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Fern Community Reassembly in Secondary Forests of Puerto Rico: Predictors, Complexity, and Niche Model Assessment

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Fern community reassembly in secondary forests of Puerto Rico: predictors, complexity, and niche model assessment.

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ABSTRACT

Approximately 94% of Puerto Rico's forests were converted into agricultural systems by 1950. Since then, extensive abandonment of agricultural land has resulted in a considerable amount of forest regeneration throughout the main island. Ferns are a major non-woody component of oceanic, tropical island forests comprising up to seventy percent of the flora. Consequently, the composition and community structure of ferns may be indicative of the relative richness of these secondary forests. I used Maximum Entropy (Maxent), a widely-used mathematical tool for distinguishing suitable versus unsuitable fern niche space, along with ENMTools, a tool that assists Maxent with proper model selection, for accurately predicting 29 common, rare, terrestrial, and epiphytic tropical fern species' distributions. Model discrimination was assessed via area under the receiver operating characteristic curve values, a common metric for model evaluation. Akaike information criteria were utilized for assessing model complexity and in selecting the most parsimonious model for each species. I highlight the importance of modeling with proper model complexity and emphasize the use of information criteria to accurately infer AUC values. Field testing of model predictions also reinforced that these models are successful at identifying suitable habitat for ferns in Puerto Rico and conservation recommendations are explored.

Key words: conservation management; Puerto Rico; secondary forests; Maxent; AUC; species distribution modeling; Akaike information criteria; complexity; fern.

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INTRODUCTION

Predictive modeling of plant and animal distributions using geographic information systems (GIS) and statistical algorithms such as Maxent, GARP, GLM, GAM, BIOCLIM, or MARS (to name a few) has become prevalent due to their accuracy in estimating unknown species distributions and has great value in decision making and conservation prioritization (Peterson et al. 2011). Incorporating biologically and ecologically relevant environmental variables into species distribution models (SDM) can lead to the identification of suitable locations for species based on previously documented occurrences at local, regional, and global scales. These models are useful to conservationists because they can provide visual probabilities of occurrence for desired species when their potential distributions are unknown (Elith et al. 2011, Rotenberry et al. 2006, Elith et al. 2006, Phillips et al. 2006).

Many predictive modeling techniques have become widely used with presence and absence location data of plant and animal species (Peterson et al. 2011, Rotenberry et al. 2006, Elith et al. 2006, Guisan et al. 2002, Guisan and Zimmerman 2000). In most cases, however, due to biased sampling and travel limitations, true absence data rarely exists among large, available museum or herbarium datasets especially for species in remote, tropical geographies where ecological modeling and conservation management has the greatest value (Elith et al. 2006, Phillips et al. 2006). Maxent has become a widely used tool designed for predictive modeling of species distributions across geographic regions with presence-only data (Phillips et al. 2006, Phillips and Dudík 2008, Elith et al. 2011). It uses the theory of maximum entropy, one that is least biased based on partial information (e.g., environmental conditions at only known species locations) for setting up probability distributions (Jaynes 1957). Maxent has become favored among spatial ecologists and is used by governmental and non-governmental organizations for biogeographical mapping projects for a number of reasons aside from its ability to utilize presence-only data: (1) it has proven robust with very few species occurrence locations (Hernandez et al. 2006, Guisan et al. 2007); (2) categorical data such as geologic substrate or soil type can be incorporated; and (3) it has consistently outperformed other modeling techniques based on discrimination success (Wisz et al. 2008, Guisan et al. 2007, Elith et al. 2006, but see Renner and Warton 2013). Maxent provides a logistic output in which cells throughout the geography contain habitat suitability values ranging from 0 to 1. Cells exhibiting values closer to 0 would be least suitable while cells closer to 1 would indicate high suitability.

Puerto Rican secondary forests are now older than most revegetating tropical landscapes found elsewhere. Thus, they provide an exceptional opportunity to study tropical forest redevelopment after large scale clearing and deforestation (Chinea and Helmer 2003). The original forests of Puerto Rico nearly disappeared completely by the early 20th century due to large-scale agriculture, primarily the production of coffee and sugarcane, and the introduction of cattle, depleting the original forest to a mere 6% of its original area (Proctor 1989, Chinea and Helmer 2003, Kennaway and Helmer 2007). Although the increase in human population in Puerto Rico over the past few decades [now totaling over 3.72 million equating to 2818 people per km^2 (2010 U.S. Census)], has put pressure on the island’s natural resources, forest cover has and continues to increase. This results from an economic shift to services and industry during the past 70 years and forest now covers over 57% of the main island of Puerto Rico, increasing

211,653 hectares since the forest inventory of 1980 (Kennaway and Helmer 2007, Brandeis et al. 2003).

Preceding human occupancy, Puerto Rico was primarily composed of tall mesophytic forests and rain forests in the wettest areas (Proctor 1989). According to Proctor (1989), Puerto Rican forests contained over 400 species of ferns, an important non-woody component to Puerto Rico's flora. The ecological significance of ferns is often underestimated due to the fact that most ecological research has been conducted in temperate zones where they are – overall – a minor component of forest flora (Mehltreter et al. 2010), but with notable exceptions (Gilliam 2007; George and Bazzaz 2003). Ferns disseminate via minute spores (20-60 μm; < 0.01 mg; Tryon 1970, Westoby et al. 1990) and are hence extremely successful at long distance dispersal. As a result, ferns are a major component of forests on remote, montane islands, comprising on average 15.3% and up to 70% of the vascular flora (Mehltreter et al. 2010). Thus, ferns are large contributors to energy, water, and nutrient dynamics in these island ecosystems, some of which include organic matter buildup, soil fertility and stability, hydraulic balance, facilitation of succession, and stabilization of slopes in areas frequently stricken by hurricanes and landslides (Drake and Pratt 2001, Walker et al. 2001).

Oceanic islands tend to have large numbers of endemic fern species resulting from geographic or elevational isolation and subsequent barriers to cross-breeding inducing speciation events (Carlquist 1974, Palmer 2003). As a result, many tropical species are more sensitive to alterations or destruction of habitat (Stevens 1989). Ferns in general are therefore of great concern for conservation management in tropical environments due to their coevolutionary history and interaction among other plant and animal species which depend upon them as sources of food, shelter, or habitable space in these unique habitats. Due to their ubiquity in tropical forests and relatively well-known taxonomy, ferns have been used as surrogates for patterns of community composition and species richness in tropical forests (Kessler 2001, Kreft et al. 2010).

Of the 400 plus species of ferns on the main island of Puerto Rico, approximately 20% are known from only one or two locations, 22 are endemic, and eight (all endemic) are endangered according to the United States Department of Agriculture (Proctor 1989, Miller and Lugo 2009). The composition and richness of fern species throughout the majority of secondary forests has yet to be assessed and may be indicative of overall species richness and abundance. Understanding the distributional patterns and environmental covariates of select fern species can lead to well developed management plans and conservation prioritization for protecting species richness in sensitive tropical areas (Gould et al. 2011).

The goals of this project were to: (1) use Maxent to predict the distributions of twenty-nine fern species that characterize a range of niche's (terrestrial and epiphytic) and frequency (rare to common); (2) to test model accuracy at differing levels of complexities; (3) to asses secondary forest structure (i.e., canopy cover and tree size) and environmental conditions (GIS variables) on fern species richness; and (4) to explore conservation recommendations in Puerto Rico.

METHODS

Study area – The study area consists of the entire main island of Puerto Rico. Puerto Rico is a small (8497 km^2), montane Caribbean island of the Greater Antilles lying between latitudes 17°45’ N and 18°30’ N, and longitudes 65°45’ W and 67°15’ W, just east of the Dominican Republic and ~810 km north of Venezuela, South America (coast to coast). The uplands peak in two distinctly separated ranges reaching heights of 1074 m in El Yunque National Forest in the northeastern end of the island, and 1338 m in the Cordillera Central or central mountain range (Figure 1). The Cordillera Central splits the island roughly into northern and southern halves causing a great range in climatic conditions throughout the year with greater average annual rainfall in the northern regions than in the southern regions due to a rain shadow effect (Daly et al. 2003). The wettest regions on the island occur in the Luquillo Mountains in El Yunque National Forest which receive up to 4500 mm of annual rainfall followed by the higher extents and foothills of the Cordillera Central with approximately 2500 mm of average annual rainfall. The southern coast is the driest region receiving less than 850 mm of average rainfall annually (Daly et al. 2003). Temperatures on the main island are highly correlated with elevation, however, the warmest temperatures are recorded in regions where relatively little precipitation occurs annually (Daly et al. 2003).

