

ECOLOGICAL NICHE MODELING OF 23 THREATENED BAT SPECIES UNDER
CURRENT AND FUTURE CLIMATE CHANGE

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THESIS: ECOLOGICAL NICHE MODELING OF 23 THREATENED BAT SPECIES UNDER
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For Jeff Mock, and the current and yet undiscovered bat species that may benefit from
timely conservation planning.

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PREFACE

This work focuses on predictive modeling under climate change in bat species, but it can be used for any species. As niche models continue to become more advanced with more precise sampling efforts and better algorithms, they can serve as a valuable resource in future conservation planning. It is the hope that misunderstood species like bats will benefit from further niche modeling research, so that they may continue to provide important ecosystem services.

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ABSTRACT

Climate change is complex and altering the geographic ranges of many species worldwide. Bats, in particular, have distributions that are not well understood, and this may put them at increased extinction risk as temperatures continue to warm. Ecological niche modeling (ENM) was used to predict which ecogeographical variables impact bat species the most under current and future climate scenarios, and whether range overlap percentage was linked to changes in elevation. Occurrences for 23 threatened bat species were modeled under current and future high carbon emission scenarios (RCP 8.5) in 2050, and the resulting range overlap percentage was compared between current to future and current to International Union for Conservation of Nature (IUCN) ranges. On average, 23 threatened bat species are estimated to lose 27% of their collective range under a high carbon emission scenario in 2050. In addition, precipitation of the driest month (BIO 14) had the most impact (~40%) on current and future bat distributions, while elevation was very weakly correlated with range shift (Spearman's $\rho = 0.09$) and not statistically significant ($p > 0.05$). These findings suggest that ENMs can more precisely predict bat distributions, which may greatly aid in conservation planning efforts needed to protect these species from further extirpation.

CHAPTER 1

INTRODUCTION

Human-Induced Climate Change and Species Distributions

Ecological niches (the set of environmental factors that determine where a species can and cannot sustain populations; Peterson et al. 2001) have long been discussed in biology. Evidence of the role of climatic thresholds in creating and modifying these niches first appeared in the early part of the 20th century (Grinnell 1917). Since then, several studies have inferred large-scale range shifts of species from small-scale observations across sections of a range. In these studies, the total study area is limited, and does not reflect the entire species range. Instead, the study area is largely circumscribed by anthropogenic political boundaries such as state and country lines. Surprisingly few studies have examined whole-range dynamics at the continental scale (Parmesan 2006). Whole-range studies are important because they illustrate how a species' response (or sensitivity) to climate change is geographically specific. After all, species responses to climate change can vary across their range. These responses would depend on the local geographical distribution and environmental conditions relative to the regional patterns of exposure to climate change (Thuiller 2004). As climate is thought to be the primary driving force in limiting species distributions (Johnston and Schmitz 1997; Stockwell and Peterson 2002), examining distributional patterns in larger areas can help to reduce the global ecological perturbations that are occurring from biodiversity losses. While there have been several syntheses detailing the direct impacts of anthropogenic climate change on shifting ranges of species in the 21st century (Chen et al. 2011; Sherwin et al. 2012; McCracken et al. 2018), the need to further evaluate the effects of global warming on species distributions is urgent: it is

estimated that by 2100, up to 50% of species are predicted to lose their ecological niche due to climate change (Trisos and Pigot 2020).

Migratory species are of particular interest in studying responses to climate change. Migration is often characterized by the annual return journey of species between geographically separate breeding and wintering regions (Newton 2011). As such, migratory species not only rely on favorable connectivity between destinations, but also on habitat suitability at either end of the journey in order to ensure both survival and fecundity at later stages in the life cycle (Gill et al. 2009; Norris et al. 2004). As climate change has been observed to disrupt a variety of biotic interactions (including reduced food supply and breeding habitat loss among others; Robinson et al. 2009), the ability of these organisms to adapt to changing conditions both to and when they arrive at their destination will greatly depend on the degree of climate change.

One such group of migratory species at risk of losing their ecological niche is bats. Bats are a highly diverse group of mammals that spend over half of their lives subjected to conditions in their roost environment (diurnal refugia such as tree cavities, caves, foliage, or man-made structures like buildings; Kunz and Fenton 2005). Insectivorous bats can also serve as bioindicators for climate change, as continual temperature fluctuations are leading to mismatches when insectivorous bats and their main food source (insects) emerge (Jones et al. 2009). These mismatches are an early indication of the many challenges that bats will face with ongoing climate change (Both and Visser 2001). As such, bat distributions may be useful in signaling current or potential inhospitable temperature fluctuations in regions where a growing number of populations face extirpation from increased geographic displacement due to climate change (Parmesan 2006).

However, collecting data on bat range distributions may prove difficult, as over half of bats (57%) assessed by the International Union for Conservation of Nature (IUCN) Red List in the past decade have unknown population trends (compared to 39% of other mammals and 8% of all birds) and another 18% are considered data deficient (compared to 13% of mammals and 1% of birds; Frick et al. 2019). This disparity in knowledge concerning the future status of bats is even more tenuous considering that most bats only produce one to two pups per year. This small brood size limits survivorship, as a reduced number of pups leave proportionately fewer offspring to survive and reproduce. Ultimately, this indicates that climate change may eventually outpace the ability of bats to adapt to their changing niche, which puts them at a higher risk of extinction.

Moreover, high-elevation species may face additional challenges as a warming climate continues to drive distributions towards the poles. As regions become colder and more unsuitable, mountain-dwelling bat species in particular may experience increased difficulty sustaining populations. In addition, this trajectory can constitute an eventual “escalator to extinction” (Freeman et al. 2018) as more bat species are extirpated to higher elevations where there is no more room to expand their range. This spatial contraction of ranges is projected to greatly impact species survival; as an example, previous studies of elevation limitation on range size in migrant landbirds estimate that around 400-500 extinctions will result from a combination of habitat loss and a 2.8° C rise in temperature (Şekercioğlu et al. 2007). To understand how far north potential distributions are likely to shift, it is useful to compare the current to future range overlap percent. If range overlap percent continues to decrease (i.e., as current and future population ranges approach maximum displacement) this is an indication that a warming climate is driving future bat populations to potentially more inhospitable habitats. As a result, subsequent

generations of bats may be sharply reduced as certain regulatory processes (such as breeding) are irreparably disrupted. As narrower elevations on mountaintops have been associated with a decreased extent of occurrence (Manne and Pimm 2001), the need to accurately identify the geographic range of future bat populations under climate change may greatly help in reducing species turnover.

Ecological Niche Modeling

Ecological niche modeling (ENM) is a powerful tool used to assess the sensitivity of species to climate change by revealing to what degree distributions are altered under current and future climate scenarios. ENM has been applied to a diversity of species including birds and plants, and in the current study, I apply this approach to bats. To predict future distributions of threatened bat species, current climatic and topographic (aspect, elevation, and slope) ecogeographical variables (EGVs) are used to extract meaningful spatial and temporal relationships in occurrence data. That is, the presence or absence of an occurrence point is correlated with the overall percent contribution of an EGV, which helps to shape the resulting distribution. Once these predictive variables have been computed for the current climate scenario, they can be projected into the future, depending on the degree of carbon emissions used in analysis (e.g., “moderate” and “high” Representative Carbon Pathways, or RCPs). Predictive habitat modeling for spatial and temporal niches has already been indispensable to conservation planning (Guisan and Zimmermann 2000) and has novel applications, such as predicting elevation gain of treeline species (Chhetri et al. 2018).

The usefulness of these models will be contingent upon the questions asked by the scientific community, with an inherent understanding that perfect validation is unrealistic (Araújo and Rahbek 2006; Araújo and New 2007). However, as the magnitude of global

emissions and climate change continue to make seasons more extreme (Hayhoe et al. 2004), the success of our capacity to make plans for conservation not only depends on reliable presence data for predictive modeling, but also on more accurate attribution of what is primarily driving bat range shifts.

