Climatic Change
https://doi.org/10.1007/s10584-019-02491-w

Climate change increases potential plant species richness on Puerto Rican uplands

Azad Henareh Khalyani[1] · **William A. Gould**[2] · **Michael J. Falkowski**[1] · **Robert Muscarella**[3] · **María Uriarte**[4] · **Foad Yousef**[5]

Received: 5 February 2018 / Accepted: 4 July 2019/

Abstract

Modeling climate change effects on species and communities is critical especially in isolated islands. We analyzed the potential effects of climate change on 200 plant species in Puerto Rico under two emission scenarios and in four periods over the twenty-first century. Our approach was based on ensemble bioclimatic modeling using eight modeling algorithms and community richness analysis. Our findings showed that the probabilities of environmental suitability decline for wet climate species and increase for drier and warm climate species in the future periods under both emission scenarios, with stronger effects under the higher emission scenario. Expansion of dry climate species to higher elevations appears to be a prominent response of species to climatic change in the island based on changes in environmental suitability but the actual species redistribution will be influenced by their life histories, potential adaptation, dispersal abilities, species introductions, and species interactions. This potential movement leads to a spatial pattern of species richness at site level that shows a positive relationship with elevation, which becomes stronger in the later periods of the century. The spatial pattern of species richness, if combined with single species projections, can provide critical information for conservation management in the island. Conservation management can support island-wide biological diversity by protecting the wet climate species on the uplands.

1 Introduction

Human effects on biodiversity through global climate change raise the need to project the threats to species and communities using modeling approaches (Nogués-Bravo and Rahbek 2011; Pecl et al. 2017). Climate-driven species redistributions have widespread consequences for economic development, food security, human health, livelihoods and culture, and

---

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10584-019-02491-w) contains supplementary material, which is available to authorized users.

✉ Azad Henareh Khalyani
ahenareh@mtu.edu

Extended author information available on the last page of the article

additional positive feedbacks on the climate itself (Pecl et al. 2017 and references within). Studying the underlying driving forces of species occurrence and community formation are at the core of modeling efforts to project the effects of global climate change. Species communities are formed by abiotic environmental conditions, biotic interactions, movement and dispersal abilities, natural and anthropogenic disturbances, and other random processes related to extinction, ecological drift, and environmental stochasticity (Soberón 2007; Peterson 2011; Chase and Myers 2011). Climate was classically assumed to have a stronger effect at the regional to continental scales and species interactions assumed to drive local community patterns. However, increasing evidence from recent studies show the importance of microclimatic variability on local distribution of species and community assembly, whereas other studies have demonstrated the importance of species interactions on species and communities at larger extents and coarser grains (D’Amen et al. 2017 and references within).

Species respond to changes in environmental conditions, notably climate change, in multiple ways. These include acclimating or adapting to new conditions, going locally extinct, or migrating/dispersing to newly favorable areas which is demonstrated by redistribution to higher latitudes, higher altitudes, and deeper in water in case of aquatic species (Moritz et al. 2008; Berg et al. 2010; Gilman et al. 2010; Harsch et al. 2017). Species redistribution is a mechanism of searching for resource availability in the new conditions imposed by climate change. For example, moisture availability was recently reported as an important driving force for westward shifts of tree species in the United States (Fei et al. 2017). In small tropical islands, species are restricted in redistributing across latitudes and longitudes and their dispersal in response to climate change is limited to higher elevations. Species responses are of great importance in tropical forests which harbor the majority of Earth’s species and are exposed to rapid rates of climate change relative to current variability (Feeley and Silman 2010a; Feeley et al. 2012).

Community richness is the number of co-occurring species in a community. It is the simplest measure of biodiversity most commonly estimated in species assemblage modeling (Guisan and Rahbek 2011). It has often been considered an indicator of conservation value (D’Amen et al. 2017) and used as a biodiversity measure for identifying priority areas for natural protection and reserve design (e.g., Young et al. 2009; D’Amen et al. 2011; Mateo et al. 2013). It has been estimated mainly by two distinct methods. Macroecological approaches focus directly on the realized characteristics of species assemblages based on theoretical expectations instead of estimating it them from the individual constituent species (Gotelli et al. 2009). Another more recent approach is the so-called stacked species distribution models (S-SDM) which aggregate the community-level properties from the properties of all individual species within the community and it is thus a ‘predict first, assemblage later’ approach resulting in a measure of community composition (Dubuis et al. 2011; Pottier et al. 2013; D'Amen et al. 2015). We used a S-SDM approach in this study based on the available species-level occurrence records across ranges of environmental conditions.

In this study, we modeled the potential effects of climate change as in Henareh Khalyani et al. (2016) on plant species of Puerto Rico. In the first step, we estimated the relative importance of potential driving forces of species occurrence by partitioning the variance in species occurrence and predictor variables. Then, we applied bioclimatic models to map the environmental suitability for each species in the contemporary and future periods, and finally, we calculated a measure of community richness and projected its future spatiotemporal changes under climate change. Species and community-level projections help in understanding potential changes in habitat suitability due to the projected climate change.

2 Methods

2.1 Study area

The island of Puerto Rico occupies 8,937 km^2 and is located at (178450–188300) N, (658450–678150) W in the Caribbean region (Fig. 1a). It includes the islands of Vieques and Culebra and several non-inhabited islands. It is a mountainous island with elevation ranges from the sea level to 1338 m above the sea level in the central mountains, which drives diversity in climatic conditions across the island. Around 55% of the island is covered with forests now (USDA 2017). The downscaled projections of the global climate models in the island showed higher warming levels and precipitation declines than the global averages (Fig. 1b; Henareh Khalyani et al. 2016).