Species and environmental data

Species data – Species presence data were collected from herbaria at the University of Puerto Rico (UPR) Río Piedras campus and UPR Mayagüez campus. Additional presence locations were obtained from the New York Botanical Garden herbarium database (NYBG 2009). All fern species with a minimum of 15 nonduplicated presence locations were used in modeling (Table 1). This minimum was chosen as a conservative threshold as Maxent predictions remain robust at sample sizes as low as ten (Guisan et al. 2007).

Environmental data – As suggested by Franklin (1995), climatic variables are the primary determinants for plant species distributions followed by geology, land cover, and finally topography. Additional research demonstrates fern richness and geographic distributions are primarily determined by rainfall and topographic complexity (Kreft et al. 2010, Mehltreter et al. 2010, Tuomisto and Poulsen 1996, 2000). Kreft et al. (2010) confirmed that fern richness was highly positively correlated with potential evapotranspiration on a global scale ($r = 0.77$ for island floras), while Kessler (2001) found precipitation and humidity to be the two primary drivers of fern species richness in montane Andean forests of Bolivia. Although edaphic factors such as pH, NO_3^-, P, K, and slope were important in determining fern niche space, Karst et al. (2005) concluded soil moisture gradients had the strongest effect.

Four primary categories of ecologically relevant predictors were chosen: climate, topography, vegetation indices, and geology (Table 2). Pearson correlation matrices were created to test collinearity among variables using the “stats” package in R version 2.15.1 (www.r-project.org). Only one predictor was selected for use in the model when two or more variables were highly correlated ($r \geq 0.8$). All transformations and calculations were performed with ArcGIS version 10 (ESRI 2011).

Temperature and precipitation data, provided by the International Institute of Tropical Forestry, were developed from 32 years of daily data collected at 47 (temperature) and 108 (precipitation) National Oceanic and Atmospheric Administration

(NOAA) stations throughout Puerto Rico (Daly et al. 2003). Data were interpolated into average monthly and annual maximum and minimum temperatures, and average monthly and annual precipitation in 450-m^2 grid raster datasets (Daly et al. 2003). Two climatic variables that promote and two climatic variables that reduce evapotranspiration were chosen. Temperature variables represent the average highs and average lows during the warmest and coldest months of the year respectively, while precipitation variables represent the average monthly rainfall during the driest and wettest months (Table 2). These variables represent extremes that likely facilitate growth and reproduction versus impose drought stress.

Differences in topographic properties have shown to be primary controls of fern richness and abundance in Amazonian communities, and hence slope and aspect variables were included in modeling (Tuomisto and Poulsen 1996, 2000). Slope and aspect were derived from NOAA Puerto Rico 1-arc-second (~30-m^2) digital elevation models (Taylor et al. 2008) and rendered operational with DEM Surface Tools (Jenness 2013). Aspect was transformed to linear variables “northness” and “eastness” ranging from 1 (closest to north or east) to -1 (furthest from north or east) with the following expressions:

$$\text{Northness} = [\text{aspect in degrees}(\pi/180)]\text{cosine}$$

$$\text{Eastness} = [\text{aspect in degrees}(\pi/180)]\text{sine}$$

Both northness and eastness were utilized as they each may have predictive value. For example, fern species in Columbia and Ecuador have been found to inhabit western slopes but not eastern slopes which may be indicative of a dispersal barrier or environmental differences among slopes (Mehltreter et al. 2010 and citations therein, Peterson et al. 2011). Additionally, some species may require increased or consistent insolation or increased evapotranspiration on southern facing slopes relative to northern facing slopes that receive less direct sunlight annually.

Despite high dispersal potential, ranges of fern species distributions have also been strongly attributed to habitat availability (Kreft et al. 2010, Mehltreter et al. 2010 and citations therein). Pearson et al. (2004) found that the inclusion of land cover data significantly improved model performance. In a highly altered landscape, such as Puerto Rico, including land cover allows incorporation of habitat availability and may aid in discrimination of climatically suitable yet physically uninhabitable areas (Gogol-Prokurat 2011, Pearson et al. 2004, Franklin 1995). Many fern species rely on moderately to almost completely closed canopies which alleviate direct insolation and regulate humidity levels (Mehltreter et al. 2010, Kessler 2001). Hence, these indices will likely improve the discrimination of realistic species distributions rather than map broad scaled climatically suitable habitats.

Tasseled cap (TC) vegetation indices were calculated in IDRISI 17.0 (Eastman 2012) using cloud-free, atmospherically corrected mosaicked Landsat satellite imagery (Helmer and Ruefenacht 2005). These TC indices include: greenness, indicating the denseness of vegetation; wetness, indicating moisture retained by vegetation and soil; and brightness, indicating exposed soil and concrete (Crist and Cicone 1984, Gogol-Prokurat 2011).

Geologic substrate (Bawiec 1999), the only categorical variable, was removed from most species' models as it erroneously swayed predicted distributions towards specific substrates during initial runs (an issue likely caused by few occurrences and biased sampling in more readily accessible locations). This variable should only be utilized for species known to specialize on specific substrates (Table 1) and was utilized on said species. All models were run at 30-m^2 grain resolutions.

Model optimization and assessment

Use of an excessive number of predictor variables can produce models that are overfit (i.e., overly restricted predicted distributions and hence unrealistically confined). Maxent uses the provided environmental variables to derive simple functions called “features.” As the number of variables used increases, more complex features are created. With small occurrence data sets, however, Maxent will match the data too closely, known as “overfitting,” creating constricted, unrealistic distributions (Phillips and Dudík 2008). The regulation multiplier, or simply beta (β), setting in Maxent can be increased which relaxes the constraints generating a predicted distribution for a species that is increasingly broad [see Phillips and Dudík (2008) for a detailed statistical discussion]. Information criteria can then be used to compare models varying in complexity. Akaike information criterion (AIC) was used to identify the most parsimonious model that maintained high predictive discrimination referred to as the most “robust” model hereon.

Each species’ distribution model was re-ran, altering complexity by setting β at 1 (default), 2, 3, 4, 5, 6, 7, and 8. ENMTools version 1.3 was utilized in generating sample size corrected AIC (AIC_c) values for identifying the most robust model as this indicator demonstrated the best average performance at estimating model complexity with fewer species’ occurrences (Warren et al. 2010, Warren and Seifert 2011).

A common approach to testing model performance is use of the receiver operating characteristic curve or commonly, area under the curve (AUC) value. The AUC reports the probability that randomly chosen presence cells (i.e., 30-m^2 cells within the geography containing species' locations used in modeling) will be ranked higher than randomly chosen absence cells (i.e., 30-m^2 cells within the geography not containing species' locations used in modeling; Phillips and Dudík 2008, Fielding and Bell 1997). Its appeal is that it quantifies a model's discrimination (i.e., measures whether presence cells have higher habitat suitability values than do randomly selected absence cells) with a single value that can be compared to other models. (Phillips et al. 2006, Peterson et al. 2011). An AUC value of 0.5 indicates that a model is no better than random at predicting species' distributions while values closest to 1 indicate optimal model discrimination of suitable vs. unsuitable habitats.

There are two main AUC values, training (AUC_{Train}) and test (AUC_{Test}). AUC_{Train} is calculated with a randomly selected set of presence locations utilized in model construction and represents how well the location data "fits" the environmental data (Phillips et al. 2006). AUC_{Train} is reported to estimate model quality, favoring models with greater variables, and therefore should be interpreted with caution (Warren and Seifert 2011). AUC_{Test} is calculated with a randomly selected set of withheld presence locations and is the true test of model predictiveness (Phillips et al. 2006, Phillips and Dudík 2008). The difference between AUC_{Train} and AUC_{Test} (AUC_{Diff}) can be used to investigate over-parameterization in models as overfit models are likely to perform well on training data but poor on test data (Sarkar et al. 2010, Warren and Seifert 2011). Average AUC values for models at default and robust settings for each species were compared.

Maxent version 3.3.3k was utilized for all model runs with the following settings for each species: "random test percentage" was set to 25% to generate AUC values;

“random seed” was selected ensuring differing test and train species’ locations for repeated model runs; “replicated run type” was set to subsample ensuring test locations are withheld and independent of training locations used during model building; “replicates” was set to 30; “maximum iterations” was set to 5000 allowing ample time for each run; and no samples were added to the background (Phillips et al. 2006). All other settings were default.

