodies of water, including creeks and rivers, channels, lagoons, and artificial lakes, and added a buffer zone of 300 m surrounding all bodies of water and the Puerto Rican coastline to the model on the assumption that iguanas occupy habitats farther from the water's edge and that especially females engage in extensive migrations.

We delimited as suitable only the habitats that complied with iguana needs (i.e. daily, seasonal or transitional) and proximity to bodies of water, at elevations of ≤ 500 m above sea level (Figure 2). Although iguanas occur at elevations to 1000 m in Colombia (e.g., Etheridge 1982, Henderson and Powell 2009) and iguanas have been observed along the shore of an artificial lake at an elevation > 500 m in the Carite National Forest in Puerto Rico (Rafael L. Joglar, personal communication), we found no iguanas at elevations ≥ 500 m during our field surveys. This should not be construed as a statement that iguanas do not occur at higher elevations, only that they are less abundant there and that such localities are unlikely to support dense populations.

In addition, we considered in one model only, all roads plus a buffer zone of 50 m, since many Puerto Rican roads are bordered by forest or vegetation fragments and are used by Green Iguanas as suitable habitat as well as corridors during migration. The problem with this layer was that it also includes developed areas along the road, many of which are not necessarily suitable for iguanas. Consequently, it might overestimate the presence of suitable habitats. To generate our final model, we combined maps showing land-cover types, bodies of water, elevations ≤ 500 m, and the presence and probable-presence hexagons.

Data analysis. We analyzed our data and constructed the final model using ESRI-ArcGIS 10 and Quantum GIS 1.5.0. To test for differences in predictability between the Green Iguana distribution models excluding and including roads, we used chi-square tests in PAST statistics (2001) and Stat Plus: Mac (2009). For statistical tests, alphas = 0.05. We also conducted an additional analysis to determine how many of the 95 terrestrial protected areas of Puerto Rico were predicted to have Green Iguanas and how many of those were confirmed in the field.

Results

The distribution model that excluded roads (Figure 3) shows a potential range throughout most of Puerto Rico and the islands of Vieques, Culebra, and adjacent keys, with concentrations mostly in suitable habitats surrounding watersheds. In areas of high urban density (San Juan metro area, Caguas, Ponce), Green Iguanas are predicted to occur in vegetation patches (e.g., parks) and adjacent to bodies of water. Green Iguana distribution, however, is patchy in the northwestern limestone formations. The model including roads (Figure 4) was generally similar, differing primarily in having a few more corridors (corresponding to roads) deemed habitable.

Model 1 (no roads) correctly predicted 137 of 172 confirmed Green Iguana presence points, an accuracy of 79.7%. The points not confirmed by this model were either in high-density urban areas or in roadside vegetation, two variables not considered by this model. Model 2 (with roads) successfully predicted 152 of 172 presence points, an accuracy of 88.4%.

When we tested, the null hypothesis was that predictive ability was independent of the model used, the null hypothesis was rejected. The alternate hypothesis, that predictive ability was related to the model used, revealed a statistically significant difference between the predictive abilities of the models ($\chi^2 = 4.8695$, p = 0.027336, df = 1), with the model including roads more efficient in predicting Green Iguana distribution where the presence of the species had been confirmed during field surveys.