2.2 Species occurrence records

The plant species occurrence records were compiled from a range of georeferenced sources including herbaria collections and plot-based studies. Specifically, we combined occurrences of Puerto Rican plants from the online database GBIF (www.gbif.org), four herbaria (UPRRP, MAPR, NY, and US), and georeferenced observations from other plot-based studies (e.g., Muscarella et al. 2016). The full dataset contains 11871 unique records, with 30–340 (mean = 57) observations for

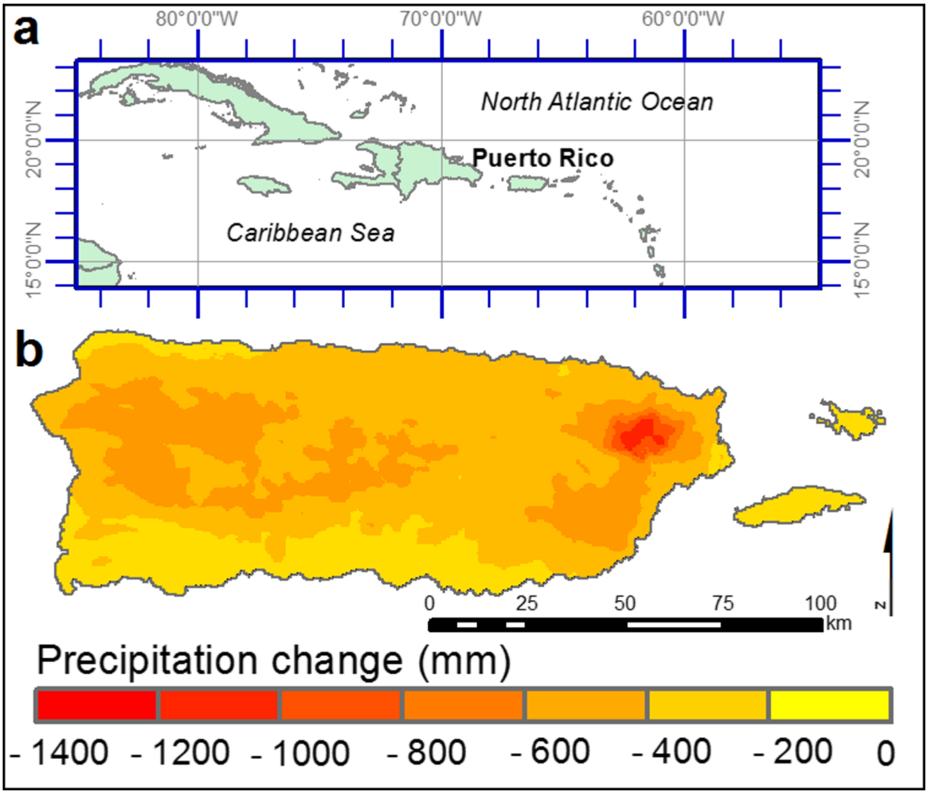


Fig. 1 **a** Location of Puerto Rico in the Caribbean region and **b** precipitation decline between the 1960–1990 and the 2071–2099 periods under the high emission scenario (Henareh Khalyani et al. 2016)

each focal species. We processed the occurrence data by first manually standardizing names based on Acevedo-Rodrıguez and Strong (2011) and then excluding observations with obvious georeferencing errors (i.e., occurrence points for trees that fell in the ocean or outside of Puerto Rico). To avoid redundant records that emerge when e.g., herbaria have duplicate specimens, we excluded duplicate records of the same species with identical geographic coordinates. We included all species forming the novel plant assemblages in the island listed in Brandeis et al. (2009) and other plant species based on occurrence record availability, a total of 200 species (Appendix I in the ESM).

2.3 Predictor variables

We used 15 predictor variables in the bioclimatic models of the plant species (Table 1). The climatic variables were 30-year average datasets at ~ 450-m resolution including mean annual precipitation (map), mean annual temperature (mat), mean maximum annual temperature (tmax), mean minimum annual temperature (tmin), and potential evapotranspiration ratio (pet). The model calibration time interval was 1960–1990 for 57 species and 1991–2010 for the remaining 143 species for which no occurrence records were available in the 1960–1990 period. We used the gridded PRISM climatic data for the 1960–1990 period (Daly et al. 2003), and the average projections of 12 models from phase 3 of the Coupled Model Intercomparison Project (CMIP3) for the four future periods under high (A2) and low (B1) emission scenarios (Henareh Khalyani et al. 2016). The terrain variables including slope, Terrain Ruggedness Index (TRI), Topographic Position Index (TPI), roughness, and aspect were calculated according to Wilson et al. (2007) using the elevation dataset from the Shuttle Radar Topographic Mission (Farr et al. 2007) and ‘terrain’ function in the *raster* package (Hijmans and van Etten 2014) in R (R Development Core Team 2017). Area Solar Radiation (arsol) was calculated using elevation data in ArcGIS ArcMap 10.3 software package (ESRI 2014). We obtained soil property variables from the Gridded Soil Survey Geographic (gSSURGO) database at 10 m resolution (USDA 2014) and used available water storage (aws) and soil organic carbon (soc) at 0–150-cm depth, which had the highest importance among the edaphic variables shown by the percent deviance in the models. Geological units were from the U. S. Geological Survey mineral resource assessment for the Commonwealth of Puerto Rico (Bawiec 1998). We resampled the edaphic, topographic, and geologic variables to climatic variables to do the modeling procedure at the resolution of the climatic variables (~ 450 m).

Table 1 Predictor variables used in all bioclimatic models

Variable	Abbr.
Mean annual precipitation	map
Maximum annual temperature	tmax
Minimum annual temperature	tmin
Mean annual temperature	mat
Potential evapotranspiration ratio	pet
Elevation	dem
Slope	slope
Transposed aspect	trasp
Topographic position index	tpi
Terrain ruggedness index	tri
Roughness	roughness
Area solar radiation	arsol
Soil organic carbon (0–150 cm)	soc
Soil available water storage (0–150 cm)	aws
Geological units	geo

2.4 Pre-modeling analysis

To get an estimate of the main driving forces shaping the distributions of species and communities, we partitioned the variance in the species occurrence data and the environmental predictor variables and estimated the proportion of variance from the environmental variables, species interactions, and random effects, i.e., the unexplained variation not predicted by environmental variables or species interactions. We used the species occurrence records with the predictor variables in a probit model applied in the Hierarchical Modelling of Species Communities (*hmsc*) R package (Ovaskainen et al. 2017) to partition the total variance in the environmental variables and occurrence records of 57 of the species with occurrence data availability in the training time period (1960–1990). The biotic interactions were estimated by pairwise species correlations as the measure of statistical co-occurrence among species (Ovaskainen et al. 2017). We also applied a Principal Component Analysis (PCA) on the environmental covariates to further partition the environmental variance between climatic, topographic, edaphic, and geologic variables. A common issue when modeling the climate change effects on the suitable areas for species is knowing the extent to which the future climatic conditions are beyond the ranges of the contemporary climatic variables used for model calibrations. A way to quantify this is creating the multivariate environmental similarity surfaces (MESS, Elith et al. 2010). We applied the MESS procedure in *ecospat* R package (Di Cola et al. 2017) and plotted the results for the two scenarios and the four periods.