Habitat suitability – The average habitat suitability map for each species were overlaid and summed displaying predicted habitat suitability of fern community reassembly. Maximum test sensitivity plus specificity was the threshold selected during modeling at robust settings to create binary maps depicting suitable versus unsuitable habitat for each species. This threshold was chosen based on results from Liu et al. (2013) stating that threshold selection should be based on maximizing the sum of sensitivity and specificity when modeling with presence-only data. The median of 30 replicated thresholds for each species was calculated and overlaid. These overlaid outputs were compared to modeled species documented in secondary forest plots as well as total fern species documented in plots. Additionally, each species was assigned a categorical variable based on Proctor (1989), 0 for rare species or species restricted to extreme habitats (e.g., restricted to steep or mountainous areas) and 1 for common species (Table 1), and a polyserial correlation was conducted on the rate at which models accurately predicted species present or absent at secondary forests sites using each species’ averaged threshold.

Field testing and secondary forest assessment

Twenty-two 20 m × 20 m plots were surveyed in secondary forest scattered across the main island of Puerto Rico from July 26th 2012 – August 25th 2012 (Figure 1). Plots were chosen based on accessibility using the latest forest stand data by Brandeis et al. (2003) prior to modeling, eliminating potential bias. All fern species were identified in each plot and a voucher specimen was submitted to the Grand Valley State University herbarium. Canopy cover was determined in the center and at four more evenly spaced positions using a densiometer at a north, south, east, and west direction within each plot. The diameter at breast height (DBH) of the ten largest trees within each plot were measured.

All statistical analyses were computed in R version 2.15.1 (www.r-project.org). Average model discrimination values were compared via Student’s t-tests, or Wilcoxon signed-rank tests when normality was not met, paired by species. Canopy cover and DBH measurements were compared to species richness in plots via Spearman rank correlations. Species richness in plots was compared to environmental variables used in modeling via Spearman rank correlations. Additionally, species richness in secondary forest plots was compared to Maxent habitat suitability and average overlaid thresholds via Pearson’s correlation and Spearman rank correlation respectively. Significance was determined at an alpha value of 0.05.

RESULTS

Model discrimination – Average AUC_{Train} values ranged from 0.835 to 0.980 and average AUC_{Test} values ranged from 0.625 to 0.961 for all species with models run at $\beta = 1$ (default). Average AUC_{Train} values ranged from 0.717 to 0.969 and average AUC_{Test} values ranged from 0.618 to 0.958 for all species run at robust β values (Table 3). Average AUC_{Train} values did not differ significantly between default and robust β settings, however, average AUC_{Test} values were significantly greater at robust settings ($n = 29$, $t = 1.85$, $P = 0.03$). Model performance therefore increased at robust settings on average for the majority of species. Ten of the twenty-nine species exhibited very similar yet slightly lower average AUC_{Test} values at robust settings rather than default settings (Table 3). AUC_{Diff} values were significantly lower at robust settings on average ($n = 29$, $V = 9$, $P < 0.0001$), indicating that models run at defaults settings are overfit creating limited suitable habitat distributions.

The species with the greatest performing models (i.e., average $AUC_{Test} > 0.9$) include *Cyathea bryophila*, *Grammitis serrulata*, *Tectaria cicutaria*, *Odontosoria scandens*, *Oleandra articulata*, *Polypodium loriceum*, and *Trichomanes scandens* respectively (Table 3). SDM have been shown to perform well on rare and endemic species in addition to species restricted to specific habitats or minute geographic ranges (McPherson and Jetz 2007, Franklin et al. 2009). These seven species are all restricted to high elevation, mountainous rain forests, aside from *T. cicutaria*, which is restricted to low elevation, calcareous substrates. Additionally, *C. bryophila* is endemic and its model performed the greatest compared to all species (average $AUC_{Test} = 0.958$). The only other endemic modeled, *Cyathea portoricensis*, also performed relatively well (average

AUC_{Test} = 0.824) but has a much broader geographic distribution and elevational range than that of *C. bryophila* (Table 1).

Although numerous species had low field success rates, model performance should not be considered poor. The ten least successful models (<60% success rate) contain five of the nine rare species used in modeling. In addition, these ten species all exhibited AUC values between 0.674 and 0.927, indicating relatively good model performance. *Polybotrya cervina* (average AUC_{Test} = 0.833) performed poorest at 32% field success rate; however, this species only occurs in wet, mountainous regions difficult to access. Similarly, *Odontosoria aculeata* (average AUC_{Test} = 0.674) with a 41% field success rate, only occurs in scattered localities across the island in mountainous regions. At 41% field success, *Oleandra articulata* (average AUC_{Test} = 0.927) was once common across the island in most moist regions. This species is now confined to mature forests due to its sensitivity to human disturbance (Proctor 1989). *Aracnioides chareophylloides* (average AUC_{Test} = 0.755; 50% field success) was found across the island in widely ranging habitat types, moisture gradients, and elevations (Schmidt *personal observation*) reducing model predictability. More occurrence data is likely necessary for this generalist species. *Polypodium crassifolium* (AUC 0.737; 55% success rate) is primarily confined to protected, mature forests which were not assessed (Proctor 1989). Finally, *Trichomanes crispum* (AUC 0.851; 59% success rate) is widely scattered across the island but uncommon in all localities (Proctor 1989).

Habitat suitability – Each species' habitat suitability and threshold map were averaged from 30 replicated runs at robust settings (Figure 2). Summed habitat suitability (all species; Figure 3) was positively correlated with modeled species documented in secondary forest plots (*r* = 0.58, *P* = 0.002, Figure 4), validating the accuracy of Maxent to detect suitable habitat for species at robust settings. Total fern species documented in secondary forest sites was not significantly correlated with neither summed habitat suitability nor number of species predicted present. The polyserial correlation coefficient was 0.551 indicating that common species were more frequent in plots than were rarer species (test of bivariate normality: *chisquare* = 1.275, *df* = 5, *P* = 0.937).

Field testing and secondary forest assessment – Species richness decreased with increasing variation in canopy cover (*rho* = -0.49, *P* = 0.01), which was primarily driven by terrestrial species (*rho* = -0.53, *P* = 0.005). Species richness increased on northern facing slopes (*rho* = 0.35, *P* = 0.05). Species richness decreased with increasing average annual temperature (*rho* = -0.45, *P* = 0.01). There was a weak, positive correlation between species richness and elevation (*rho* = 0.33, *P* = 0.06). Epiphyte species richness increased as February precipitation increased (*rho* = 0.49, *P* = 0.01). Surprisingly, there was a negative correlation between total species richness and average annual precipitation (*rho* = -0.43, *P* = 0.02).

DISCUSSION

Increasing β to find proper complexity is necessary for model accuracy and reliable AUC interpretation, indicated by significantly greater AUC_{Test} values for the majority of species at robust settings. Few SDM studies investigate complexity and treat it as unimportant in Maxent. Results here demonstrate that model complexity affects performance in Maxent and likely most applications, coinciding with Warren and Seifert (2011). Models run at the default β setting possessed significantly greater AUC_{Diff} values than robust models and were by this measure overly-complex, utilizing too many environmental features relative to the number of occurrences for a given species. None of the models exhibited maximum parsimony at $\beta = 1$ (Table 3). AUC_{Diff} values may be useful in revealing overfit models; however, information criteria should be the primary tool for identifying and adjusting for optimal model complexity, especially when modeling with few species' locations (Warren and Seifert 2011). Warren and Seifert (2011) found that slightly overly complex models were less problematic than under-parameterized models in most cases, however, models with appropriate complexity performed best. Complex models may produce conservative distributions, but overly complex models will likely only predict areas known to the modeling algorithm as present (or rather, areas adjacent to know presence locations) rather than identifying potential, fundamental niche space on revegetating landscapes (Peterson et al. 2011). It may be necessary to run and test models with large datasets at higher β values. With few occurrences and relatively few predictors (i.e., 16 – 46 and 10 respectively), increasing β greater than eight was not necessary for the species utilized here as lowest AIC_c values were observed at β values between two and seven (Table 3).

Summed logistic habitat suitability for the twenty-nine modeled fern species positively correlated with their occurrence in the twenty-two secondary forests plots surveyed throughout the main island of Puerto Rico. The success of these models to predict occurrence supports their use for identifying areas of conservation value. In contrast, total fern species richness observed in the survey plots did not correlate with summed logistic nor summed threshold habitat suitability maps. The disconnect between the ability to predict species occurrence versus the ability to predict community richness may be due to a number of factors including, but not limited to, the number of species modeled relative to the number of species that occur on the island (>400), the rarity of some of the modeled species, or geographic sampling bias (e.g., inability to access montane regions). Supporting the hypothesis that the rarity of some of the modeled species may have compromised the ability of summed (logistic or threshold) maps to predict community richness in the survey plots, a polyserial correlation revealed that, not surprisingly, common species dominated the secondary forests in which these plots occurred.