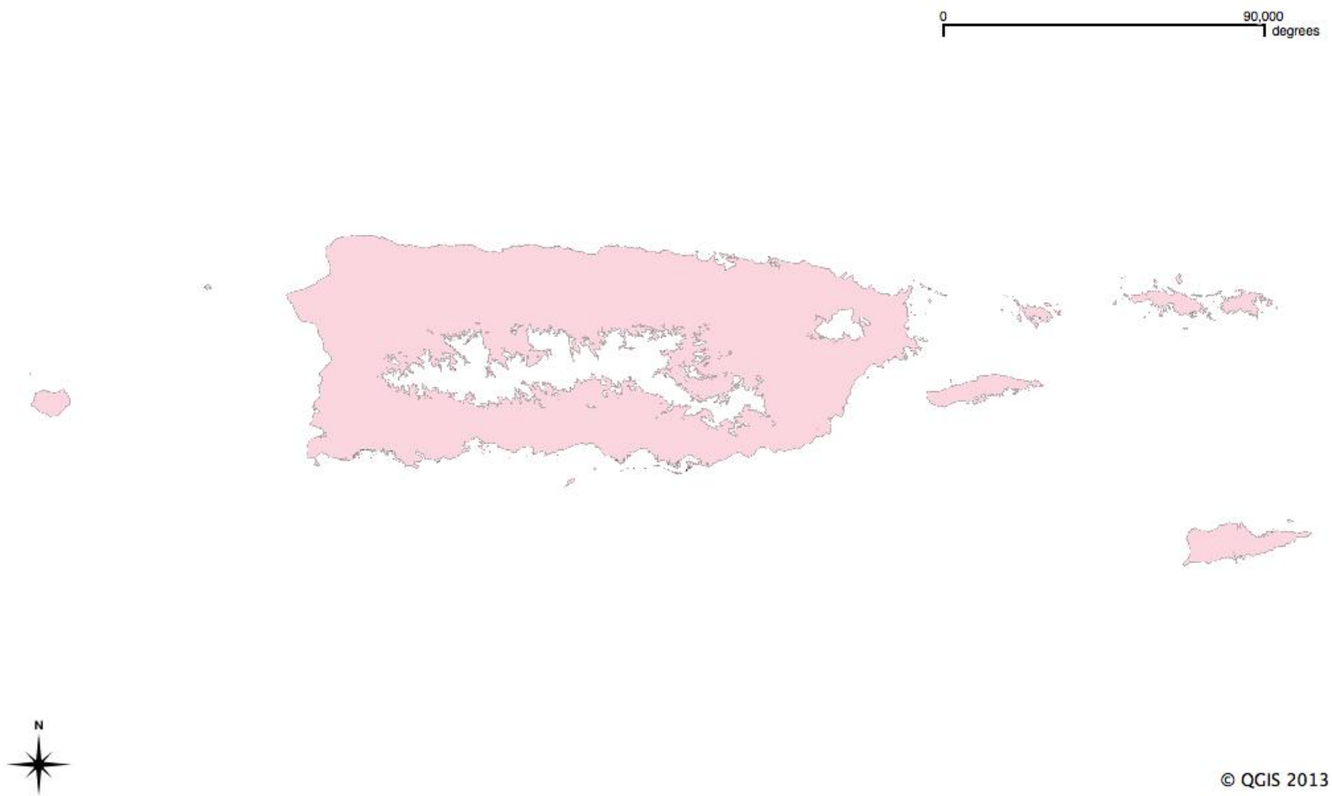

Figure 2. Map of Puerto Rico detailing the elevational distribution of Green Iguanas. Areas colored in light pink represent elevations equal to or below 500m above sea level. Areas in white represent areas above 500m above sea level, which are possibly without Green Iguanas.

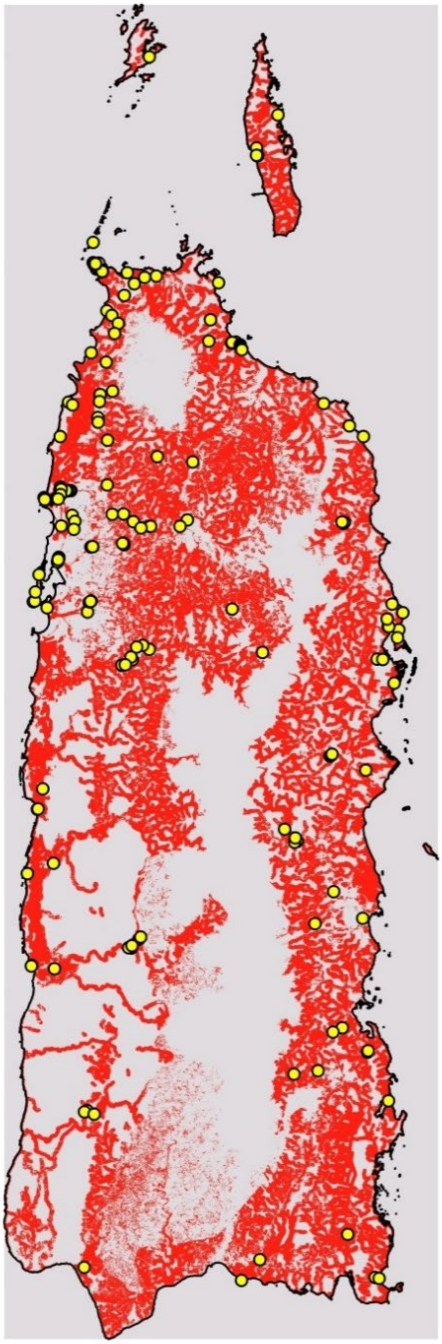

Figure 3. Model 1 for Green Iguana distribution in Puerto Rico. Yellow filled in circles represent confirmed GPS points with Green Iguana presence. Proposed Green Iguana distribution is represented in red.