2.5 Bioclimatic modeling

To help account for the fact that model projections generally vary with modeling methods, we used an ensemble approach of eight algorithms using *BIOMOD* and the *biomod2* R packages (Thuiller 2003; Thuiller et al. 2016). The applied models were Generalized Linear Model (GLM), Surface Range Envelop (SRE), Flexible Discriminant Analysis (FDA), Classification Tree Algorithms (CTA), Artificial Neural Networks (ANN), Multivariate Adaptive Regression Splines (MARS), Generalized Boosted Regression Models (GBM), and Random Forest (RF). The predictive performances of models were evaluated by randomly splitting the data into calibration (or training, 70%) and evaluation (or testing, 30%) subsets. We repeated the data splitting procedure four times for each modeling algorithm. We used randomly generated 10,000 pseudo-absences with the entire island as the study extent and repeated the procedure three times for each model. This procedure resulted in 96 models runs for each species (8 methods × 4 data splitting repetitions × 3 pseudo-absence construction repetitions). Then a weighted ensemble forecasting approach was used in *BIOMOD* to consolidate all 96 predictions for each species to a single prediction weighted by their predictive performances based on the True Skill Statistic (TSS). We repeated these steps for each species for four future time intervals and two high (A2) and low (B1) climate change scenarios substituting the climatic predictor variables with the climatic model projections under each emission scenario.

2.6 Model evaluation

The lack of true absences in presence-background models hinders the use of common presence-absence evaluation indices, which evaluate models' ability to discriminate between occupied and unoccupied cells. Model evaluation must access only presences in this case. We assessed the final model performances based on the Boyce index as in Hirzel et al. (2006)

calculated in *ecospat* package. Boyce index is a threshold-independent evaluator which is considered the most appropriate metric for model performance evaluation in case of presence-only occurrence data. It calculates ratios of the numbers of predicted evaluation points to what is expected from a random distribution for a range of continuous habitat suitability values and measures the correlation between the ratio and the habitat suitability. The index values are Spearman Rank Correlation Coefficient between the continuous ranges of suitability and the predicted/expected ratio, with values closer to 1 indicating a good model (Hirzel et al. 2006). It measures how much model predictions differ from the distribution of the observed presences (Boyce et al. 2002; Hirzel et al. 2006).

2.7 Species richness

We calculated community richness by applying the Spatially Explicit Species Assemblage Modeling (SESAM) framework (Guisan and Rahbek 2011) in *ecospat* package. The procedure summed the probabilities of habitat suitability for individual species as obtained from the bioclimatic models. Then, it ranked the species at each site in decreasing order of probabilities and retained the most probable species down the list until the sum of the probabilities of the retained species at each site reached the total probability summed at each site in the previous step (D'Amen et al. 2015). We did not use a constraint on the number of species because related macroecological studies were not available and recent studies show that species richness in many communities can be unsaturated (e.g., Mateo et al. 2017). There is no theoretical support for the belief that species interactions set an upper limit to the number of species that can coexist in a community at any scale (e.g., Loreau 2000). The SESAM procedure retained all species with a predicted probability at each site. We then summed the retained species at each site as a measure of site-level richness.

3 Results

3.1 Underlying factors and model extrapolations

Variance partitioning showed that 68% of the total variance in the predictor variables was from the environmental covariates (Fig. 2a). The further analysis of variability within the environmental predictor variables using PCA showed that the first two axes with highest loadings from climatic variables and elevation formed 55.82% of variance in the environmental covariates. Geological units had high loading on the third axis, which formed 14.70% of the variance. The remaining 29.48% of the variance in environmental variables was related to topographic and edaphic variables (Fig. 2b). The 19% random was the total variance that was accounted for as ‘hidden factors’ in the model and could be from any other unknown or unmeasured covariates and also from purely stochastic processes which were not included as predictors in our models. Biotic interactions as measured from the species by species correlations formed 13% of the total variance (Fig. 2a). The MESS plots showed that the areas with future climatic variables unpresented in the calibration period increase under both high and low emission scenarios with stronger increases under the high emission scenario. The number of climatic variables which changed beyond the contemporary ranges also increases through time (Fig. 3).