Here, I tested how climate change will impact the geographic range of 23 threatened bat species (Fig. 1, 2). Bats were selected based on IUCN threatened status (CR—Critically Endangered, E—Endangered, and V—Vulnerable) and further filtered to remove duplicate, spatially autocorrelated and non-useable records without coordinates. For each species, I created climate models using EGVs and current geographic occurrences to predict species distributions for the current climate scenario and one “high” carbon emission scenario in 2050. I used 19 historical bioclimatic variables and 4 topographic variables to run both current and future models and generated 23 current models and 23 “high” carbon (RCP 8.5) scenario models for 2050. IUCN species distributions are characterized by ongoing assessments which provide a framework for measuring species conservation success. As such, the IUCN Red List considers the global population of a species, and uses specific categories and criteria (e.g., population reduction) to assess overall extinction risk. However, IUCN assessments are not completely comprehensive, as new information about species occurrences are not always updated. Therefore, in order to obtain a more reliable estimate of species distributions under climate change, I used occurrence data to predict future distributions. I then measured range shift by comparing the percentage of range overlap between current to future and current to IUCN species distributions. Lastly, I tested whether elevation was correlated with current and future range overlap percentage to ascertain whether shifting altitudinal ranges affected distributions.

In sum, the four aims of this study were to: (i) predict which ecogeographical variables impact bat populations in different geographical regions; (ii) compare range maps of current ENM and IUCN bat distributions; (iii) quantify range overlap percentage between current and future climate scenarios; and (iv) determine if range overlap percentage varies across elevation.

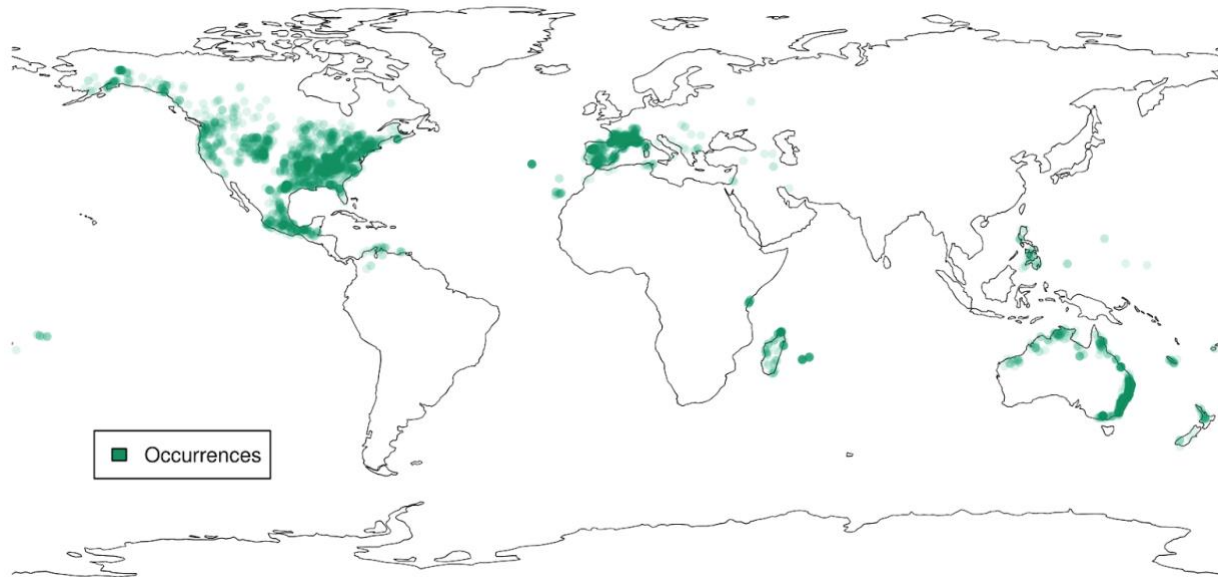


Figure 1. Current Global Occurrences of 23 Threatened Bat Species. Darker green areas suggest a higher density of bat occurrences, while lighter green areas denote lower bat occurrence density. According to the map, these threatened bat species primarily occupy the Nearctic, Palearctic, Indo-Malay, Madagascar, and Australasian biogeographical regions (Global Map. Threatened bat cases [occurrence map]. Copenhagen, Denmark: Global Biodiversity Information Facility (GBIF); accessed 2020 Aug 25).

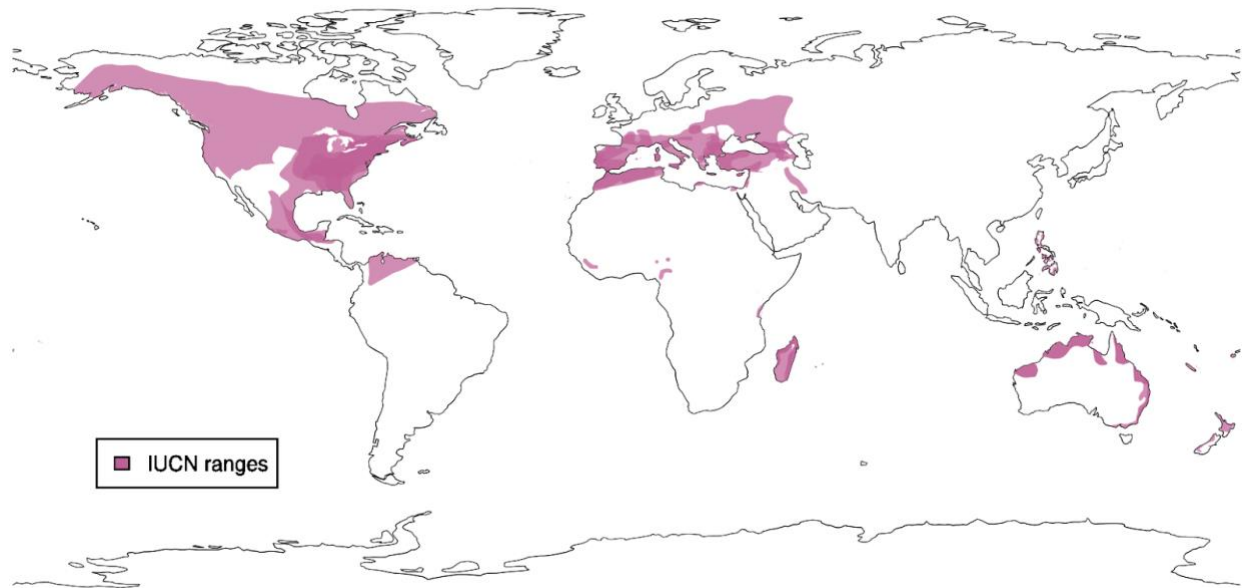


Figure 2. Current IUCN Global Ranges of 23 Threatened Bat Species. Darker pink areas suggest a greater number of bat species occupying an area, while lighter pink areas suggest fewer species occupying an area. The 23 species included in this study occupy a wide range of biomes which include temperate broadleaf and mixed forests, woodlands, and scrub. Most bat species tend to avoid extremely cold or dry biomes (Frick et al. 2019; Global Map. Threatened Bat Cases [range map]. Gland, Switzerland: International Union for Conservation of Nature (IUCN); accessed 2020 Aug 25).

CHAPTER 2

METHODS

Selection of Bat Species

I selected bats based on their threatened status (Vulnerable—VU, Endangered—EN, and Critically Endangered—CR) according to the IUCN Red List guidelines (iucnredlist.org). At the time of access (August 25, 2020), there were 106 VU, 77 E, and 22 CR bats for a total of 205 threatened species.

Presence-Only Data

Species distribution models are based on known occurrence records for a given species; to access this occurrence data, I used the `rgbif` (Chamberlain and Boettiger 2017) and `maptools` (Bivand and Lewin-Koh 2020) libraries in R to download and visualize occurrence records for each bat species from the Global Biodiversity Information Facility (GBIF; gbif.org), a global aggregator of museum records and ecological surveys for a wide number of species. Of these, 80 species returned records totaling 30,530 observations. I removed duplicate records and records without coordinates. I then used the `CoordinateCleaner` (Zizka et al. 2019) library in R to flag non-usable records (tests: “capitals,” “centroids,” “equal,” “gbif,” “institutions,” “zeros”) in addition to removing records with low coordinate precision (less than 100km grain size), fossil records (basis of records: “human observation,” “observation,” “preserved specimen”) and those with suspicious individual counts (greater than 99 observations) following recent approaches in predicting species distributions (Maldonado et al. 2015). To reduce spatial correlation among presence records, I thinned the remaining species to 1km² extent using the `spThin` (Aiello-Lammens et al. 2019) library in R and filtered the remaining records to include those with 15 or

more unique records (Raes and ter Steege 2007). The final count was 23 species that were suitable for analysis; of which, 6 are Endangered and the remaining 18 are classified as Vulnerable according to the IUCN Red List (Table 1).