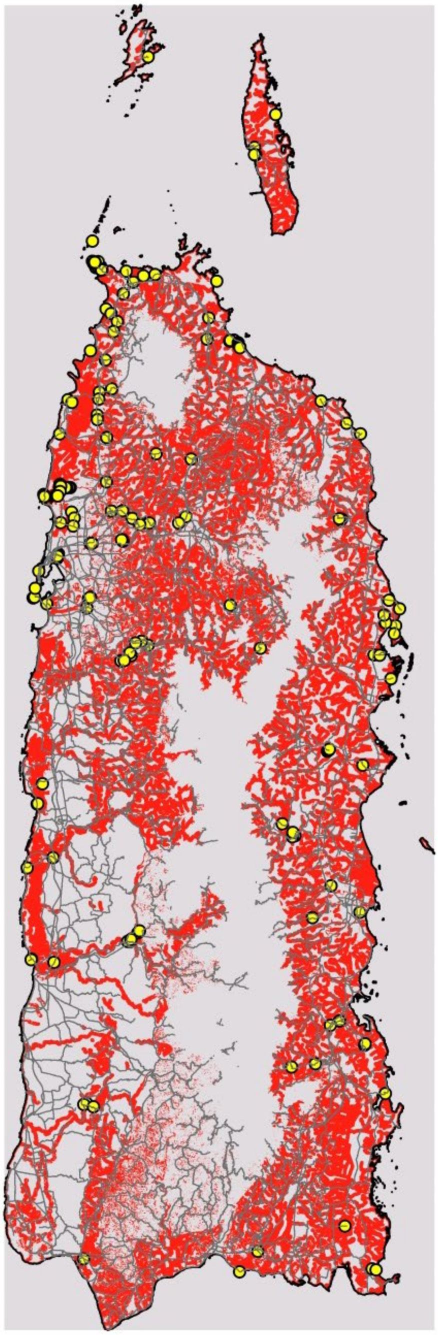

Figure 4. Model 2 for Green Iguana distribution in Puerto Rico. Yellow filled in circles represent confirmed GPS points with Green Iguana presence. Proposed Green Iguana distribution is represented in red and grey. The grey lines represent roads and roadside habitats.