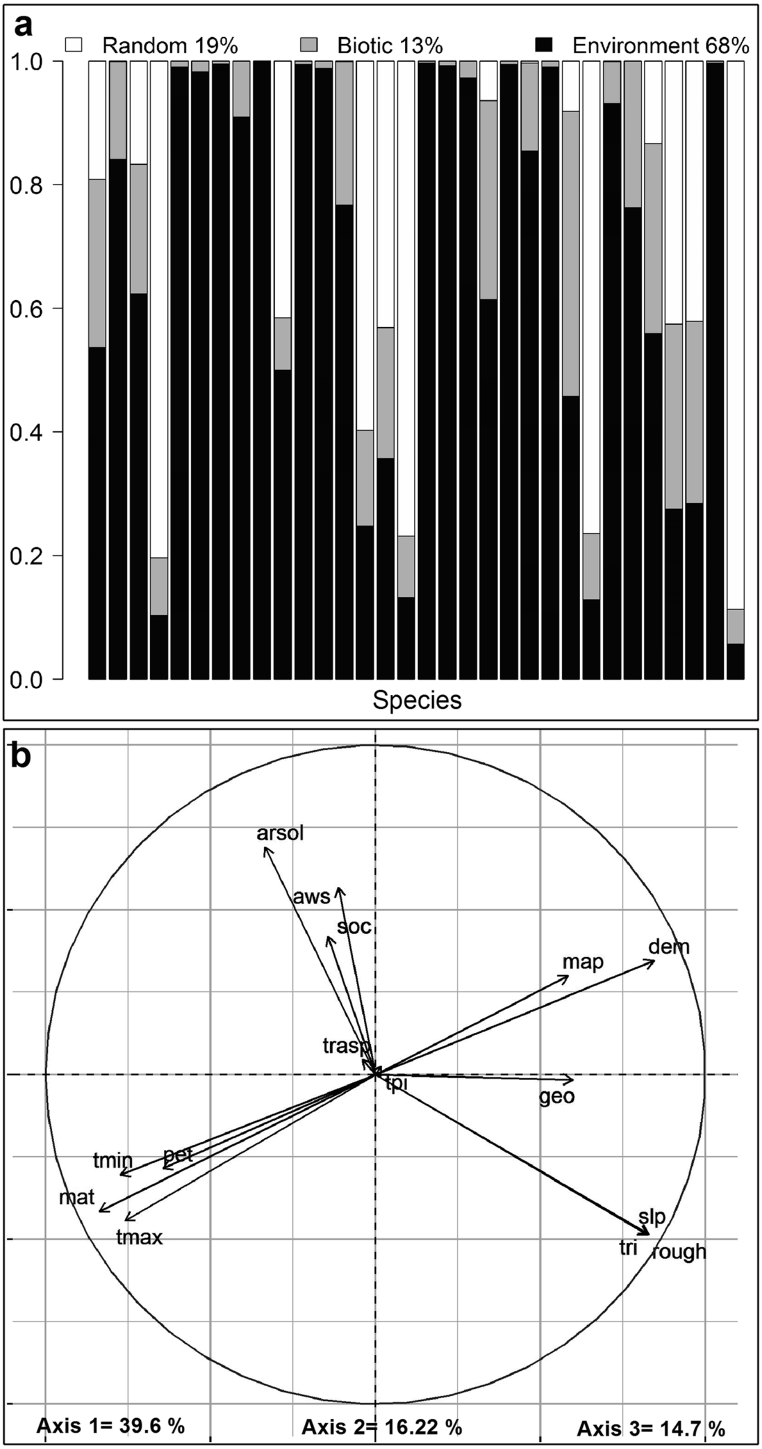


Fig. 2 **a** Partitioning the total variance in the environmental predictor variables and the occurrence records of 57 species in the 1960–1990 period and **b** further partitioning the variance only in the predictor variables using PCA

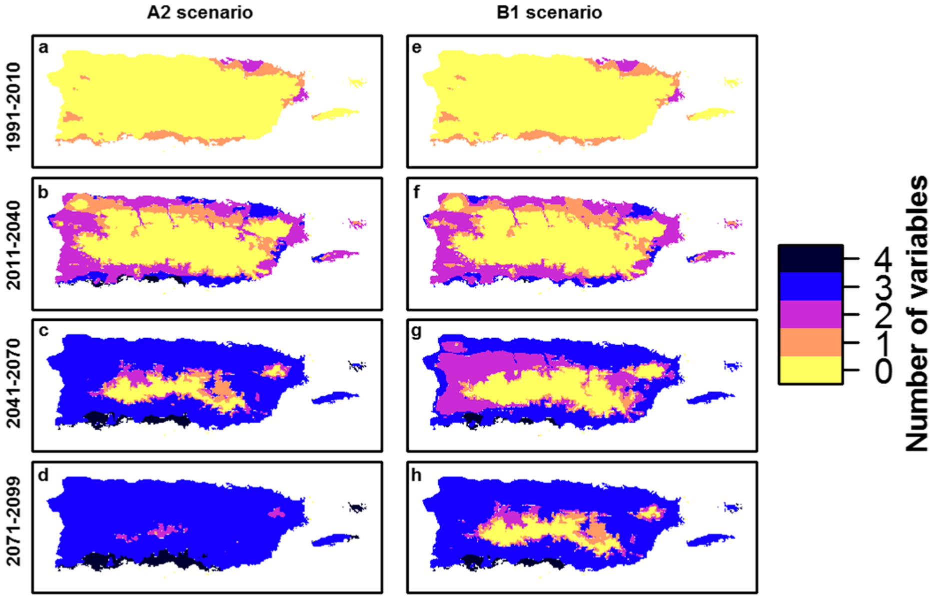


Fig. 3 Multivariate environmental similarity surfaces (MESS) of the predictor variables in the four future periods under **a**–**d** high and **e**–**h** low emission scenarios. Colors at each pixel indicate the number of variables with values outside of their calibration range

3.2 Species changes

Calculating mean changes in environmental suitability at the island scale from the 1991–2010 period to the end-of-century period (2071–2099) showed that all 200 species show either increasing or decreasing pattern of change in this century with stronger effect under the higher emission scenario (Fig. 4). Environmental suitability generally decreased for humid and wet zone species and increased for dry zone species in the future periods. We included the projected probabilities of environmental suitability for sweet acacia (*Acacia farnesiana)* which was identified as the indicator species of one of the tree assemblages by Brandeis et al. (2009), as an example of dry area species (Appendix II in the ESM). We also include the projections for *Casearia sylvestris* which was the indicator species of a wet area community (Brandeis et al. 2009; Appendix II in the ESM). Model performance evaluation results showed that the final model of most species obtained a high model performance shown by a positive Boyce index value above 0.9 (Appendix I in the ESM).

3.3 Community changes

Species within each tree assemblage in Brandeis et al. (2009) showed the same direction of change depending on their current climates. Specifically, potential future distributions areas were decreased for wet zone species and increased for dry zone species. However, some species within the same assemblage showed changes in opposite directions. For example, while *C. sylvestris*, as the indicator species of a wet forest community (importance value = 20.5, Brandeis et al. 2009), showed gradual decrease of potential distribution from the first to the end-of-century period (Appendix II in the ESM)*, H. courbaril* (a less important species in