There are over 3098-km^2 of secondary forest throughout the main island of Puerto Rico, of which, over 96% is unprotected as of May 2011 [Gould et al. 2011(2)]. Approximately 214-km^2 of that unprotected forest lies along the Cordillera Central surrounding Monte Guilarte, Toro Negro, and Tres Picachos State Forests, in higher elevations surrounding Carite State Forest, and just west, south west of El Yunque National Forest where fern species richness is predicted to be greatest (Figure 5). These areas exhibited the greatest average habitat suitability scores of 0.5 or greater predicting fern community reassembly to be highest in these localities. These protected areas are likely source locations for population reintroductions in these montane, wet forests. Expanding protected boundaries to lower elevations could increase overall species richness for source locations in these revegetating forests and should be explored.

Secondary forest stand assessment further solidified that total species richness increases with reduced water stress. Species richness decreased as variation in canopy cover increased in secondary forest plots, primarily driven by terrestrial species. This is not surprising as many pteridophyte species cannot tolerate prolonged exposure to direct insolation and most tropical species rely on moist substrates. Species richness increased on northern facing slopes in secondary forest stands. Loriot et al. (2006) found a species of fern to be restricted to northern slopes in low light habitats in France, likely due to reduced water stress. Species richness decreased with average annual temperature and increased with elevation. These results are likely due to cooler temperatures subsequently alleviating evapotranspiration. The unexpected negative association between average annual rainfall and total species richness may indicate in addition to reduced water stress, ferns are likely dependent upon forest structure and canopy coverage. As secondary forests mature and canopies close, both moisture retention and habitable space for epiphytes increase.

All models performed relatively well; however, this study began with 36 species. *Plebodium aureum*, *Pityrogramma calomelanos*, *Pteris longifolia*, *Tectaria incisa*, *Thelypteris hildae*, *Thelypteris poiteana*, and *Thelypteris reticulata* performed poorly (i.e., average $AUC_{Test} \leq 0.5$ meaning no better than random) across all models regardless of the β setting and therefore, were removed from the study. This likely resulted from too few occurrence locations (18-21 records) for species that may have broad distributions and may be tolerant to extensive habitat types. For example *T. incisa* and *T. poiteana* were found in secondary forests throughout the entire main island in vastly differing habitats (Schmidt *personal observation*).

CONCLUSION

This study highlights the importance of understanding complexity while modeling in Maxent, especially when modeling with few species occurrences (one of the main reasons Maxent is utilized and advocated). Extensive areas of realistically suitable habitat for species would not be accounted for without adjusting β and testing for parsimony, potentially leading to erroneous management decisions for rare, threatened, or endemic species. This could lead to unprotected or unmonitored patches of secondary forest suitable for select species of interest. Furthermore, a shortcoming of AUC values is that even overfit, unrealistic models may exhibit high discrimination values which may mislead management decisions and therefore other parameters should be considered for assessing model discrimination such as the true skill statistic proposed by Allouche et al. (2006). This statistic is independent of prevalence and thus, is not subjected to the same limitations as AUC values; however, when interpreted with caution and tested for parsimony, AUC values for models with fewer species occurrences can be utilized in management practices. Not surprisingly, total fern species richness in secondary forest plots was primarily dependent by reduced water stress.

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Table 1. Puerto Rican fern species used for predictive model assessment along with the number of occurrences, physiognomy, elevational range, commonality, and field success rate.

Species	Number of Occurrences	Physiognomy	Elevational Range (m)	Commonality	Field Success Rate (%)
Adiantum latifolium (Lamarck)	23	terrestrial	0 - 500	C	77
Adiantum pyramidale (Linnaeus)	39	terrestrial	0 - 940	C	64
Arachniodes chaerophylloides (Poiret)	43	terrestrial	200 - 1070	C	50
Blechnum occidentale (Linnaeus)	31	terrestrial	20 - 950	C	68
Cyathea bryophila (R. Tryon)*	26	tree	750 - 1300	C	91
Cyathea horrida (Linnaeus)	23	tree	220 - 1000	C	64
Cyathea portoricensis (Sprengel ex Kuhn)*	24	tree	175 - 1240	C	73
Cyclopeltis semicordata (Swartz)	26	terrestrial; epipetric	10 - 250	C	86
Dennstaedtia bipinnata (Cavanilles)	19	terrestrial	65 - 900	C	59
Grammitis serrulata (Swartz)	19	terrestrial; epiphytic; epipetric	175 - 1300	C	77
Lastreopsis effusa (Swartz)	16	terrestrial	180 - 1300	C	82
Nephrolepis exaltata (Linnaeus)	16	terrestrial; epiphytic	300 - 1200	R	68
Nephrolepis rivularis (Vahl)	17	terrestrial; epiphytic	220 - 970	C	64

Odontosoria aculeata (Linnaeus)	23	terrestrial	0 - 950	R	41
Odontosoria scandens (Desvaux)	17	terrestrial	850 - 1300	C	82
Oleandra articulata (Swartz)	31	epiphytic; epipetric	200 - 1065	R	45
Olfersia cervina (Linnaeus)	20	terrestrial	200 - 1000	R	32
Pecluma pectinata (Linnaeus)	30	epiphytic; epipetric	175 - 860	C	41
Polypodium crassifolium (Linnaeus)	21	epiphytic; epipetric	300 - 1100	R	55
Polypodium dissimile (Linnaeus)	17	epiphytic	430 - 900	R	64
Polypodium heterophyllum (Linnaeus)	24	epiphytic	10 - 550	R	82
Polypodium loriceum (Linnaeus)	26	epiphytic	600 - 1300	C	59
Polypodium lycopodioides (Linnaeus)	36	epiphytic	0 - 1200	C	73
Polypodium piloselloides (Linnaeus)	31	epiphytic; epipetric	130 - 1100	C	59
Tectaria cicutaria (Linnaeus)†	17	terrestrial; epipetric	ca. 100	C	95
Tectaria heracleifolia (Willdenow)	46	terrestrial	10 - 450	C	82
Thelypteris guadalupensis (Wikström)†	19	terrestrial	10 - 350	C	91
Trichomanes crispum (Linnaeus)	16	epiphytic	200 - 900	R	59

Trichomanes scandens (Linnaeus)	20	epiphytic	500 - 1300	R	68

† indicate species restricted to limestone or calcareous substrate (geology predictor used in mapping distribution).

* indicate endemic species

Table 2. Detailed descriptions of environmental predictors in each category utilized during modeling along with the cell size of the original data set and source in which it was provided and created. Elevation was not used in modeling.

Category	Predictor	Cell (m^2)	Source
Climate	Average August (max) temperature	450	PRISM*
	Average February (min) temperature	450	PRISM*
	Average October (max) precipitation	450	PRISM*
	Average February (min) precipitation	450	PRISM*
Topography	Elevation	30	NOAA DEM†
	Slope	30	NOAA DEM†
	Northness [aspect in radians(cosine)]	30	NOAA DEM†
	Eastness [aspect in radians(sine)]	30	NOAA DEM†
Vegetation Indices	Tasseled Cap - Greenness	30	Landsat Mosaic•
	Tasseled Cap - Wetness	30	Landsat Mosaic•
	Tasseled Cap - Brightness	30	Landsat Mosaic•
Geology+	Geologic substrate	NA	USGS°

*Parameter-elevation Regressions on Independent Slopes Model (see Daly et al. 2003).

†National Oceanic and Atmospheric Administration Digital Elevation Models (see Taylor et al. 2008).

•Mosaicked Landsat satellite imagery (see Helmer and Ruefenacht 2005).

°United States Geologic Survey (see Bawiec 1999).

+Only used for select species (see Table 1).

Table 3. Average Test and Train AUC values for each species at default (D) and robust (R) settings along with the regulation multiplier (β) setting for parsimony.