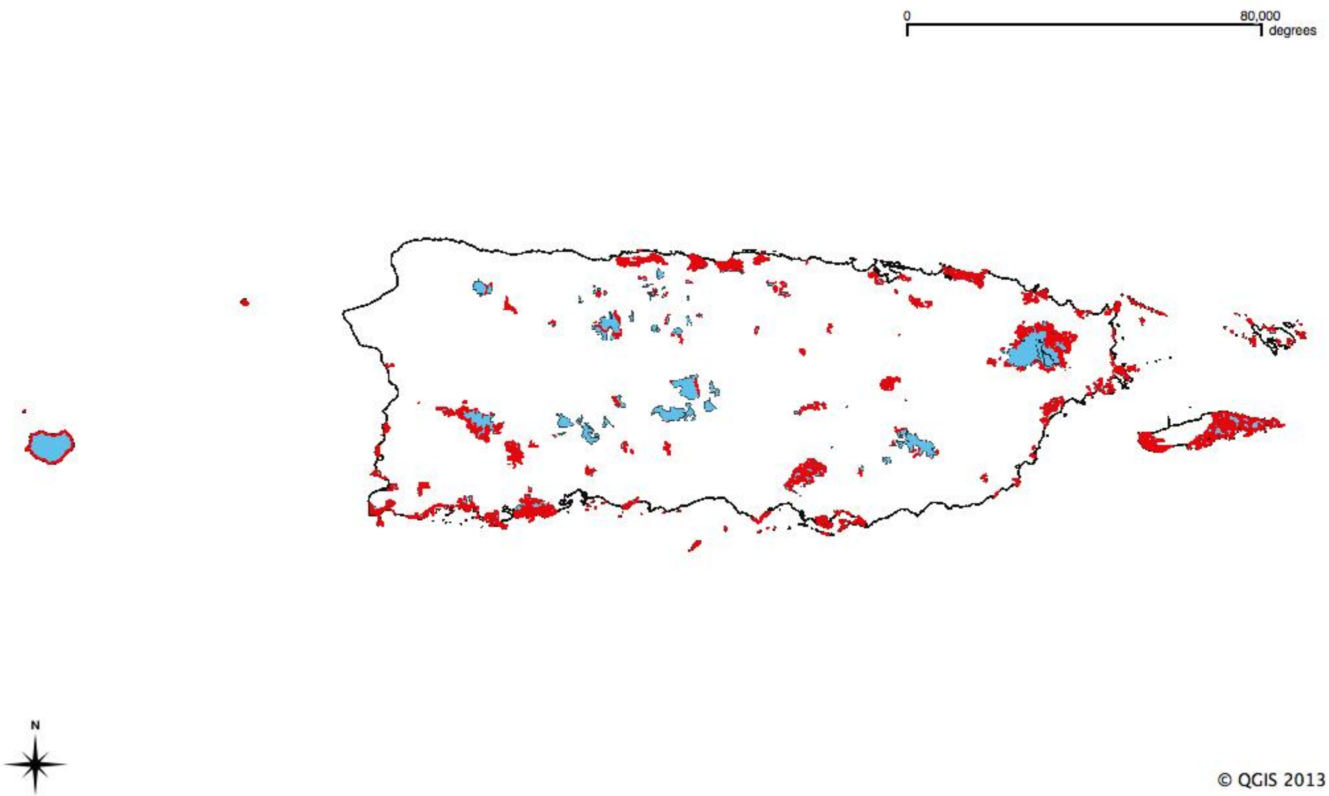

Figure 5. Map of Puerto Rico's protected areas with probable Green Iguana presence. Areas in Blue represent all of Puerto Rico's protected areas. The portions in red represent the protected areas where iguanas are predicted to be present with model 1.

Discussion

Both models were very efficient in predicting potential Green Iguana distribution in Puerto Rico, with that including roads having a slightly greater predictive ability. The inclusion of roads in the model has its pros and cons. Harris (1982) documented a phenomenon he termed "highway madness" in Green Iguanas of northern Colombia and Rodda (1990) described a similar pattern in Venezuela, both noting that the attractiveness of roads accounts for a high incidence of road-killed iguanas. Roadsides seem to be ideal nesting sites for females, but also offer vantage points for males to display and thermoregulate.

In Puerto Rico, hundreds of road-killed Green Iguanas are seen along the roads during the mating and egg-laying seasons. On 8 April 2009, we counted 36 road-killed Green Iguanas (mostly gravid females) on one side of a 13-km stretch of highway. Field surveys indicate that Green Iguanas use roadsides and adjacent habitats for perching, thermoregulation, displaying, courtship, and nesting. Roads also appear to serve as both barriers and corridors. Roads as barriers fragment habitats, but in doing so create edges, similar to habitats along rivers, mangroves, and lakes, used by iguanas (Carlo and García-Quijano 2008). However, we also think that roads and the adjacent fragmented habitats provide an extensive corridor system for the movement, migration, and possible dispersal into new habitats in Puerto Rico. More research on the effect of roads on Green Iguana populations in Puerto Rico may warrant attention, for example differences in population density and habitat use along roadside habitats in the reproductive season versus the non-reproductive season.

Although the model including roads efficiently predicts Green Iguana distribution in Puerto Rico, it might overestimate available habitats and thus numbers of iguanas. Not all roadsides contain crucial habitats as many roads are bordered by intensely developed urban areas uninhabitable by iguanas. Consequently, because of the possibility of falsely predicting the presence of Green Iguanas in many urban areas, we are inclined to prefer the model that excludes roads. Future models should incorporate fine-scale analyses that differentiate between different kinds of roads or perhaps a preference for one model over the other should be determined by a consideration of roadside conditions.