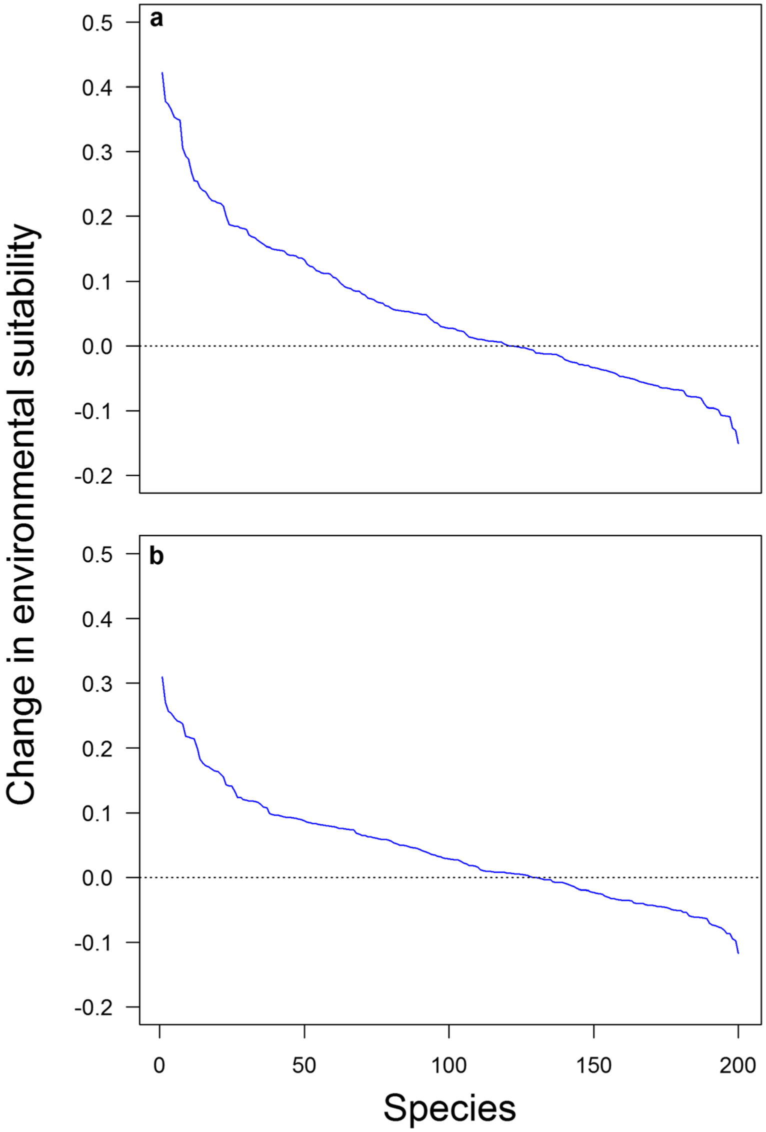


Fig. 4 Changes in the probability of environmental suitability for all 200 species from the 1991–2010 period to the 2071–2099 period under **a** high and **b** low emission scenarios. Species are ordered from increases to decreases in the projected environmental suitability

the same community, importance value = 3.6, Brandeis et al. 2009), showed a gradual increase in the future periods. The occurrence records of *H. courbaril* were on lower ranges of mean annual precipitation and higher ranges of mean annual temperature compared with *C. sylvestris* (Appendix II in the ESM). The site (cell)-level species richness was projected to increase and its spatial distribution was projected to change strongly as upland areas appear to harbor a larger number of species. Changes in the environmental suitability and consequently the number of species from the first time period to the last period under both climate change scenarios illustrates the projected increases in the number of species on the upland areas with highest effects on the two main upland areas, namely Luquillo mountains in the northeast and the interior mountain region (Central mountains or *la Cordillera Central*) which slices the island down the middle expanding west to east (Fig. 5). Plotting the number of species against elevation for future periods showed that the relationship became stronger in future periods under both emission scenarios. The relationship of the number of species and elevation were compared between different time intervals by fitting standard generalized linear models (GLM). Relationships became stronger both statistically (R^2) and visually under both climate change scenarios showing a higher number of species on higher elevations in the later periods of the century (Fig. 6).

4 Discussion

Puerto Rican forest communities have undergone a long history of disturbances and recovery. The island was mostly forested in the sixteenth century but it was largely cleared for agriculture from 1930 to 1950 (e.g., del Mar López et al. 2001). Since then, rapid losses of agricultural lands and increase in forest recovery due to the shift of the economy to industry and services were reported (e.g., del Mar López et al. 2001; Brandeis et al. 2009). Environmental factors specifically the climatic variables had an overarching effect on variation in species composition of plant communities in the secondary tropical forests emerged through reforestation (Brandeis et al. 2009). Given this important role of climatic variables, it is critical for management to project the potential emergent future effects of climate change on the current forest communities. Our future projections showed that the probabilities of environmental suitability generally increased for hot and dry climate communities and decreased for cold and wet climate communities. Wet climate species mainly occur in the central mountains and Luquillo Mountains. They are the main plant species in the subtropical rain forest life zone in El Yunque National Forest, which is the only rain forest in the island (Henareh Khalyani