IUCN Range Maps

To understand the best estimate of current bat ranges, I downloaded range map shapefiles (.shp) for all 23 species from the IUCN Red List (<https://www.iucnredlist.org/>, accessed August 25, 2020). Shapefiles were visualized in R using the raster (Hijmans 2020), rgdal (Bivand et al. 2020) and rgeos (Bivand and Rundel 2020) libraries. In addition to the Red List threatened categories, the IUCN provides data concerning population trends and current threats that may be contributing to these ranges.

Historical Climate Data

To assess bat distributions under current climate scenarios, I used WorldClim v. 2.1 (Fick and Hijmans 2017) to download current 1970-2000 Bioclimatic variables (Bio 1-19) at 1 km² spatial resolution (Table 2). These variables are derived from averages of monthly temperature and rainfall values that are used to represent annual trends. These trends are grouped into four categories: annual mean temperature and precipitation (Bio 1,12); seasonal temperature range and precipitation (Bio 2,3,4,7,15); mean or min/max temperatures of the warmest and coldest months or quarters (Bio 5,6,10,11,18,19); and precipitation of the wettest and driest quarters or months (Bio 8,9,13,14,16,17). I then converted these climate raster files into ASCII (.asc) format using the raster (Hijmans 2020), maps (Becker and Wilks 2018) and mapdata (Becker and Wilks 2018) libraries in R. WorldClim was used because it is easily accessible and used in many species distribution studies.

Future Climate Data

To predict how distributions of bat populations will be affected by climate change, I modeled a potential carbon scenario in 2050 that is considered to be a very high baseline for greenhouse gas emissions. This was done primarily to get a sense of the maximum displacement of geographic range that bats may experience under a “high” carbon environment in 2050. In order to simulate the effects of warming temperatures in the future, I used the raster library in R to download the same bioclimatic variables (1-19) from WorldClim at 1 km² spatial resolution at a Representative Concentration Pathway (RCP) that examined a very high baseline future carbon scenario (RCP 8.5) following recent climate forecasting practices in niche modeling (Chhetri et al. 2018; Zamora-Gutierrez et al. 2018). These 19 variables were derived from the Coupled Model Intercomparison Project Phase 5 (CMIP5) 2010-2014 using data collected from the Intergovernmental Panel on Climate Change Assessment Report 5 (IPCC AR5). In order to more accurately simulate the earth’s climate system in 2050, it was necessary to use a downscaled Global Climate Model (GCM) which translates coarse-resolution climate data into fine-resolution outputs used for modeling. From the nine available GCMs, I chose the Community Climate System Model version 4 (CCSM4) from the National Center for Atmospheric Research in the United States (NCAR).

Topographic Variables

Digital Elevation Models (DEMs) were downloaded from WorldClim at 1km spatial resolution derived from NASA’s Shuttle Radar Topography Mission version 4 (SRTM v.4) data. In addition, I used Earth Env (<https://www.earthenv.org/topography>) to download slope and aspect (east and north components) based on 1km spatial grain (aggregation) from the Global Multi-resolution Terrain Elevation data 2010 (GMTED2010) from the U.S. Geological Survey

(USGS) and National Geo-Spatial Intelligence Agency (NGA). The same four topographic variables (elevation, slope, aspect/north, aspect/east) were used in both current and future 2050 climate models.

Ecological niche model

Because bats are distributed across the globe, using spatial data from modeling to create maps is a useful tool for projecting future distributions affected by climate change. Both current and future species distribution models for all 23 bat species were built in Maxent (v. 3.4.1), which is a robust presence-only regression program that predicts species distributions with relatively low sample sizes (<100) (Elith et al. 2006; Phillips et al. 2006; Phillips et al. 2009). Figure 3 illustrates an overview of my approach. To reduce overfitting and collinearity of BioClim variables in the model, I used the usdm library (Naimi et al. 2014) in R to construct a stepwise Variance Inflation Factor analysis (>10 indicating highly inflated) to eliminate highly correlated variables from the model following recent techniques in niche modeling (Zeng et al. 2016).

Since Maxent is a presence-only algorithm, a leave-one-out cross validation (LOOCV) resampling approach was used to validate the model which makes better use of small datasets (Phillips et al. 2006). I also increased the number of background points to 10,000 and increased the number of replicates to 15 (Phillips and Dudík 2008) but set all other parameters to default. When all 46 models were completed, I converted probability of occurrence into a binary presence (1) and absence (0) prediction using the 10th percentile training presence (10% omission rate) logistic threshold (Peterson et al. 2007) following recent approaches in the study of bats (Santos et al. 2013). I then reclassified current and future maps according to threshold values, and converted them into shapefiles using the raster, rgdal and rgeos libraries in R.

Model Evaluation

Several methods were used to evaluate model performance of current and future climate scenarios. First, I recorded the area under the curve (AUC) value of the receiver operator characteristic (ROC), which is an indicator of how well Maxent ranks presence values from random background points, and was therefore a good measure of predictive accuracy (Phillips et al. 2006, Merow et al. 2013). AUC values range between 0 and 1, with greater than 0.75 considered to be good model performance (Elith et al., 2006), and 0.5 and below considered to be no better than random (Phillips et al. 2006).

In order to evaluate how influential the EGVs were in distinguishing between presence and random background points, a statistical jackknife analysis of gain (a resampling technique that uses subsets of the original data) was used to measure which variables contributed the most to model performance based on percentage. In other words, this is a statistical method that resamples (takes random subsets from) the sample data in order to estimate which EGVs contribute the most to current and future distributions (Phillips 2007, Nisbet 2018).

Lastly, a binomial p-test ($p < 0.05$, statistically significant) for 10% omission training presence was used to test for statistical significance of omission rate between all 23 current and future models.

Testing Hypothesis

To test if current and future percent range overlap varied across elevation, a Spearman's rank correlation (correlation coefficient, r_s) test was performed in R to measure the correlation between percent range overlap and elevation as well as the strength of association. That is, I hypothesized that either (1) range overlap percentage and elevation both increase or (2) range overlap percentage decreases as elevation increases (or vice-versa).

Table 1. IUCN Status and Last Year of Assessment for 23 Threatened Bat Species. Out of 23 species (“Bat Species”) used in this study, 7 have not been assessed (“Last year of IUCN assessment” in bold) within the last decade. In total, there were 6 endangered (“Status” = EN) and 17 vulnerable (“Status” = VU) bat species at the time of access (August 25, 2020).

Bat Species	IUCN	Last year of IUCN assessment
<i>Acerodon jubatus</i>	EN	2016
<i>Emballonura semicaudata</i>	EN	2008
<i>Leptonycteris nivalis</i>	EN	2015
<i>Myotis leibii</i>	EN	2018
<i>Myotis lucifugus</i>	EN	2018
<i>Pteropus niger</i>	EN	2017
<i>Balantiopteryx io</i>	V	2014
<i>Chalinolobus tuberculatus</i>	V	2008
<i>Eidolon dupreanum</i>	V	2008
<i>Leptonycteris curasoae</i>	V	2015
<i>Macroderma gigas</i>	V	2019
<i>Miniopterus schreibersii</i>	V	2019
<i>Mormopterus norfolkensis</i>	V	2008
<i>Musonycteris harrisoni</i>	V	2015
<i>Myotis grisescens</i>	V	2017
<i>Nyctalus lasiopterus</i>	V	2016
<i>Perimyotis subflavus</i>	V	2018
<i>Pipistrellus maderensis</i>	V	2016
<i>Pteropus ornatus</i>	V	2008
<i>Pteropus poliocephalus</i>	V	2008
<i>Rhinolophus mehelyi</i>	V	2016
<i>Rousettus madagascariensis</i>	V	2018
<i>Taphozous hildegardeae</i>	V	2008

Table 2. Description of Ecogeographical Variables (EGVs) Used in This Study. Bioclimatic variables (“EGV”, BIO 1-19 which are averages from 1970-2000) were downloaded at 1km² spatial resolution from WorldClim v 2.1. For future bioclimatic variables, a high emission scenario (RCP 8.5) was taken from the Community Climate System Model 4 (CCSM4) General Circulation Model (GCM). Variables that were drawn from both the current (“Time period”, C) and future (“Time period”, F) periods are noted. Digital Elevation Models (“EGV”: elev) were taken from NASA’s Shuttle Radar Topography Mission version (SRTM v.4), while the other topographic variables (“EGV”: slope, east (E) and north (N); aspect is the direction of the slope) were taken from the Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010) from the U.S. Geological Survey (USGS) available on EarthEnv. All topographic variables were only available for the current climate.