Regardless, both models indicate that Green Iguanas are widely distributed throughout Puerto Rico. Even more impressive is the realization that 86.3% (82/95) of Puerto Rico's protected areas are intersected by the distribution model excluding roads. That iguanas were not predicted to occur in protected areas at elevations > 500 meters was to be expected since the model was limited to elevations ≤ 500 m, but what we did not expect was finding protected areas at elevations < 500 m without Green Iguanas. Particularly interesting was the fact that all but one of these lowland protected areas, excepting Servidumbre de Conservación Montes Oscuros, were concentrated in the northwestern limestone region of Puerto Rico. These limestone formations, characterized by vast cave systems and subterranean rivers, possibly limiting the extent of extensive riparian corridors, supports unique habitats exploited by native and endemic flora and fauna. This region is also under constant threat from development. As a consequence, a high concentration of protected areas in this region serve to protect species like the critically endangered Puerto Rican Parrot, *Amazona vittata* Boddaert, 1783; the Puerto Rican Boa, *Chilabothrus inornatus* (Reinhardt, 1843); and are sites of efforts to reintroduce depleted populations of the Puerto Rican Crested Toad, *Peltophryne lemur* Cope, 1869. The models not predicting the presence of Green Iguanas in these protected areas should not be interpreted to imply that they are not present (although suboptimal habitat probably limits numbers). Nevertheless, for a region of such high conservation importance, this may be a good sign. Federal, state, and private land managers should pay special attention to the possible dispersal of Green Iguanas into the regions of Puerto Rico and apply their limited available resources to develop clear objectives regarding the management of this species.

The models presented herein should be useful for land managers, who can determine what crucial habitats exist for Green Iguanas in a given protected area and use that information to make important decisions regarding where to survey Green Iguana populations and where to most effectively control the populations (e.g., nesting sites). Nevertheless, we would consider including mean annual precipitation and temperature into the Green Iguana distribution models. High population densities and reproductive season in Puerto Rico appear to be correlated with temperature (López-Torres et al. 2011), so including temperature and precipitation layers into our models should enhance their predictive ability. In the future, we also propose increasing the elevational buffer to 1000 m and analyzing the extended suite of variables using MaxEnt (as in Falcón et al. 2012, 2013).

Acknowledgements

We want to thank Sebastian G. Rodríguez, Stephanie M. Rodríguez, Mariely Rodríguez Medina, and Mario Cancel for help in gathering Green Iguana presence data. We also thank the municipal mayoral and emergency management offices of the Commonwealth of Puerto Rico for providing useful information on the presence of iguanas in their communities. We also want to thank Dr. Robert Powell for his insightful comments and opinions on this paper. The University of Puerto Rico, Río Piedras Campus provided funding via the Puerto Rico Louis Stokes Alliance for Minority Participation -Bridge to the Doctorate Scholarship (Grant number: HRD-0601843), Department of Biology Formative Academic Experiences Program and the Dean of Graduate Studies and Research - Golf Tournament Scholarship. We also are immensely thankful to the USFS-International Institute of Tropical Forestry GIS lab for expert advice and for the use of equipment and software. All research at the USDA International Institute of Tropical Forestry was done in collaboration with the University of Puerto Rico.

Literature Cited

Belongie, C. 2008. Using GIS to Create a Gray Wolf Habitat Suitability Model and to Assess Wolf Pack Ranges in the Western Upper Peninsula of Michigan. Volume 10. *Papers in Resource Analysis*. 15pp. Saint Mary's University of Minnesota Central Services Press. Winona, Minnesota, USA. Retrieved on February 22, 2020 from http://www.gis.smumn.edu, http://www2.smumn.edu/ra/gis/gradprojects/belongiec.pdf

Bock, B. C. and G. F. McCracken. 1988. Genetic structure and variability in the Green Iguana (*Iguana iguana*). *Journal of Herpetology* 22(3): 316–322. https://doi.org/10.2307/1564155

Bock, B. C., V. P. Páez, and S. A. Rand. 1998. Temperaturas del suelo atípicas en áreas de anidación de la iguana verde (*Iguana iguana*) en Colombia y Panamá. *Crónica Forestal y del Medio Ambiente*13(1):55-70.

Breuil, M., B. Vuillaume, D. Schikorski, U. Krauss, M. N. Morton, P. Haynes, J. C. Daltry, E. Corry, G. Gaymes, J. Gaymes, N. Bech, M. Jelic, and F. Grandjean. 2019. A story of nasal horns: Two new subspecies of *Iguana* Laurenti, 1768 (Squamata, Iguanidae) in Saint Lucia, St Vincent & the Grenadines, and Grenada (southern Lesser Antilles). *Zootaxa* 4608: 201–232. https://doi.org/10.11646/zootaxa.4608.2.1

Brotons, L., W. Thuiller, M. B. Araújo, and H. Hirzel. 2004. Presence-absence versus presence-only modeling methods for predicting bird habitat suitability. *Ecography* 27:437–448. https://doi.org/10.1111/j.0906-7590.2004.03764.x

Carlo, T. A. and C. G. Garía-Quijano. 2008 (September 20). Assessing ecosystem and cultural impacts of the Green Iguana (*Iguana iguana*) invasion in the San Juan Bay Estuary (SJBE) in Puerto Rico. Unpublished Final Report for SJBE.