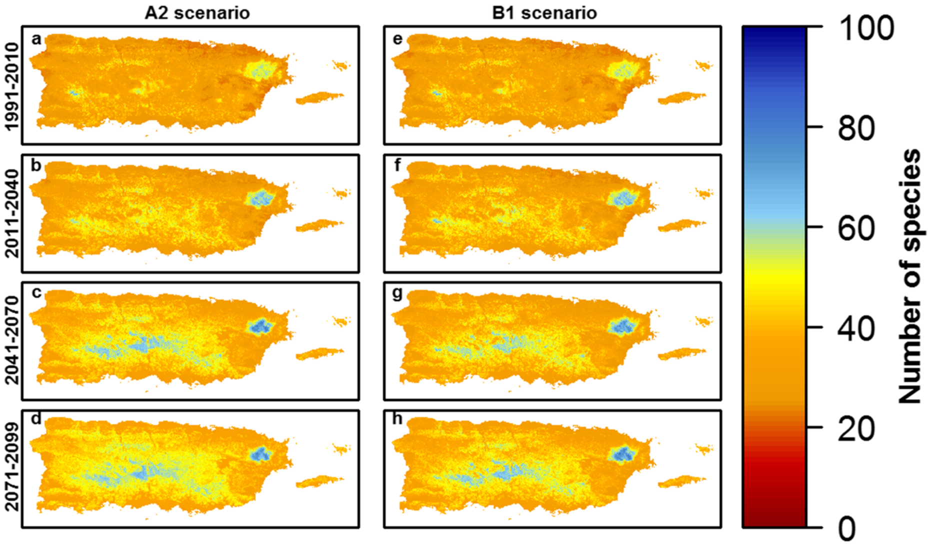


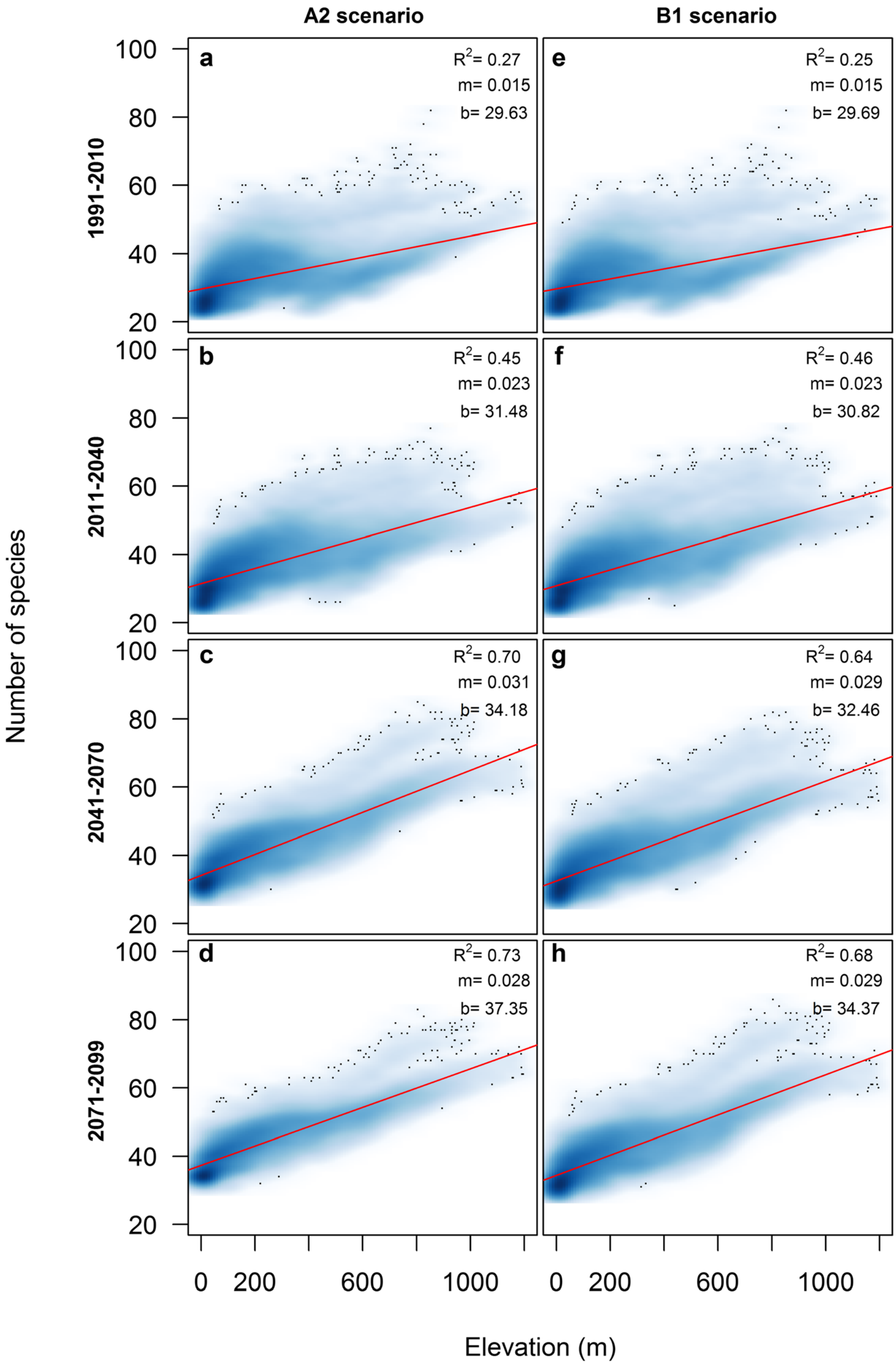
Fig. 5 Changes in the number of species as calculated from SESAM framework for future periods under **a–d** high and **e–h** low emission scenarios

et al. 2016). Some communities may also experience within community changes in species composition, i.e., ecological reorganization due to difference in the potential responses of specific species to climate change. For example, the future climatic conditions will support ecological reorganization within the community dominated by *C. sylvestris* (Brandeis et al. 2009). This implies potential emergence of novel community compositions in later periods of the century.

Species move to new regions due to altered climates and some species appear to benefit from the changes with more available favorite climates. Potential upward movement of the dry and hot climate species can increase competition for resources on the uplands. This will place additional pressure on the wet and cold climate species, which will be stressed under the projected decrease in environmental suitability (Harsch et al. 2017). However, the extent to which species can redistribute in response to climate change induced warming depends directly on their dispersal abilities, disturbances, and human activities (Feeley and Silman 2010b; Feeley et al. 2012). There is a great deal of uncertainty about the migration capabilities of tropical forest plant species at the rates required to keep pace with climate change (Feeley et al. 2012). Species and communities may also adapt to the new climatic conditions instead of redistributing to other areas. Adaptive responses include non-genetic phenotypic acclimation, genetically based evolution, and ecological reorganization (Webster et al. 2016). Conservation management should promote natural adaptation of species and communities. Recent studies suggest that conservative approaches that protect biological diversity can increase the probabilities of adaptation to climate change (e.g., Schindler et al. 2015; Webster et al. 2016). The projected richness is related to the scale of observations and analyses. We calculated the changes in species richness at the site level. While the site-level species richness increases on the uplands, the island-wide richness does not change or may decrease due to increasing pressures on the species adapted to cooler and wetter conditions.

The patterns of changes in species richness will provide information for conservation management. If species can migrate to newly favorable areas, the increase in species richness at upland sites, and changes in spatial evenness of species will cause different spatial patterns of biodiversity in the later periods of the century. Increases in relative abundance of adult and juvenile trees on higher elevations were reported at rates consistent with concurrent climate change (e.g., Duque et al. 2015). These increases were at the expense of “biotic attrition” or decrease in species diversity in areas which become less favorable for species (Feeley and Silman 2010b). However, in this study, the increase in species richness on the uplands did not decrease the richness on lower dry areas because the new conditions further increased the suitability for hot and dry climate species on the lowlands. Since the calculated richness is merely the counted number of species, it alone does not include any detail on the individual species and their properties. If combined with detailed projections at the species level, it can provide the basis for adaptive approaches to mitigate the threats from the species redistributions. For example, Australia’s Queensland government considered maximizing habitats for range-shifting species in prioritizing areas for new protected areas (Pecl et al. 2017). The proactive management approaches based on model projections should not be limited to the species that are projected to do better under the future conditions. They must also consider promoting species that will be potentially stressed such as the wet and cold climate species currently on the Puerto Rican uplands to protect the biological diversity.