EGV	Description	Time period	Source
BIO 1	Annual Mean Temperature	C/F	WorldClim
BIO 2	Mean Diurnal Range	C/F	WorldClim
BIO 3	Isothermality (BIO 2/BIO 7)(*100)	C/F	WorldClim
BIO 4	Temperature Seasonality (standard deviation *100)	C/F	WorldClim
BIO 5	Max Temperature of the Warmest Month	C/F	WorldClim
BIO 6	Min Temperature of the Coldest Month	C/F	WorldClim
BIO 7	Temperature Annual Range (BIO 5 - BIO 6)	C/F	WorldClim
BIO 8	Mean Temperature of the Wettest Quarter	C/F	WorldClim
BIO 9	Mean Temperature of the Driest Quarter	C/F	WorldClim
BIO 10	Mean Temperature of the Warmest Quarter	C/F	WorldClim
BIO 11	Mean Temperature of the Coldest Quarter	C/F	WorldClim
BIO 12	Annual Precipitation	C/F	WorldClim
BIO 13	Precipitation of the Wettest Month	C/F	WorldClim
BIO 14	Precipitation of the Driest Month	C/F	WorldClim
BIO 15	Precipitation Seasonality	C/F	WorldClim
BIO 16	Precipitation of the Wettest Quarter	C/F	WorldClim
BIO 17	Precipitation of the Driest Quarter	C/F	WorldClim
BIO 18	Precipitation of the Warmest Quarter	C/F	WorldClim
BIO 19	Precipitation of the Coldest Quarter	C/F	WorldClim
Elevation	SRTM v.4	C	WorldClim
Slope	GMTED2010	C	EarthEnv
Aspect (E)	GMTED2010	C	EarthEnv
Aspect (N)	GMTED2010	C	EarthEnv

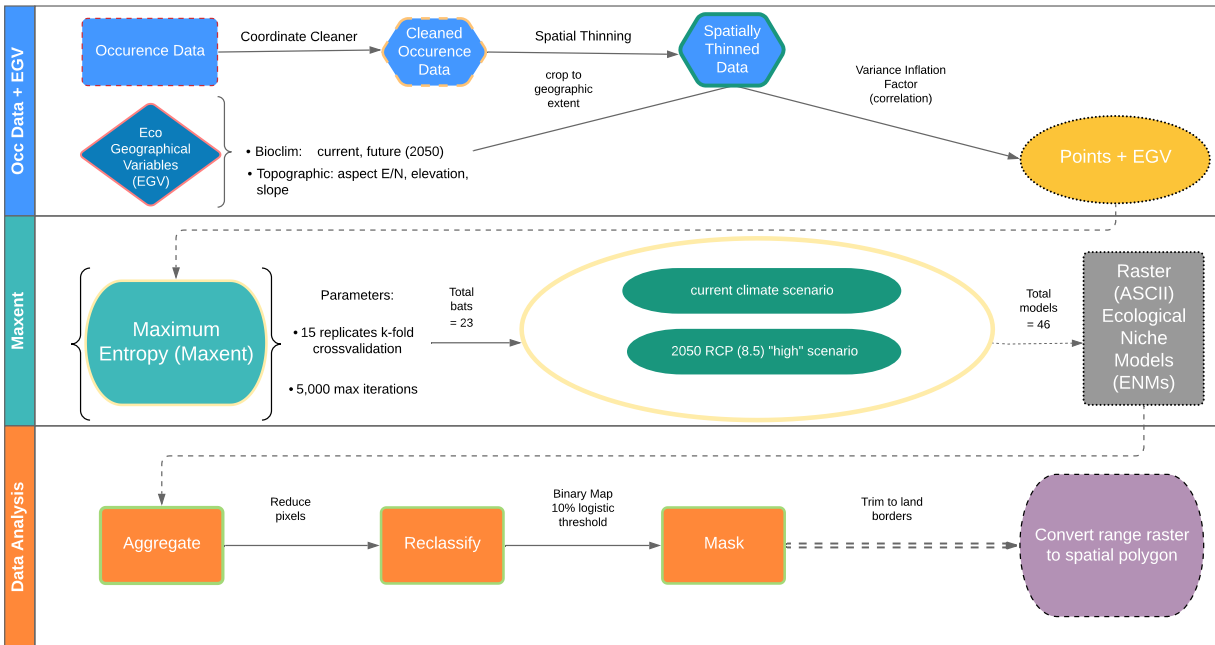


Figure 3. Workflow of Constructing Ecological Niche Models (ENMs) for 23 Threatened Bat Species. The top box shows how occurrence data and ecogeographical variables (EGVs) were prepared for Maxent. The middle box illustrates the approach used to generate two models (one current and one 2050 “high” carbon scenario) for each of 23 bat species. The third box shows how Maxent niche models were converted into current and future range maps.

CHAPTER 3

RESULTS

Ecological Niche Modeling Results

For each of 23 analyzed bat species, I inferred current ecological niche models and projected them onto future climates. To evaluate how well these niche models performed, I recorded average AUC (area under the curve) values, TTP (tenth percentile training presence) and jackknife analysis of EGV contribution across 15 replicate runs in Maxent (Table 3).

For current climate scenarios, “Mean AUC current” (Table 3) shows that the average AUC value for all models was 0.806 (standard deviation = 0.098) with a minimum of 0.572 (for *P. niger*) and a maximum of 0.998 (for *E. semicaudata*). In general, AUC values greater than 0.75 suggest high predictive power (indicating true positives) while values less than 0.5 indicate less predictive power (indicating false positives), and a value of 0.5 provides no information (Peterson et al. 2007).

For “high” (RCP 8.5) climate scenarios in 2050, “Mean AUC 2050” (Table 3) had a slightly higher average AUC value of 0.849 (+ 0.043, standard deviation=0.084) with a slightly lower minimum of 0.556 (-0.016 for *P. niger*) and the same maximum (0.998) for the same species (*E. semicaudata*).

TTP provides a threshold for classifying species presence (1) or absence (0) when ten percent of the total presence points are omitted from the model. The average logistic threshold for TTP was 0.251 for the current climate (“Mean TTP current”, Table 3), and a similar 0.258 (+0.007) for the future climate in 2050 (“Mean TTP 2050”, Table 3), indicating that the model is omitting similar presence points in both current and future 2050 climate scenarios that are not likely contributing to distributions.

Jackknife analysis of gain indicates to what degree the EGVs contributed to overall species distribution. This method helps to account for sampling errors that may have resulted from biased partitioning of occurrence data. The mean percent contribution of the EGV that affected the greatest number of species was used in the final analysis.

BIO14 (precipitation of the driest month) had the greatest mean percent contribution to ENMs in both the current and future climates. The current climate was slightly higher (39.7%; “EGV max current”, Table 3) while the future climate in 2050 showed a slightly lower (-1.68) mean percent contribution (38.02%; “EGV max 2050”, Table 3).

In contrast, “north”, the y-component (along with the x-component, “east”) of the earth’s (circular) aspect, had the least mean percent contribution to ENMs in both the current climate (0.2%; “EGV min current”, Table 3) and a slightly higher (+0.3) mean percent contribution in the future climate (0.5%; “EGV min 2050”, Table 3).

Of the species most affected by BIO14, 4 were in the current climate (*M. grisescens*, *M. leibii*, *P. subflavus* and *P. ornatus*) and the same 4 were in the future climate plus an additional bat species (*A. jubatus*).

Of those affected by “north” aspect, 7 species were in the current climate (*M. grisescens*, *N. lasiopterus*, *P. subflavus*, *P. maderensis*, *P. ornatus*, *R. mehelyi*, *R. madagascariensis*) and the same 4 species (*M. grisescens*, *N. lasiopterus*, *P. maderensis*, *P. subflavus*) plus an additional 5 species (*B. io*, *L. nivalis*, *M. gigas*, *P. niger*, *P. poliocephalus*) were in the future climate. Overall, percent contributions for all EGVs ranged from 0% to 78.2% in both the current and future climates.