Species	Avg Train AUC (D)	Avg Test AUC (D)	Avg Train AUC (R)	Avg Test AUC (R)	Beta Value (R)
A. latifolium	0.892	0.705	0.716	0.693	5
A. pyramidale	0.839	0.691	0.716	0.643	7
A. chaerophylloides	0.867	0.748	0.805	0.755	5
B. occidentale	0.896	0.749	0.782	0.733	6
C. bryophila	0.980	0.953	0.965	0.958	5
C. horrida	0.924	0.786	0.873	0.799	4
C. portoricensis	0.919	0.816	0.874	0.824	6
C. semicordata	0.906	0.758	0.826	0.786	4
D. bipinnata	0.906	0.745	0.851	0.836	5
G. serrulata	0.977	0.917	0.966	0.953	5
L. effusa	0.857	0.657	0.821	0.727	2
N. exaltata	0.892	0.802	0.874	0.791	4
N. rivularis	0.880	0.836	0.878	0.806	2
O. aculeata	0.899	0.745	0.758	0.674	5
O. scandens	0.972	0.911	0.968	0.938	4
O. articulata	0.964	0.916	0.957	0.927	5
O. cervina	0.936	0.818	0.866	0.833	5
P. pectinata	0.863	0.678	0.790	0.783	5
P. crassifolium	0.896	0.677	0.781	0.737	4

P. dissimile	0.917	0.785	0.880	0.787	2
P. heterophylla	0.899	0.739	0.762	0.751	5
P. loriceum	0.956	0.898	0.935	0.924	5
P. lycopodioides	0.835	0.695	0.777	0.751	4
P. piloselloides	0.886	0.764	0.826	0.808	5
T. cicutaria	0.977	0.961	0.958	0.951	4
T. heracleifolia	0.844	0.624	0.748	0.617	3
T. guadalupensis	0.906	0.648	0.760	0.647	5
T. crispum	0.929	0.880	0.917	0.851	3
T. scandens	0.971	0.916	0.943	0.921	4

Table 4. Summary of twenty-two secondary forests plots sampled July 26th 2012 – August 25th 2012 including all species average habitat suitability (HS), predicted species present, species observed, physiognomy of species observed, and forest age.

Site	Species HS (average)	Species HS (Sum)	Species Predicted Present (Threshold)	Modeled Species Present	Total Species Present	Total Terrestrial	Total Epiphytic	Forest Age (years)
1	0.43	13.5	13	9	15	8	7	36 - 62
2	0.39	12.2	8	5	15	11	4	36 - 62
3	0.35	11.0	2	4	16	12	4	23 - 35
4	0.41	12.8	15	6	14	9	5	14 - 22
5	0.53	16.3	22	10	16	7	9	36 - 62
6	0.43	13.4	11	9	21	11	10	36 - 62
7	0.60	18.3	24	9	27	24	3	23 - 35
8	0.37	11.7	5	7	19	17	2	23 - 35
9	0.51	15.7	18	9	14	7	7	14 - 22
10	0.34	11.0	2	7	21	14	7	14 - 22
11	0.48	14.8	21	9	22	21	1	23 - 35
12	0.45	14.0	16	10	22	15	7	23 - 35
13	0.46	14.5	19	8	18	15	3	23 - 35

14	0.45	14.0	17	10	24	13	11	23 - 35
15	0.51	15.7	21	11	21	17	4	23 - 35
16	0.52	16.0	21	9	19	14	5	23 - 35
17	0.34	10.9	6	7	21	13	8	23 - 35
18	0.33	10.5	5	9	24	13	11	36 - 62
19	0.42	13.1	13	8	14	10	4	23 - 35
20	0.41	12.8	11	6	22	13	9	23 - 35
21	0.39	12.3	10	9	19	13	6	23 - 35
22	0.49	15.1	14	8	18	8	10	23 - 35

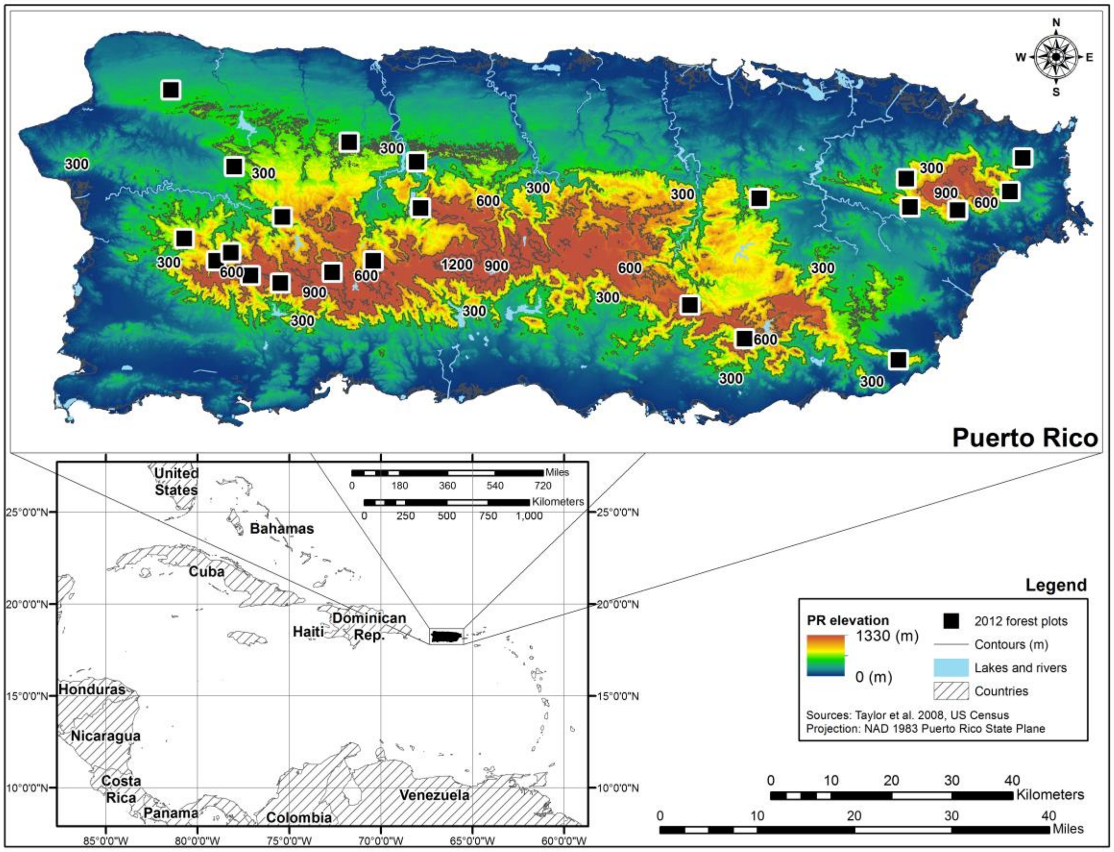
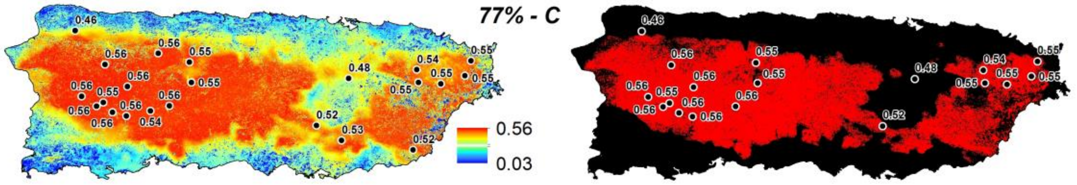
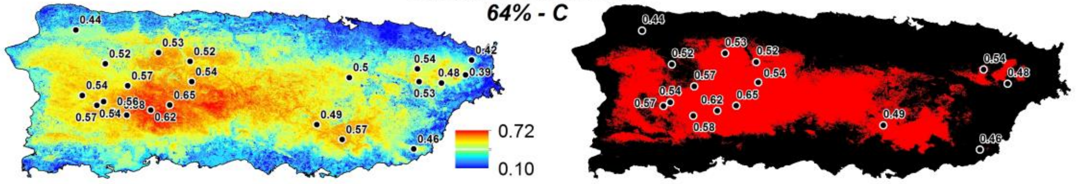


Figure 1. Study area: topography of the main island of Puerto Rico along with its location in the Caribbean, surrounding geographies, and secondary forest plots sampled in summer 2012.