Corsi, F., J. de Leeuw, and A. K. Skidmore. 2000. Modeling species distribution with GIS. pp. 320-339. In, Boitani, L., and T. K. Fuller (Editors). *Research Techniques in Animal Ecology: Controversies and Consequences.* Columbia University Press. New York, NY, USA. 442 pp.

Dugan, B. 1982 The mating behavior of the Green Iguana, *Iguana iguana*. pp. 320-339. In, Burghardt, G. M. and A. S. Rand (Editors). *Iguanas of the World: Their Behavior, Ecology, and Conservation*. Noyes Series in Animal Behavior, Ecology, Conservation and Management. Park Ridge, New Jersey, USA. 474 pp.

Etheridge, R. 1982. Checklist of the iguanine and Malagasy iguanid lizards. pp. 7-37. In, Burghardt, G. M. and A. S. Rand (Editors). *Iguanas of the World: Their Behavior, Ecology, and Conservation*. Noyes Series in Animal Behavior, Ecology, Conservation and Management. Park Ridge, New Jersey, USA. 474 pp.

Falcón, W., J. D. Ackerman, and C. C. Daehler. 2012 (September). March of the Green Iguana: Non-native distribution and predicted geographic range of *Iguana iguana* in the greater Caribbean region. *IRCF* (*International Reptile Conservation Foundation*) *Reptiles and Amphibians*10(3): 150–160. https://www.researchgate.net/publication/231521613_March_of_the_green_iguana_Non-native_distribution_and_predicted_geographic_range_of_Iguana_iguana_in_the_Greater_Caribbean_Region

Falcón, W., J. D. Ackerman, W. Recart, and C. Daehler. 2013. Biology and impacts of Pacific island invasive Species. 10. *Iguana iguana*, the Green Iguana. *Pacific Science* 67(2):157-186. https://doi.org/10.2984/67.2.2

Gassó, N., W. Thuiller, J. Pino, and M. Vilà. 2012. Potential distribution range of invasive plant species in Spain. *NeoBiota* 12: 25 – 40. https://doi.org/10.3897/neobiota.12.2341

Gibson, L. A., B. A. Wilson, D. M. Cahill, and J. Hill. 2004. Spatial prediction of rufous bristlebird habitat in a coastal heathland: a GIS – based approach. *Journal of Applied Ecology* 41:213-223. https://doi.org/10.1111/j.0021-8901.2004.00896.x

Gould, W. A., C. Alarcón, B. Fevold, M. E. Jiménez, M. Martinuzzi, G. Dotts, M. Quiñonez, M. Solórzano, and E. Ventosa. 2008. The Puerto Rico Gap Analysis Project. Volume 1. Landcover, Vertebrate Species, Distributions and Land Stewardship. United States Department of Agriculture. Forest Service. General Technical Report. International Institute of Tropical Forestry General Technical Report IITF-GTR-39. 165 pp. Published online. https://doi.org/10.2737/IITF-GTR-39

Harris, D. M. 1982. The phenology, growth, and survival of the Green Iguana, *Iguana iguana* pp. 150-161. In, Burghardt, G. M. and A. S. Rand (Editors). *Iguanas of the World: Their Behavior, Ecology, and Conservation*. Noyes Series in Animal Behavior, Ecology, Conservation and Management. Park Ridge, New Jersey, USA. 474 pp.

Henderson, R. W. and R. Powell. 2009. *Natural History of West Indian Reptiles and Amphibians*. University Press of Florida. Gainesville, Florida. USA. 528 pp.