Comparison of Current ENMs to IUCN Ranges

To compare current ENMs to IUCN ranges, I visualized their overlap. I show this overlap for three randomly chosen bat species in Figure 4. As illustrated in the figure, overlap varies across species (*R. madagascariensis*: 22.1%, *P. subflavus*: 57.6 %, *A. jubatus*: 36.8%). On average, overlap between the IUCN and current ENM ranges for all 23 species was 34% (“Mean ICPO”, which represents the mean IUCN to current range overlap percent, Table 3) with a minimum of 5.91% for *T. hildegardeae* and a maximum of 83.4% for *M. leibii*.

Comparison of Current to Future ENM Range Overlap

I calculated current to future range percent overlap as the percent overlap between the intersection of current to future range area over the current area. I then compared overlap between current ENM distributions and future distributions (Figure 6). The average current to future percent overlap was 72.7%, with a minimum of 39.7% (for *E. semicaudata*) and a maximum of 95.97% (for *P. niger*) as depicted in “Mean CFPO” (mean current to future range percent overlap, Table 3). Approximately five of the 23 species (22%) were projected to occupy less than 60% of their original niche. Of these, two are currently classified as endangered (*A. jubatus*, 54.7%; *E. semicaudata*, 39.7%) and three are classified as vulnerable (*L. curasoeae*, 51.3%; *M. harrisoni*, 51.6%; *P. maderensis*, 48.5%).

Changes in Elevation and Current to Future Range Overlap

Elevation (meters) appears to be very weakly correlated with current to future percent overlap (Figure 7; Spearman's $\rho = 0.09$, $p\text{-value} = 0.6935$, $n = 23$). This suggests that elevational shift itself is not a strong indicator of future displacement under climate change.

Table 3. Individual and Average Values of Model Performance in 23 Threatened Bat Species. From left to right: bat taxa grouped by IUCN status, Data Points (total presence points used in the model), Mean AUC current (average area under the curve values per bat), Mean TTP current (average tenth percentile training values in the current climate), Mean TTP 2050 (average TTP values per bat species in 2050), Mean CFPO (average current to future percent overlap), Mean ICPO (average IUCN to current percent overlap), EGV max current (ecogeographic variable with the highest percent contribution in the current climate), EGV min current (variable with the lowest percent contribution in the current climate), EGV max 2050 (variable with the highest percent contribution in 2050), EGV min 2050 (variable with the lowest percent contribution in 2050). Elevation = “elev”. Mean values for all 15 runs in 23 bat species are represented in bold according to IUCN status (EN = Endangered, VU = Vulnerable).

Bat Species	Data Points	Mean AUC current	Mean AUC 2050	Mean TTP current	Mean TTP 2050	Mean CFPO	Mean ICPO
EN		0.806	0.794	0.279	0.292	0.754	0.384
<i>Acerodon jubatus</i>	29	0.774	0.72	0.3	0.396	0.547	0.368
<i>Emballonura semicaudata</i>	19	0.998	0.998	0.349	0.33	0.397	0.164
<i>Leptonycteris nivalis</i>	145	0.824	0.836	0.201	0.19	0.83	0.556
<i>Myotis leibii</i>	74	0.854	0.835	0.218	0.236	0.91	0.591
<i>Myotis lucifugus</i>	719	0.814	0.817	0.249	0.258	0.879	0.321
<i>Pteropus niger</i>	25	0.572	0.556	0.36	0.34	0.96	0.305
VU		0.858	0.868	0.241	0.246	0.718	0.324
<i>Balantiopteryx io</i>	50	0.903	0.894	0.087	0.167	0.694	0.493
<i>Chalinolobus tuberculatus</i>	28	0.682	0.748	0.385	0.281	0.736	0.53
<i>Eidolon dupreanum</i>	25	0.702	0.712	0.071	0.123	0.687	0.834
<i>Leptonycteris curasoae</i>	23	0.897	0.904	0.163	0.203	0.513	0.109
<i>Macroderma gigas</i>	153	0.881	0.884	0.175	0.235	0.719	0.338
<i>Miniopterus schreibersii</i>	509	0.92	0.915	0.275	0.279	0.745	0.151
<i>Mormopterus norfolkensis</i>	85	0.918	0.922	0.354	0.376	0.826	0.562
<i>Musonycteris harrisoni</i>	15	0.902	0.94	0.187	0.327	0.516	0.155
<i>Myotis grisescens</i>	90	0.8	0.844	0.28	0.331	0.66	0.402
<i>Nyctalus lasiopterus</i>	368	0.964	0.958	0.22	0.203	0.659	0.049
<i>Perimyotis subflavus</i>	957	0.783	0.793	0.313	0.305	0.954	0.576
<i>Pipistrellus maderensis</i>	28	0.688	0.804	0.274	0.188	0.485	0.376
<i>Pteropus ornatus</i>	14	0.844	0.749	0.327	0.382	0.754	0.21
<i>Pteropus poliocephalus</i>	1315	0.929	0.93	0.322	0.328	0.882	0.208
<i>Rhinolophus mehelyi</i>	100	0.918	0.913	0.257	0.212	0.851	0.229
<i>Rousettus madagascariensis</i>	56	0.895	0.885	0.127	0.088	0.895	0.221
<i>Taphozous hildegardeae</i>	15	0.959	0.971	0.285	0.15	0.624	0.059

Table 3. (continued)

Bat Species	Data Points	EGV max current	EGV min current	EGV max 2050	EGV min 2050
EN					
<i>Acerodon jubatus</i>	29	2	east	14	19
<i>Emballonura semicaudata</i>	19	17	19	17	north
<i>Leptonycteris nivalis</i>	145	13	18	13	18
<i>Myotis leibii</i>	74	slope	elev	slope	12
<i>Myotis lucifugus</i>	719	2	east	2	east
<i>Pteropus niger</i>	25	east	7	east	7
VU					
<i>Balantiopteryx io</i>	50	6	18	6	north
<i>Chalinolobus tuberculatus</i>	28	11	10	7	north
<i>Eidolon dupreanum</i>	25	19	slope	19	slope
<i>Leptonycteris curasoae</i>	23	5	7	5	east
<i>Macroderma gigas</i>	153	4	6	4	11
<i>Miniopterus schreibersii</i>	509	14	north	14	north
<i>Mormopterus norfolkensis</i>	85	14	east	14	east
<i>Musonycteris harrisoni</i>	15	6	4	elev	18
<i>Myotis grisescens</i>	90	slope	north	slope	north
<i>Nyctalus lasiopterus</i>	368	14	north	14	north
<i>Perimyotis subflavus</i>	957	11	north	11	north
<i>Pipistrellus maderensis</i>	28	7	east	7	north
<i>Pteropus ornatus</i>	14	10	17	elev	13
<i>Pteropus poliocephalus</i>	1315	14	north	14	north
<i>Rhinolophus mehelyi</i>	100	11	north	6	18
<i>Rousettus madagascariensis</i>	56	12	north	12	slope
<i>Taphozous hildegardeae</i>	15	elev	east	11	14