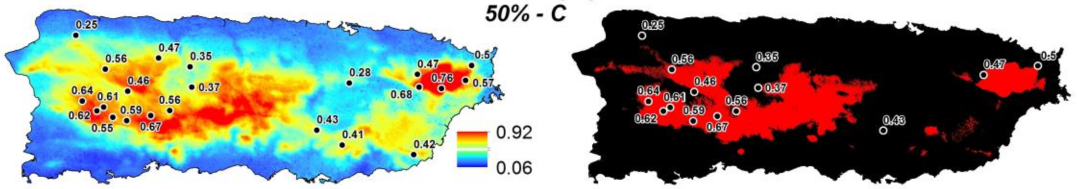
Adiantum latifolium
77% - C



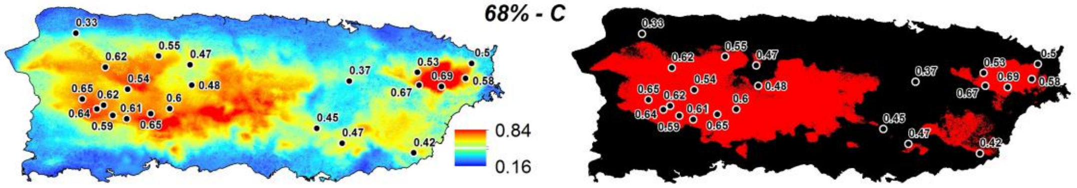
Adiantum pyramidale
64% - C



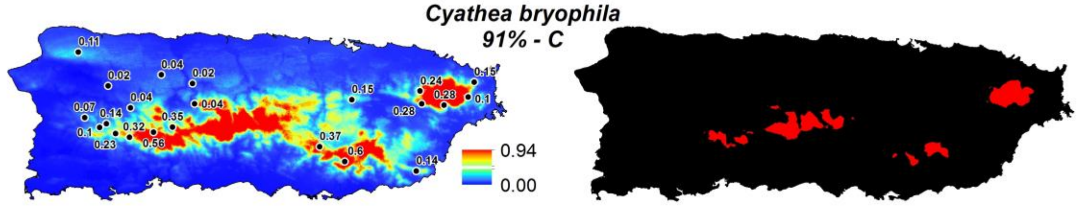
Adiantum chaerophylloides
50% - C



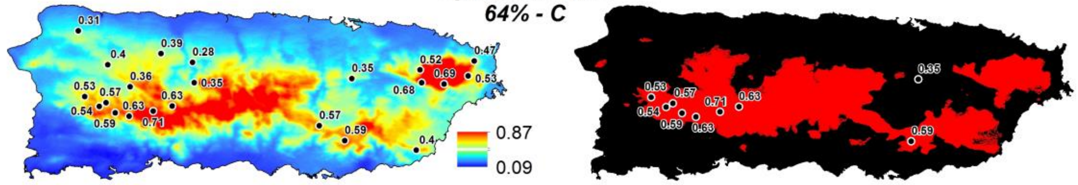
Blechnum occidentale
68% - C



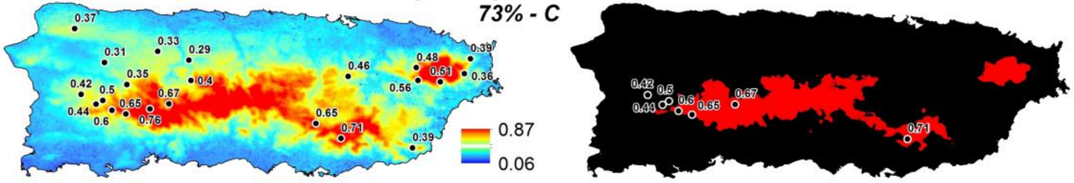
Cyathea bryophila
91% - C



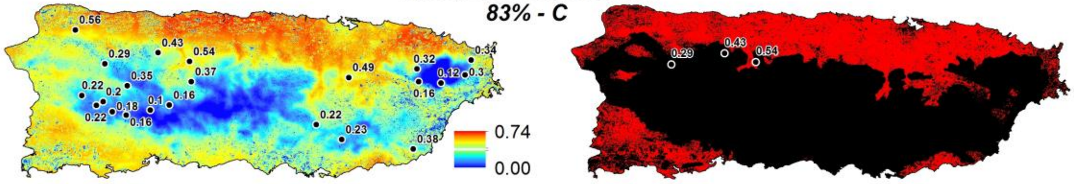
Cyathea horrida
64% - C



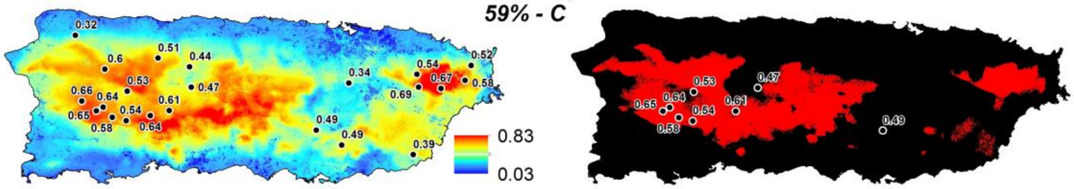
Cyathea portoricensis
73% - C



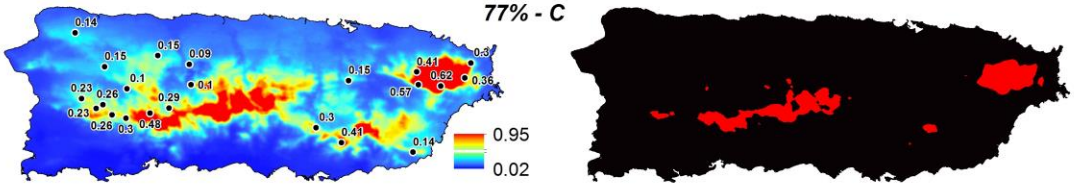
Cyclopeltis semicordata
83% - C



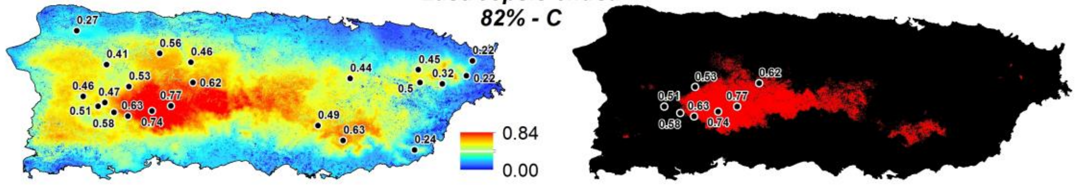
Dennstaedtia bipinnata
59% - C



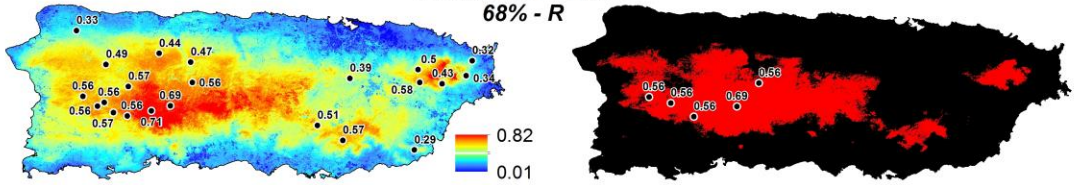
Grammitis serrulata
77% - C



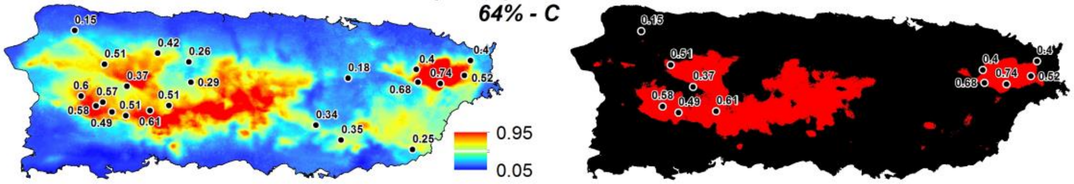
Lastreopsis effusa
82% - C



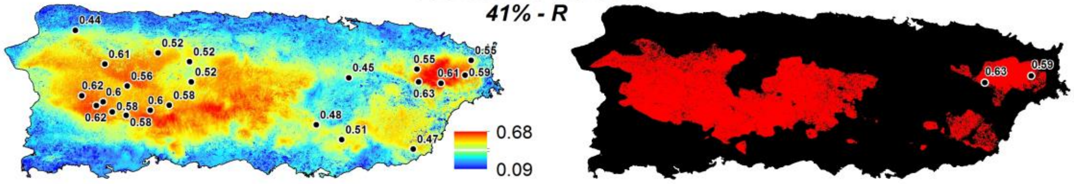
Nephrolepis exaltata
68% - R



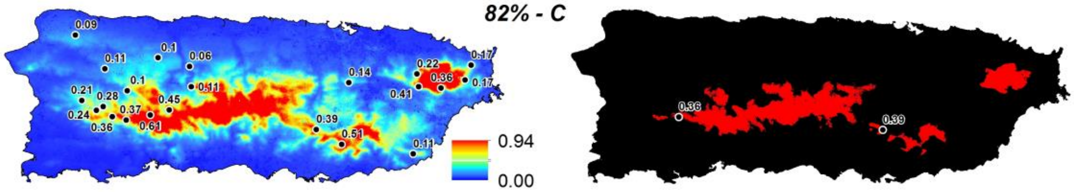