The strength of changes in environmental suitability in the future periods is also partly caused by model extrapolations since all future model projections required extrapolations into changed climates in the future time intervals with the largest extents of extrapolations in the later periods (Fig. 3). Given the limitations of the correlative approaches especially in the small


A2 scenario
B1 scenario
Number of species
1991-2010
2011-2040
2041-2070
2071-2099
a
R^2= 0.27
m= 0.015
b= 29.63
b
R^2= 0.45
m= 0.023
b= 31.48
c
R^2= 0.70
m= 0.031
b= 34.18
d
R^2= 0.73
m= 0.028
b= 37.35
e
R^2= 0.25
m= 0.015
b= 29.69
f
R^2= 0.46
m= 0.023
b= 30.82
g
R^2= 0.64
m= 0.029
b= 32.46
h
R^2= 0.68
m= 0.029
b= 34.37
20
40
60
80
100
0
200
600
1000
Elevation (m)

◀ **Fig. 6** Number of species plotted against elevation for all pixels of the projected species richness maps under **a**–**d** high and **e**–**h** low emission scenarios. The red line represents the regression line of a standard generalized linear model (GLM) across the cloud of points. R^2, m, and b represent coefficient of determination, slope, and intercept of the fitted regression model respectively

islands with limited possibility for including areas with different climatic conditions in model training, integrating results from mechanistic modeling approaches will complement these projections especially for interpreting the effects of climatic conditions in the future. The projections of potential species distributions presented here reflect abiotic environmental changes, which outline the fundamental niches of species. They are based on the assumption that the environmental filtering is properly captured by the environmental variables used in the models. They are thus not in absolute but rather relative values because not all potential environmental variables were included in our models and the overall prevalence of each species is not known. Although in relative values, they do represent changes in environmental suitability for species under the future climatic conditions. Species are likely to respond in more complex ways than these projections in future environmental conditions based on their colonization history, evolutionary processes, biotic interactions, dispersal abilities, strength of human effects, and policy changes. Study of functional traits in Puerto Rico has shown that species occurrence in the island is linked to their local community weighted mean functional traits (Muscarella and Uriarte 2016). The pool of available approaches and analytical abilities will be improved by future progress in methods, data availability and quality, and richer knowledge on the underlying processes obtained from experimentation. Future works should include the effects of management and land use policies and other socioeconomic factors. The correlative approach applied here and the future projections based on abiotic filtering do not test the hypotheses but rather define the hypotheses that should be further evaluated, completed, and tested by mechanistic approaches and by including other driving forces of species and communities not incorporated here.

5 Conclusions

We projected the twenty-first century climate change effects on 200 Puerto Rican plant species using bioclimatic models and estimated the future changes in community richness under two emission scenarios. The probabilities of environmental suitability were projected to increase for low-altitude dry and warm climate species while it was decreased for the high-altitude colder and wet climate species. This implies potential movement of species to higher altitudes if species do not adapt to the new conditions and if their migration capabilities permit movement. This will increase species richness at the site level on the uplands putting competition pressure on the wet and cold climate species in addition to the altered climatic conditions. Conservation management can protect island-wide biological diversity by promoting the wet climate species currently occurring on the uplands. Our correlative approach based on abiotic environmental filtering should be evaluated by other approaches adding more species and potential driving forces and experimentations for more complete insights on climate change effects on plant species and communities in Puerto Rico.

Acknowledgments We thank Dr. Ariel Lugo for his cases of advice and Dr. Thomas Brandeis for sharing the Puerto Rico tree assemblages data in Brandeis et al. (2009).

Funding information This study was funded by the USDA Caribbean Climate Hub.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Acevedo-Rodrıguez P, Strong MT (2011) Flora of the West Indies: catalogue of the seed plants of the West Indies. Smithsonian Institution, National Museum of Natural History, Washington, DC

Bawiec, W J (1998) Geology, geochemistry, geophysics, mineral occurrences, and mineral resource assessment for the Commonwealth of Puerto Rico. U S Geological Survey, Open File Report CD–ROM 98–38

Berg MP, KIERS E, Driessen G, Van Der Heijden M, Kooi BW, Kuenen F, Ellers J (2010) Adapt or disperse: understanding species persistence in a changing world. Glob Chang Biol 16(2):587–598

Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FKA (2002) Evaluating resource selection functions. Ecol Model 157:281–300

Brandeis TJ, Helmer EH, Marcano-Vega H, Lugo AE (2009) Climate shapes the novel plant communities that form after deforestation in Puerto Rico and the US Virgin Islands. For Ecol Manag 258(7):1704–1718

Chase JM, Myers JA (2011) Disentangling the importance of ecological niches from stochastic processes across scales. Philos Trans R Soc Lond Ser B Biol Sci 366:2351–2363

D’Amen M, Bombi P, Pearman PB, Schmatz DR, Zimmermann NE, Bologna MA (2011) Will climate change reduce the efficacy of protected areas for amphibian conservation in Italy? Biol Conserv 144(3):989–997

Daly C, Helmer EH, Quiñones M (2003) Mapping the climate of Puerto Rico, Vieques and Culebra. Int J Climatol 23(11):1359–1381

D'Amen M, Dubuis A, Fernandes RF, Pottier J, Pellissier L, Guisan A (2015) Using species richness and functional traits predictions to constrain assemblage predictions from stacked species distribution models. J Biogeogr 42(7):1255–1266

D'Amen M, Rahbek C, Zimmermann NE, Guisan A (2017) Spatial predictions at the community level: from current approaches to future frameworks. Biol Rev 92(1):169–187

del Mar Lopez T, Aide TM, Thomlinson JR (2001) Urban expansion and the loss of prime agricultural lands in Puerto Rico. AMBIO 30(1):49–54

Di Cola V, Broennimann O, Petitpierre B, Breiner FT, D'Amen M, Randin C, Pellissier L (2017) ecospat: an R package to support spatial analyses and modeling of species niches and distributions. Ecography 40(6):774–787

Dubuis A, Pottier J, Rion V, Pellissier L, Theurillat JP, Guisan A (2011) Predicting spatial patterns of plant species richness: a comparison of direct macroecological and species stacking modelling approaches. Divers Distrib 17(6):1122–1131

Duque A, Stevenson PR, Feeley KJ (2015) Thermophilization of adult and juvenile tree communities in the northern tropical Andes. PNAS 112(34):10744–10749

Elith J, Kearney M, Phillips S (2010) The art of modelling range–shifting species. Methods Ecol Evol 1:330–342

Farr TG, Rosen PA, Caro E, Crippen R, Duren R, Hensley S, Kobrick M, Paller M, Rodriguez E, Roth L, Seal D, Shaffer S, Shimada J, Umland J, Werner M, Oskin M, Burbank D, Alsdorf D (2007) The shuttle radar topography mission, Rev Geophys 45(2), RG2004. https://doi.org/10.1029/2005RG000183

Feeley KJ, Silman MR (2010a) Modelling the responses of Andean and Amazonian plant species to climate change: the effects of georeferencing errors and the importance of data filtering. J Biogeogr 37(4):733–740