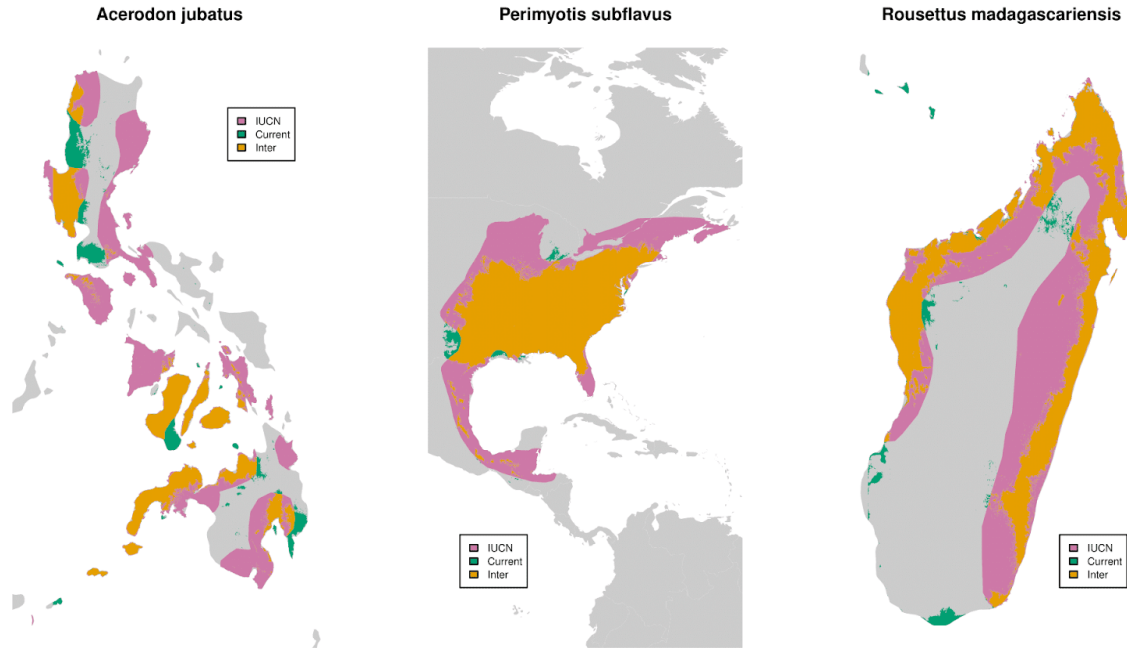


Figure 4. Map of Current ENM and IUCN Range Overlap for Three Randomly Chosen Threatened Bat Species. Pink areas represent IUCN ranges (“IUCN”), green areas represent current estimates of range based on ecological niche modeling (“Current”), and orange areas represent the intersection between these two ranges (“Inter”). *P. subflavus* (middle panel) had an approximate overlap of 57.6%, while *A. jubatus* (left panel) had 36.8% overlap, and *R. madagascariensis* (right panel) had the least overlap (22.1%). This figure also indicates that ENM ranges (green areas) for all three species extended beyond the IUCN ranges to varying degrees. This reveals that ENM range maps tend to be more precise than IUCN range maps, possibly due to under-sampling of occurrence records by the IUCN.

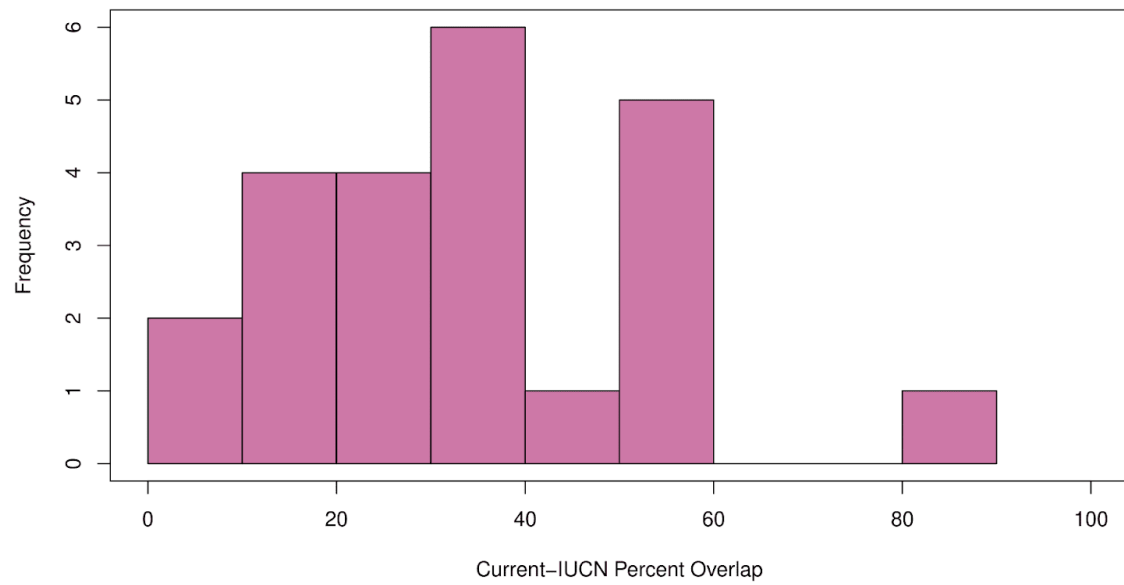


Figure 5. Percent Overlap between Current ENM and IUCN Ranges for 23 Threatened Bat Species. The highest range percent overlap was 80% (*L. nivalis*) while more than half of the bat species (14 species) had a range overlap between 30-60%.

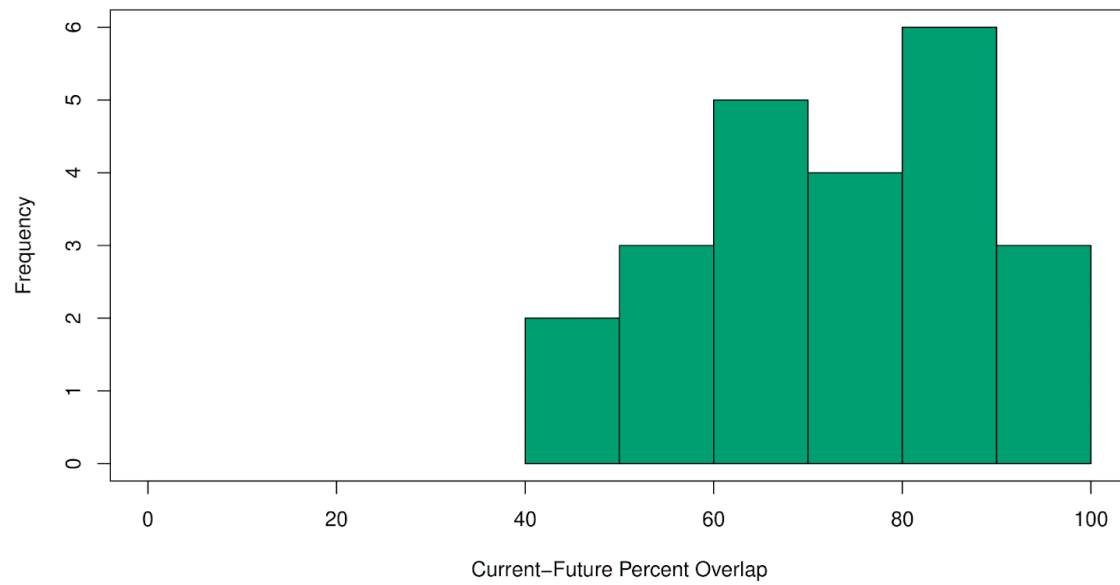


Figure 6. Percent Overlap between Current and Future ENM Ranges for 23 Threatened Bat Species. The data indicates that of the 23 species studied here, at least 18 are projected to occupy between 60-100% of their original niche, despite a high carbon scenario in 2050. This leaves 5 species occupying less than 60% of their original niche in 2050. These results suggest that climate change is expected to decrease overall range overlap percent, but these patterns are heterogeneous across species.

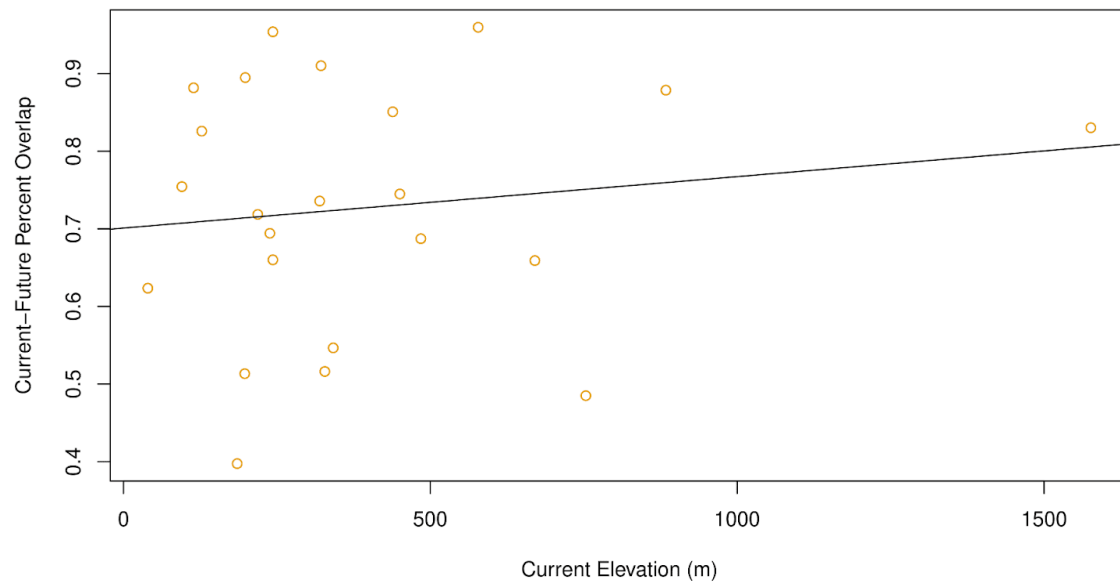


Figure 7. Current Elevation and Percent Overlap between Current and Future ENM Ranges for 23 Threatened Bat Species. The scatterplot shows a very weak correlation between elevation and current to future percent overlap (Spearman's $\rho = 0.09$, $p = 0.6925$, $n = 23$), with one value at 1576 meters (*L. nivalis*). These values indicate that increased elevation is not strongly associated with greater current to future range percent overlap.