Nephrolepis rivularis
64% - C



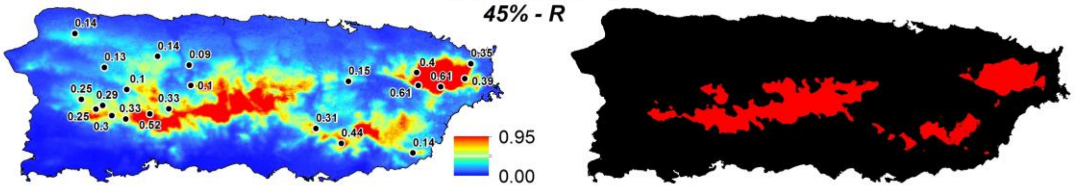
Odontosoria aculeata
41% - R



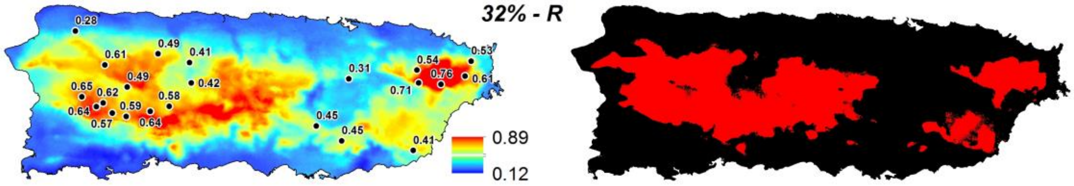
Odontosoria scandens
82% - C



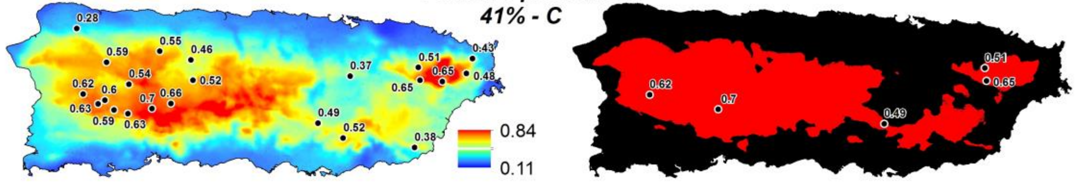
Oleandra articulata
45% - R

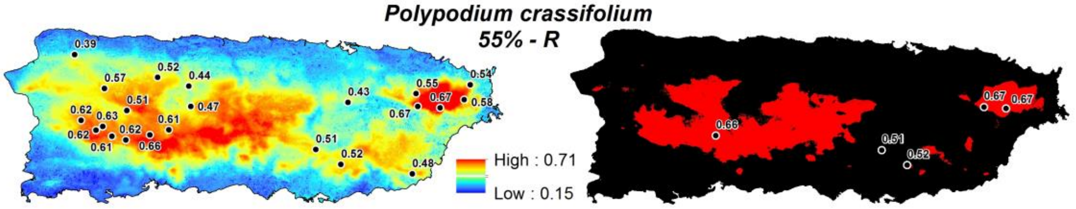


Olfersia cervina
32% - R

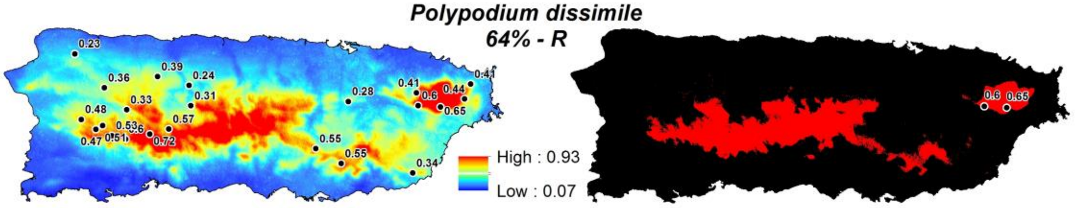


Pecluma pectinata
41% - C

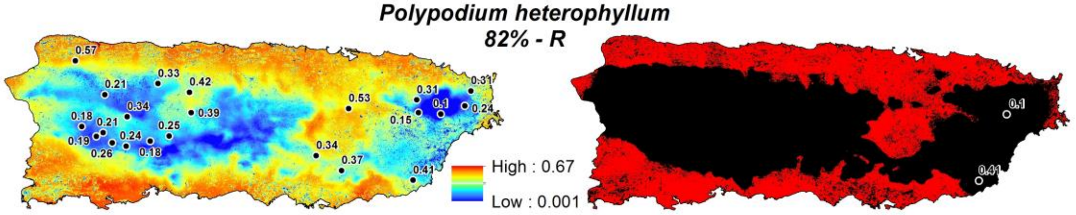




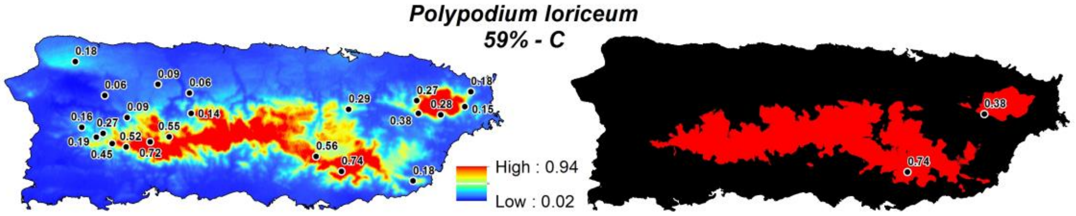
Polypodium crassifolium
55% - R



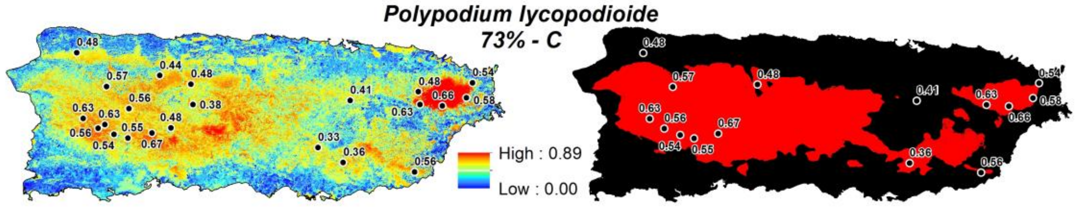
Polypodium dissimile
64% - R



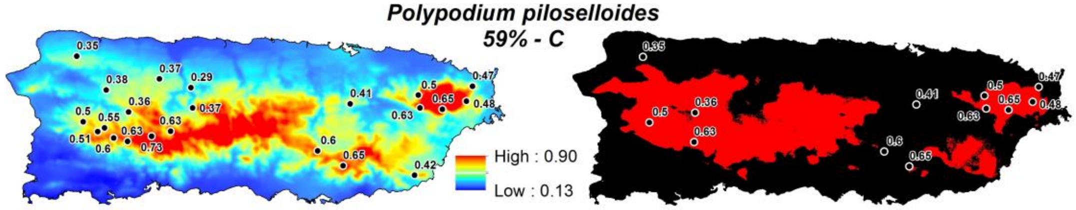
Polypodium heterophyllum
82% - R



Polypodium loriceum
59% - C



Polypodium lycopodioide
73% - C



Polypodium piloselloides
59% - C

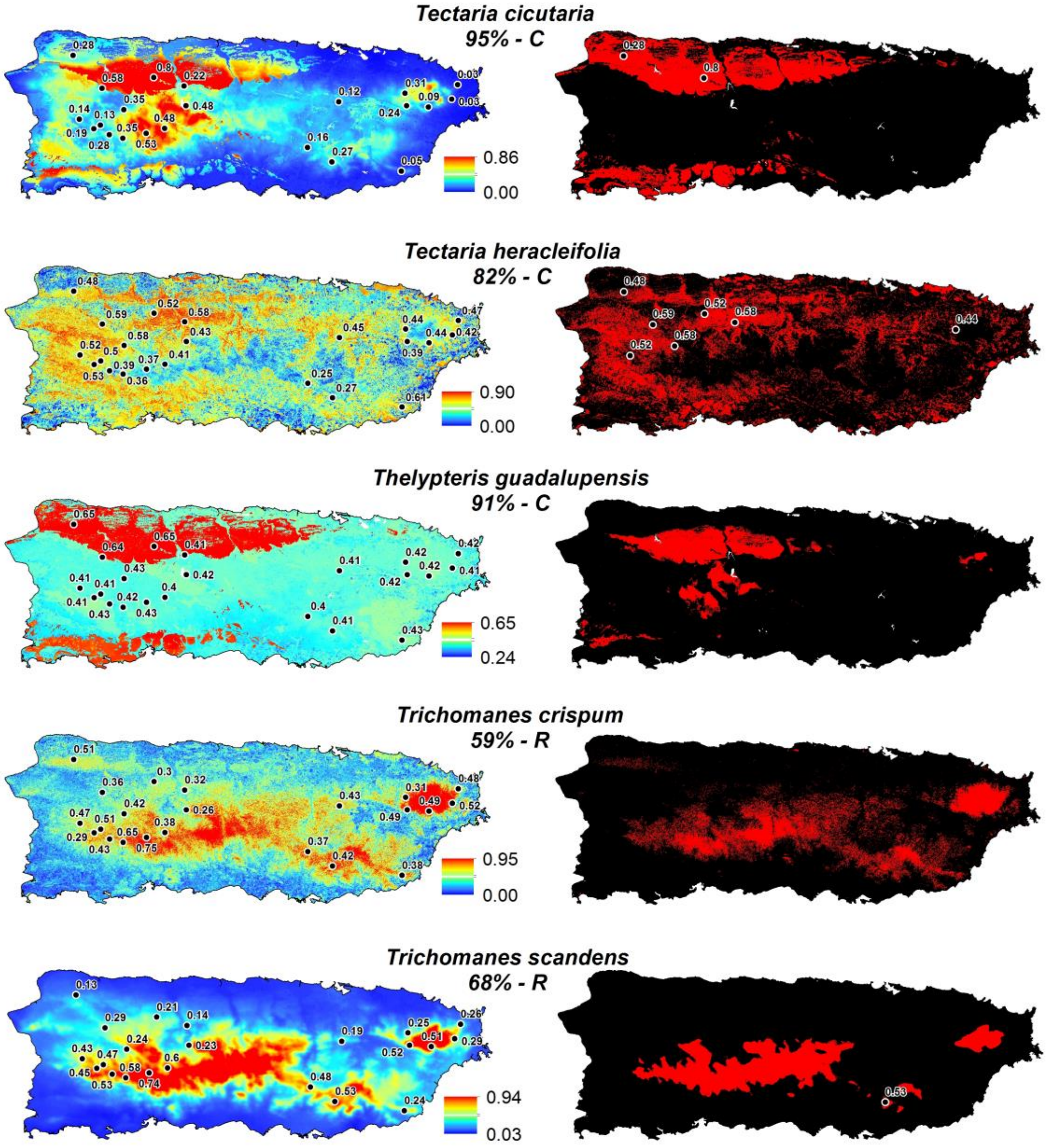