Feeley KJ, Silman MR (2010b) Biotic attrition from tropical forests correcting for truncated temperature niches. Glob Chang Biol 16(6):1830–1836

Feeley K, Rehm EM, Machovina B (2012) Perspective: The responses of tropical forest species to global climate change: acclimate, adapt, migrate, or go extinct? Front Biogeogr 4(2):69–84

Fei S, Desprez JM, Potter KM, Jo I, Knott JA, Oswalt CM (2017) Divergence of species responses to climate change. Sci Adv 3(5):e1603055

Gilman SE, Urban MC, Tewksbury J, Gilchrist GW, Holt RD (2010) A framework for community interactions under climate change. Trends Ecol Evol 25(6):325–331

Gotelli NJ, Anderson MJ, Arita HT, Chao A, Colwell RK, Connolly SR, Grytnes JA (2009) Patterns and causes of species richness: a general simulation model for macroecology. Ecol Lett 12(9):873–886

Guisan A, Rahbek C (2011) SESAM–a new framework integrating macroecological and species distribution models for predicting spatio-temporal patterns of species assemblages. J Biogeogr 38(8):1433–1444

Harsch MA, Phillips A, Zhou Y, Leung MR, Rinnan DS, Kot M (2017) Moving forward: insights and applications of moving-habitat models for climate change ecology. J Ecol 105(5):1169–1181

Henareh Khalyani A, Gould WA, Harmsen E, Terando A, Quinones M, Collazo JA (2016) Climate change implications for tropical islands: interpolating and interpreting statistically downscaled GCM projections for management and planning. J Appl Meteorol Climatol 55(2):265–282

Hijmans RJ, van Etten J (2014) raster: Geographic data analysis and modeling. R package version 2, 15

Hirzel AH, Le Lay G, Helfer V, Randin C, Guisan A (2006) Evaluating the ability of habitat suitability models to predict species presences. Ecol Model 199:142–152

Loreau M (2000) Are communities saturated? On the relationship between α, β and γ diversity. Ecol Lett 3(2): 73–76

Mateo RG, de la Estrella M, Felicísimo ÁM, Muñoz J, Guisan A (2013) A new spin on a compositionalist predictive modelling framework for conservation planning: a tropical case study in Ecuador. Biol Conserv 160:150–161

Mateo RG, Mokany K, Guisan A (2017) Biodiversity models: what if unsaturation is the rule? Trends Ecol Evol 32(8):556–566

Moritz C, Patton JL, Conroy CJ, Parra JL, White GC, Beissinger SR (2008) Impact of a century of climate change on small–mammal communities in Yosemite National Park, USA. Science 322(5899):261–264

Muscarella R, Uriarte M (2016) Do community-weighted mean functional traits reflect optimal strategies? Proc R Soc B 283:20152434. https://doi.org/10.1098/rspb.2015.2434

Muscarella R, Uriarte M, Erickson DL, Swenson NG, Kress WJ, Zimmerman JK (2016) Variation of tropical forest assembly processes across regional environmental gradients. Perspect Plant Ecol Syst 23:52–62

Nogués-Bravo D, Rahbek C (2011) Communities under climate change. Science 334(6059):1070–1071

Ovaskainen O, Tikhonov G, Norberg A, Guillaume Blanchet F, Duan L, Dunson D, Abrego N (2017) How to make more out of community data? A conceptual framework and its implementation as models and software. Ecol Lett 20(5):561–576

Pecl GT, Araújo MB, Bell JD, Blanchard J, Bonebrake TC, Chen IC, Falconi L (2017) Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. Science 355(6332):eaai9214

Peterson AT (2011) Ecological niches and geographic distributions. Princeton University Press, Princeton

Pottier J, Dubuis A, Pellissier L, Maiorano L, Rossier L, Randin CF, Guisan A (2013) The accuracy of plant assemblage prediction from species distribution models varies along environmental gradients. Glob Ecol Biogeogr 22(1):52–63

R Development Core Team (2017) R version 330: a language and environment for statistical computing R foundation for statistical computing, Vienna, AustriaURL http://wwwR–projectorg/. Accessed March to December 2017.

Schindler DE, Armstrong JB, Reed TE (2015) The portfolio concept in ecology and evolution. Front Ecol Environ 13(5):257–263

Soberón J (2007) Grinnellian and Eltonian niches and geographic distributions of species. Ecol Lett 10(12):1115–1123

Thuiller W (2003) BIOMOD – optimizing predictions of species distributions and projecting potential future shifts under global change. Glob Chang Biol 9:1353–1362

Thuiller W, Georges D, Engler R, Breiner F, Georges MD, Thuiller CW (2016) biomod2: ensemble platform for species distribution modeling. R package version 3.3–7

USDA (2017) Forest inventory and analysis database forest service available at: http://appsfsfedus/fiadbdownloads/datamarthtml. Accessed Feb 2017

USDA Soil Survey Staff (2014) Gridded Soil Survey Geographic (gSSURGO) Database for Puerto Rico United States Department of Agriculture, Natural Resources Conservation Service Available online at https://www.gdgscegovusdagov/. Accessed June 2016.

Webster MS, Madhavi AC, Darling ES, Armstrong J, Pinsky ML, Knowlton N, Schindler DE (2016) Who should pick the winners of climate change? Trends Ecol Evol 32:3

Wilson MFJ, O'Connell B, Brown C, Guinan JC, Grehan AJ (2007) Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope marine. Geodesy 30:3–35

Young BE, Franke I, Hernandez PA, Herzog SK, Paniagua L, Tovar C, Valqui T (2009) Using spatial models to predict areas of endemism and gaps in the protection of Andean slope birds. Auk 126(3):554–565

Affiliations

Azad Henareh Khalyani[1] **· William A. Gould**[2] **· Michael J. Falkowski**[1] **· Robert Muscarella**[3] **· María Uriarte**[4] **· Foad Yousef**[5]

[1] Natural Resource Ecology Laboratory, Colorado State University, 1499 Campus Delivery, Fort Collins, CO 80523, USA

[2] International Institute of Tropical Forestry, USDA Forest Service, San Juan, PR, USA

[3] Department of Bioscience - Ecoinformatics and Biodiversity, Aarhus University, Aarhus, Denmark

[4] Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY, USA

[5] Foad Yousef, Department of Biology, Westminster College, Salt Lake City, UT, USA