CHAPTER 4

DISCUSSION

Overall Findings

While IUCN assessments are a useful metric for measuring extinction risk among species, the occurrence data used to create species range maps for the IUCN are frequently not up-to-date. For instance, the last assessments for *E. semicaudata* and *T. hildegardeae* were in 2008 at the time of access (August 25, 2020). ENMs provide a useful alternative to IUCN species range maps, as they can be updated as new occurrence data are uploaded. This study reveals that ENMs work well for non-terrestrial volant species such as bats, and not only emphasizes the need to utilize more updated presence points for modeling, but to increase sample size to more accurately forecast potential distributions under climate change.

In this study, ENMs predicted geographic range as a subset of the region outlined by the IUCN range (Figure 2). However, the relatively low average percent overlap between current ENMs and IUCN range maps (53.4%) suggests that ENMs can also provide a more precise characterization of where bat species can be found. This is especially important for tropical island endemic bat species (range-restricted species that are native to that island only) that are threatened by habitat fragmentation and extreme weather events (heat waves, cold spells, cyclones) which are exacerbated by climate change (Şekercioğlu et al. 2011; Frick et al. 2019). As studies suggest that neotropical bat species may be keystone taxa as well as important components of biodiversity (Kaufman and Willig 1998), the loss of these species may significantly alter global ecosystems.

In addition, low current to future range overlap percentage for several bat species in this study signals an increased need to protect those species that stand to lose a larger portion of their

range due to climate change. For endangered bats like *E. semicaudata* that are projected to lose up to 60% of their range under high carbon emission scenarios in 2050, the results of this study further highlight the need to obtain accurate occurrence records in order to create better and more robust predictive models.

EGVs That Impact Bat Distributions in Different Geographic Regions

On average across all bat species, precipitation of the driest month (BIO14) had the highest percent contribution in both current (39.7%) and future (38.02%) climate scenarios. Of the four bat species whose distributions were primarily influenced by BIO14 in the current climate (*M. grisescens*, *M. leibii*, *P. subflavus*, and *P. ornatus*), one is endangered (*M. leibii*).

Water is an important variable which determines favorable foraging areas in bats. Studies reveal that high ambient temperature combined with low relative humidity in dry Mediterranean regions can increase evaporative water loss in bats (Rainho and Palmeirim 2011). Further, the finding that BIO14 is a major predictor of species distributions in both the current and future climate in 2050 parallels previous studies linking the availability of drinking water with potential use of space in bat species (Korine and Pinshow 2004; Salsamendi et al. 2012; Jachowski et al. 2014).

The mean temperature of the coldest quarter (BIO11) had the second highest percent contribution to the current climate (44.7%) affecting three vulnerable bat species (*M. gigas*, *R. mehelyi*, and *P. maderensis*). This variable had slightly more contribution in the future climate (48.6%), impacting the ranges of *P. maderensis* and one more vulnerable bat species (*T. hildegardeae*). The importance of this variable could be connected to the scarcity of food resources for hibernating bats in the winter. As cold weather reduces overall nocturnal prey

abundance, hibernating bats must rely on their fat stores in order to survive cold temperatures as food becomes scarce (Lyman et al. 1982; Meyer et al. 2016).

Range Maps of Current ENM and IUCN Distributions

I found that the average range percent overlap between current ENMs and IUCN range maps was 53.4% for all 23 bat species. The overlap was relatively low because IUCN range maps tend to extrapolate data (inferring unknown occurrences from known occurrences) as up-to-date species records are not always available (Escobar et al. 2016). In addition, larger IUCN range distributions may be due to other contributing factors, such as under-sampling.

The wide IUCN range of *A. jubatus* (36.8% overlap with current ENM ranges) may be explained by this species' large foraging area, as these frugivorous bats often travel 20 km from day roosts (Palmer and Woinarski 1999) to feed on fruits. This may account for large numbers of *A. jubatus* potentially occurring between patches of suitable habitat at any given time (McConkey and Drake 2006). In addition, while *P. subflavus* had the highest average percent overlap between current ENM and IUCN ranges (57.6%), migratory distributions of females to males in this species have been observed to vary seasonally (Davis 1959) which may account for some inflation of IUCN range distributions.

Lastly, *R. madagascariensis* had the lowest IUCN average range percent overlap (22%) among the three bat species measured in Figure 4. Along with *A. jubatus*, *R. madagascariensis* is an island endemic species, and may be particularly vulnerable to more extreme weather events such as cyclones (Carroll and Mace 1988) which can alter future distributions in new and unforeseen ways. When compared with a much higher degree of current to future range percent overlap (89%) in ENM models for this species in this study, the low average range percent

overlap between current ENM and IUCN ranges in *R. madagascariensis* reveals possible under-sampling of occurrences by the IUCN (as Figure 4 shows ENM occurrences on the Comoros and Mayotte islands, just northwest of Madagascar, which are outside of the IUCN range). This low average range percent overlap in current ENM and IUCN range for this species is somewhat surprising considering that the last IUCN assessment was conducted in 2019 (Table 1).

Range Overlap Percentage between Current and Future Distributions

On average, the current to future range percent overlap (CFPO) for all 23 bat species was 72.7%, indicating that these 23 bat species will lose approximately 27% of their current range under high carbon emission scenarios in 2050. Two endangered bat species showed the most pronounced change in current to future distributions: *E. semicaudata* had the highest AUC values for both current and future climate scenarios (AUC = 0.998) but reported the least amount of current to future range percent overlap (39.7%), while *P. niger* had the lowest current and future AUC values (0.572, 0.556, respectively) but the highest current to future range percent overlap (95.97 %). While the AUC values provide a useful metric for gauging model consistency when predicting presences from random background points, they do not necessarily provide validation that the resulting ranges are accurate. For example, since background points may contain both presences and absences (since Maxent only uses presence data), AUC values may not reliably distinguish true occurrences, especially if sampling records are low (Merow et al. 2013). In addition, as AUC values do not provide any additional ecological information pertaining to species habits and preferences, they should be interpreted with caution when evaluating future species distributions (Jiménez-Valverde et al. 2008; Elith et al. 2011).

In spite of this, there may be a couple of reasons for why the AUC values between *E. semicaudata* and *P. niger* differ. First, distance to resources may have a variable impact on species distributions as climate change continues to alter prey abundance and forest composition. The insectivorous *E. semicaudata* is primarily cave-dwelling but also roosts in nearby native forests (Bonaccorso and Allison 2008), while the frugivorous *P. niger* primarily roosts in forests, but like most flying fox species, can travel long distances (more than 10 km; Corlett 2009) between their roost and feeding sites. The low AUC values for *P. niger* indicate that the model had difficulty distinguishing between presences and background points in both current and future climate scenarios, while the high AUC value in *E. semicaudata* suggests just the opposite. As climate change continues to alter landscapes, it is possible that the uncertainty of environmental variables may be compounded over greater foraging distances, as model learning ability declines in an increasingly heterogeneous environment (Zollner and Lima 1999; Patenaude-Monette et al. 2014). Hence, the high current to future overlap percent in *P. niger* does not necessarily reflect higher predictive power, as the input variables used for modeling may be unreliable due to a large foraging range.