Figure 2. Individual species’ average habitat suitability (HS; left) and threshold (T; right) map from 30 replicated runs at robust settings. Success rate (present or absent) is indicated below species’ names along with a rarity factor (C = common and R = rare). HS scores for each species at all secondary forest plots are displayed on HS maps. Points on T maps indicate where each species was documented in plots.

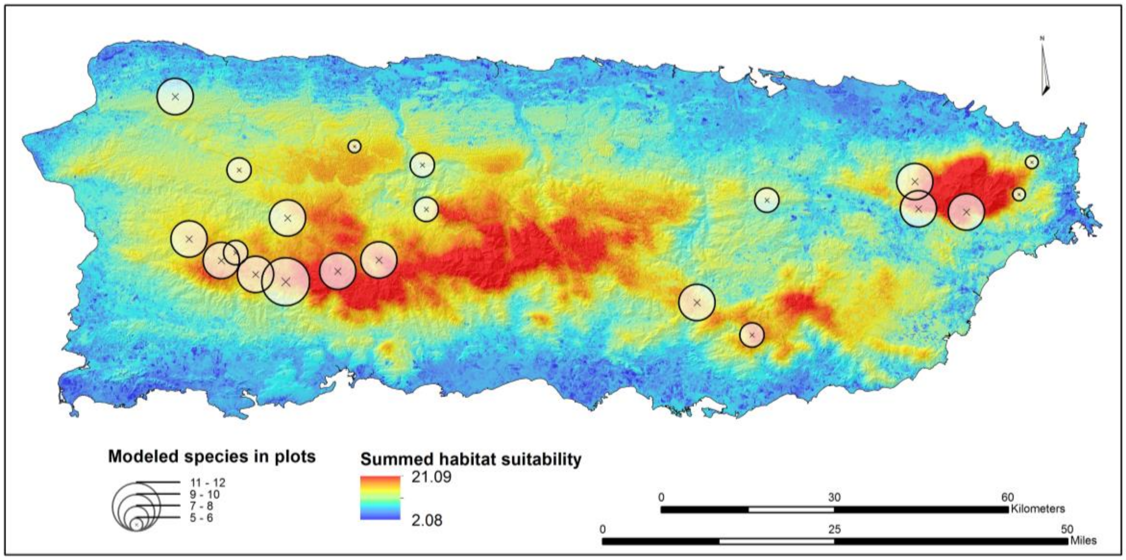


Figure 3. Summed logistic habitat suitability map for all modeled species along with secondary forest plots depicting number of modeled species observed.

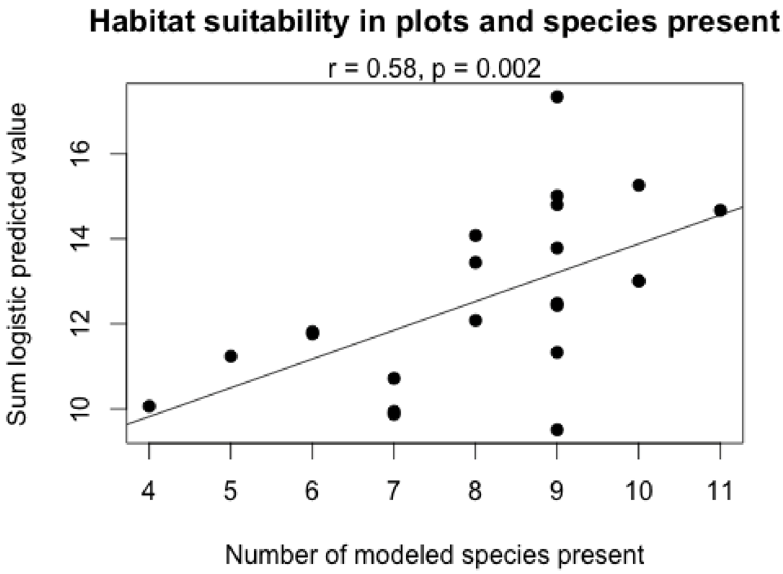


Figure 4. Correlation between logistic habitat suitability and modeled species documented in secondary forest plots.

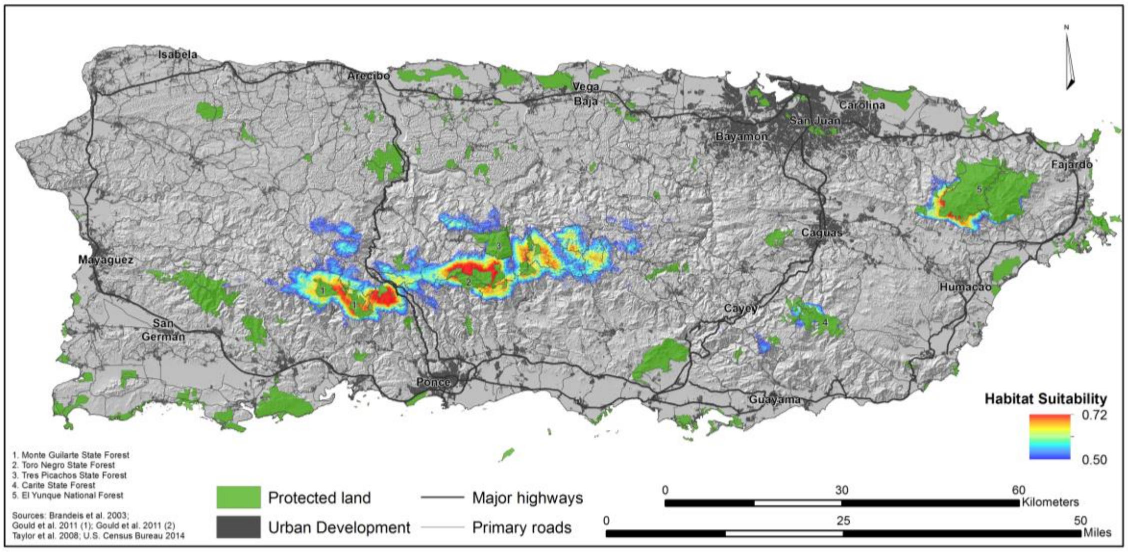


Figure 5. Study area depicting protected land as of May 2011, urban development, and areas with highest predicted fern community reassembly along the Cordillera Central and surrounding Carite State and El Yunque National Forests.