Buckley, L. J., K. De Queiroz, T. D. Grant, B. D. Hollingsworth, J. B. Iverson, S. A. Pasachnik, and

C. L. Stephen (Iguana Taxonomy Working Group). 2016. A checklist of the Iguanas of the World (Iguanidae; Iguaninae). In, Iverson, J. B., T. D. Grant, C. R. Knapp, and S. A. Pasachnik (Editors). *Iguanas: Biology, Systematics, and Conservation. Herpetological Conservation and Biology* 11 (Monograph 6):4-46. http://www.herpconbio.org/Volume_11/Monograph_6/2-Iguana_Taxonomy_Working_Group_2016.pdf

Krysko, K. L., K. M. Enge, E. M. Donlan, J. C. Seitz, and E. A. Golden. 2007. Distribution, natural history and impacts of the introduced Green Iguana (*Iguana iguana*) in Florida. *Iguana* 14(3): 142-151.

López-Torres, A. L., H. J. Claudio-Hernández, C. A. Rodríguez-Gómez, A. V. Longo, and R. L. Joglar. 2011. Green Iguanas (*Iguana iguana*) in Puerto Rico: is it time for management? *Biological Invasions* 14(1):3 –45. https://doi.org/10.1007/s10530-011-0057-0

Lugo, A. E. and J. M. Wunderle Jr. 2012 Natural mixing of species: novel plant – animal communities on Caribbean Islands. *Animal Conservation* 15:233-241.https://doi.org/10.1111/j.1469-1795.2012.00523.x

McPherson, J. M. and W. Jetz. 2007. Effects of species' ecology on the accuracy of distribution models. *Ecography* 30:135–151. https://doi.org/10.1111/j.0906-7590.2007.04823.x

Meshaka Jr., W. E., H. T. Smith, E. Golden, J. A. Moore, S. Fitchet, E. M. Cowan, R. M. Engeman, and S. R. Sekscienski. 2007. Green Iguanas (*Iguana iguana*): The unintended consequence of sound wildlife management practices in a South Florida. *Herpetological Conservation and Biology* 2:149–156.

Meyerson, L. and H. A. Mooney. 2007. Invasive alien species in an era of globalization. *Frontiers in Ecology and the Environment* 5(4):199–208. https://doi.org/10.1890/15409295(2007)5[199:IASIAE]2.0.CO;2

Montgomery, G. G. 1973. Post-nesting movements of iguanas from a nesting aggregation. *Copeia* 3:620–622. https://doi.org/10.2307/1443141

Rand, A. S., E. Font, D. Ramos, D. I. Werner, and B. C. Bock. 1989. Home range in Green Iguanas (*Iguana iguana*) in Panama. *Copeia* 1989(1):217–221. https://doi.org/10.2307/1445631

Rivero, J. A. 1998. *Los Anfibios y Reptiles de Puerto Rico*. Segunda Edición Revisada. *The Amphibians and Reptiles of Puerto Rico*. Editorial de la Universidad de Puerto Rico. San Juan, Puerto Rico. 510 pp.

Rodda, G. H. and A. Grajal. 1990. The nesting behavior of the Green Iguana, *Iguana iguana* in the llanos of Venezuela. *Amphibia-Reptilia* 11: 31–39. https://doi.org/10.1163/156853890X00294

Savage, J. M. 2002. *The Amphibians and Reptiles of Costa Rica: A Herpetofauna between Two Continents, between Two Seas*. The University of Chicago Press. Chicago, Illinois, USA. 934 pp.

Stephen, C. L., V. H. Reynoso, W. S. Collet, C. R. Hasban, and J. W. Breinholt. 2013. Geographical structure and cryptic lineages within common green iguanas, *Iguana iguana. Journal of Biogeography* 40:50–62. https://doi.org/10.1111/j.1365-2699.2012.02780.x

Strayer, D. L. 2012. Eight questions about invasions and ecosystem functioning. *Ecology Letters* 15(10):1199-1210. https://doi.org/10.1111/j.1461-0248.2012.01817.x

Townsend–Peterson, A. and D. A. Vieglais. 2001 Predicting species invasions using ecological niche modeling: new approaches from bioinformatics attack a pressing problem. *BioScience* 51(5):363–371. https://doi.org/10.1641/0006-3568(2001)051[0363:PSIUEN]2.0.CO;2

Vuillaume, B., V. Valette, O. Lepais, F. Grandjean, and M. Breuil. 2015. Genetic evidence of hybridization between the endangered native species *Iguana delicatissima* and the invasive *Iguana iguana* (Reptilia, Iguanidae) in the Lesser Antilles: Management implications. *PLoS One* 10(6).e0127575. https://doi.org/10.1371/journal.pone.0127575