Second, the results may be related to model parameterization in Maxent. While the AUC value provides a single measure for Maxent to accurately identify presence points using a single threshold (DeLeo 1993), the choice of threshold value has been shown to significantly alter the projection of species range shifts (Nenzén and Araújo 2011). In this study, I used a ten percent training logistic threshold (TTP, where 10% of the occurrence data is assumed to suffer from errors) as opposed to a minimum training logistic threshold (MTP, where 0% of the occurrence data is omitted) because it more accurately reflects errors of commission (false positives). This was due to the fact that occurrence data was gathered over several geographical regions and time

periods where precision has probably varied (Rebelo and Jones 2010). Therefore, it is possible that the low level of current to future range overlap in *E. semicaudata* was due to an error of commission in Maxent that was contributing to a very high AUC value. This is not surprising considering that both *E. semicaudata* and *P. niger* had very few occurrence records to begin with (19 and 25, respectively), which may have increased the standard deviation in both current and future models.

Case Study for Certain Bat Species

In this study, I took a broad comparative approach, finding that the impacts of climate change on future bat species distributions may have greater implications for certain species. Now, I will take a focused look at patterns for a couple select bat species.

M. leibii is predicted to lose 9% of its range under future climate scenarios according to the ENMs presented in this study. Insectivorous bat species like *M. leibii* can serve as surrogates for lower trophic organisms (e.g., herbivorous insects or birds) by revealing the consequences of climate-induced disturbances in advance (Jones et al. 2009). As insectivorous mammals occupy higher trophic levels (characterized by increased dietary accumulation and metabolic capacity at higher positions in the food chain; Alleva et al. 2006), this suggests that asynchronous mismatches in resources for these bat species may increase as climate continues shift ecological processes. And, as phenological traits (the timing of important biological processes, such as mating and hibernation) are more commonly shifting to earlier dates than in the past (Radchuk et al. 2019), this may put *M. leibii* at a higher risk for extirpation as insect abundance declines.

A. jubatus is predicted to lose approximately 45% of its range in future climate scenarios according to the ENMs in this study (note that this does not also account for predicted habitat loss due to other anthropogenic factors). As the geographic range of *A. jubatus* is restricted to the

Philippines, the clearing of native forests in this region has also resulted in sharp population declines for *A. jubatus*, which rely on *Ficus* trees for food and diurnal roosting sites (Stier and Middelstein 2005). These anthropogenic disturbances, in addition to climate change, might further exacerbate population declines. With regards to forest ecosystems, previous studies reveal that the functional extinction of a key disperser may significantly affect plant community composition (Christian 2001), as successional trajectories may be disrupted following the loss of important pollinators and seed dispersers. This is especially pronounced in island ecosystems where food resources can be limited. Hence, the loss of a key player may irreparably alter forest dynamics, as evidenced by forests that are shifting to small-seeded vegetation as the primary dispersers are on the decline (McConkey and Drake 2006).

Elevation Change and Range Overlap

Elevation did not seem to influence range percent overlap between current and future climate scenarios ($p = 0.6935$). While research indicates that temperature and precipitation EGVs can significantly influence shifts over a larger geographic range for avian species (Tingley et al. 2012), there is currently a lack of consensus as to whether elevation is a significant predictor variable for mammal ranges. However, while the majority of bat species distributions were not influenced by elevation, for one species in the current climate (*T. hildegardeae*) and two species in the future climate (*M. harrisoni*, *P. ornatus*), elevation was the most important predictor variable. A possible explanation for this may be related to food availability along a latitudinal gradient (Remonti et al. 2009). Research surrounding the density of lowland and highland faunas in montane tropical bat species has found that the most significant variation in food assemblages is around 750m (Patterson et al. 1998), suggesting that trophic flexibility may ensure better survival for species living above this range (Schluter and Repasky 1991; Grant and Grant 1996).

Given the fact that these three bat species have different altitudinal limits and food requirements (*T. hildegardeae* is insectivorous and has the lowest current mean elevation [40 m], followed by the frugivorous *P. ornatus* [95 m] and the nectivorous *M. harrisoni* [328 m]), this suggests that elevation can serve as a crude surrogate for biotic processes that affect distributions when species interactions are not well understood or more data is not available (Cianfrani et al. 2011).

For the tropical bat species with the highest elevation (*L. nivalis*, 1576 m), precipitation of the wettest month (BIO13) contributed the most to predicting distributions in both current and future climates. A likely explanation for why elevation was not a significant predictor variable for a nectar-feeding bat species like *L. nivalis* may be that water availability on subtropical mountains is highest at mid-slope (where higher rainfall and runoff from steep slopes are at their greatest; McCain 2007) and this increased vegetation drives species occurrence. However, there may be other reasons why it may become increasingly difficult for higher elevation species like *L. nivalis* to expand their ranges northward. Research has revealed that unfavorable migration conditions are a primary driver of northward edge contractions in montane birds (Rushing et al. 2017), suggesting that populations of tropical montane bat species like *L. nivalis* may decline as a result of breeding constraints imposed by seasonal disruptions due to climate change. Furthermore, declining availability of preferred prey resources along a higher elevational gradient (where there is increasing ice and snow) can make it more difficult for some insect and plant species to survive, which limits food availability even further (Ruiz Olmo et al. 1998).

Limitations

There were some limitations in this study, particularly in regard to presence data and modeling parameters. While Maxent predictions are generally considered to be robust across all sample sizes (Wisz et al. 2008), modeling reliability was primarily limited by lack of suitable bat

species presence data (according to Wisz et al. 2008, $n = 10$ is considered a “low” sample size, while $n = 30$ and $n = 100$ are considered “medium” and “large” sample sizes, respectively). In order to avoid an over-simplistic representation of species ranges and create more useful maps to aid in management plans, future niche models would benefit from exact and abundant species occurrences which are necessary to predict the likelihood of a species’ presence or absence (Stebbins 1988; Barnhart and Gillam 2016). As for modeling parameters, I did not use a bias file, which may have contributed to some sampling bias resulting from over-representation of regions within occurrence data records (Phillips et al. 2009; Kramer-Schadt et al. 2013). Lastly, while I focused primarily on climatic and topographic variables for both current and future scenarios, studies suggest that vegetation type as well as habitat structure and heterogeneity are also considered to be predictors of species distributions (Curran et al. 2012; Linden et al. 2014; Weier et al. 2017).

Future Directions

Accurately forecasting future distributions of bat species will most likely involve a combination of improved modeling techniques and a broader understanding of dynamic species interactions as complex climate changes continue to disrupt ecological processes. For example, research suggests that using discriminant factor analysis (determining which EGVs most define niches for two species) to differentiate among cryptic (morphologically similar) bat species’ niches may help elucidate species-specific habitat requirements to aid in conservation efforts (Sattler et al. 2007).

Moreover, while several studies stress the importance of reducing collinearity among EGVs to increase model predictive accuracy (Phillips et al. 2009; Elith et al. 2011; Merow et al. 2013) there is some evidence that redundancy in EGVs does not significantly alter model

performance but does affect model transferability and environmental novelty (Feng et al. 2019). That is, Maxent is robust enough to parse through multiple linear variables, but the results should be interpreted with caution when assessing different time periods or geographic regions (as well as environmental conditions that are outside the range of normal variability).

In addition, distance to resources can be a useful metric for determining which species should be prioritized for conservation. This is especially true for dynamic foragers whose ranges span large areas (a few thousand square km) where uniform habitat suitability maps may be more difficult to create due to patchy and heterogeneous habitats (Rainho and Palmeirim 2011). Determining thresholds of available habitat suitability and assessing how many locations can potentially sustain bat populations will become important questions as climate change continues to shift these species upslope.

Lastly, it is important to consider that Maxent primarily utilizes realized niche (the actual set of conditions that a species experiences in its habitat) and that forecasting distributions solely based on temperature and precipitation excludes the idea that deforestation and other human-induced land use changes may alter niche dynamics in new and unforeseen ways (Sánchez-Cordero 2005). It is therefore important to take a more holistic approach in predicting distributions of threatened bat species by pairing niche theory with ecological functional processes in order to correctly ascertain which vegetative and climatic factors are most affecting distributions.

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