Monarch Butterfly (Danaus plexippus) Roost Site-Selection and Viability East of the Appalachian Mountains

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MONARCH BUTTERFLY (DANAUS PLEXIPPUS) ROOST SITE-SELECTION
AND VIABILITY EAST OF THE APPALACHIAN MOUNTAINS

By
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B.S. United States Military Academy at West Point, 2010
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(in Ecology and Environmental Science)

The Graduate School
The University of Maine
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The Monarch butterfly is a flagship species and pollinator whose populations have declined by approximately 85% in the last two decades. Their largest population overwinters in Mexico, then disperses across the eastern United States and Canada during April to August. Between September-December, the butterflies return south using two migratory flyways, one spanning the central United States and another following the Atlantic coast. They fly during the day and at night roost in large groups. Roosting habitat is essential to the continuation of the Monarchs’ migration, however, threats such as anthropogenic habitat disturbance and climate change potentially endanger sustainability of these habitats. The criteria that Monarchs use to select specific roost sites, and the landscape context where those sites are found, have received little study. I developed ecological niche models for the Atlantic Flyway roost sites using modeling algorithms, citizen scientist observations, and environmental variables that are known to affect Monarchs in the adult stage prior to migration. MaxEnt variable jackknifing identified proximity to surface water (Euclidean Distance to Coast, Lakes, and Rivers), elevation (Above Mean Sea Level), and vegetative cover (Land and Crop Cover Type) as the most important criteria. My model predicts 2.6 million ha of suitable roosting habitat in the Atlantic flyway, with
greatest availability along the Atlantic coastal plain and Appalachian Mountain ridges. These models can be used to help prioritize survey and conservation efforts for Monarchs in areas most suitable for their roosting. I developed two novel methods for validating the models: a smartphone application to engage citizen scientists, and peer-informed comparisons with Google Earth imagery. I conducted a vulnerability assessment of predicted suitable roost habitat, assessed the connectivity of the habitat with Morphological Spatial Pattern Analysis, used Zonation software to create a relative value ranking of the Atlantic flyway region for Monarch roost site conservation, and mapped areas of high conservation value in the flyway in regards to their current predicted vulnerability. Predicted suitable roost habitats occurring in coastal areas (1 million ha) were more vulnerable than those further inland (1.6 million ha), where they parallel the Appalachian Mountains chain. The majority (73%) of roosting habitat occurs within non-fragmented core patches, and many of these patches are within the average daily flight distance (45 km) of migrating Monarchs. Although the flyway contains 18.5 million hectares of lands in conservation management, there was little overlap between the areas of high conservation value for migrating Monarch butterflies and current conservation lands, with only 7% of predicted suitable roost habitat currently in conservation holdings. These findings suggest that conservation of the Monarch migratory phenomenon may benefit most from land management action outside of current conservation lands to promote roost habitat.
ACKNOWLEDGEMENTS

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CHAPTER 1

MONARCH BUTTERFLY (*Danaus plexippus* L.) ROOST SITE-SELECTION CRITERIA AND LOCATIONS EAST OF THE APPALACHIAN MOUNTAINS, U.S.A.

The Monarch butterfly is a flagship species and pollinator whose populations have declined by approximately 85% in the last two decades. Their largest population overwinters in Mexico, then disperses across the eastern United States and Canada during April to August. Between September-December, the butterflies return south using two migratory flyways, one spanning the central United States and another following the Atlantic coast. They fly during the day and at night roost in large groups. The criteria that Monarchs use to select specific roost sites, and the landscape context where those sites are found, have received little study. This makes conservation of this species difficult, as protecting these roost sites will support the continued migration of Monarchs. We developed ecological niche models for the Atlantic Flyway roost sites using modeling algorithms, citizen scientist observations, and environmental variables that are known to affect Monarchs in the adult stage prior to migration. MaxEnt variable jackknifing identified proximity to surface water (Euclidean Distance to Coast, Lakes, and Rivers), elevation (Above Mean Sea Level), and vegetative cover (Land and Crop Cover Type) as the most important criteria. We developed two novel methods for validating the models: a smartphone application to engage citizen scientists, and peer-informed comparisons with Google Earth imagery. Our model predicts 2.6 million ha of suitable roosting habitat in the Atlantic flyway, with greatest availability along the Atlantic coastal plain and Appalachian Mountain ridges. These models can be used to help prioritize survey and conservation efforts for Monarchs in areas most suitable for their roosting.
Introduction

Animal migration can be a dramatic phenomenon. Migratory species that spend most of their lives in a local area will, with some predictability, travel great distances often surrounded by conspecifics during their journey. This action is participated in by myriad taxa at variable scales, from blue whales (Abrahams 2019) and wildebeest (Musiega et al. 2006), to aphids (Ghosh et al. 2019) and jellyfish (Kaartvedt et al. 2007). These movements have drawn the attention of humans from the times of the Judeo-Christian Bible (Exodus 10:13-14) and Ancient Greeks (Aristotle 350 B.C.E.), and they continue to garner significant attention today (Kido and Seidl 2008, Oscan et al. 2009, Larsen el. 2020). There are many reasons why animals have evolved to migrate, and there are many associated challenges and hazards (Dingle and Drake 2007), which can be exacerbated by habitat loss and fragmentation. The challenge of conserving habitat for the survival and well-being of species increases when that species is migratory and requires suitable habitat over a greater extent (Gurarie et al. 2017). Compounding this challenge still further, migrants must navigate between the endpoints of their journey, which necessitates habitat connectivity (Xu et al. 2019) with suitable stop over habitat for rest and nourishment (Schaub et al. 2008). Implementing conservation actions is made more complex when the migration spans geopolitical boundaries, where conservation goals, priorities, resources and methods may differ between governments (Kull et al. 2007).

The needs of migrants, like all species, can be described by their fundamental ecological niche, which describes the biotic and abiotic suite of resources that define its function and survival within the biosphere. The scope and specificity of niches varies among species, as does the sensitivity to changes in factors that define them. Some species can survive in only a narrow set of conditions, whereas others thrive in more diverse environments (Hutchinson 1957). While
a migrating species’ niche describes the full suite of habitat conditions needed before, during, and after migration, the specifics of those conditions may vary among its starting and ending points, the route it takes between them, and the stop over locations it uses along the way (Gurarie et al. 2017). A species’ ecological niche reflects the species’ geographic range, resource use, and its resilience to environmental change (Ferrer-Sanchez and Rodriguez-Estrella 2016).

Ecological niche modeling accounts for both deterministic and stochastic factors that affect a species’ use of its niche (Chase and Myers 2011). These models represent algorithms that relate environmental conditions at a species occurrence location to predict the probability of presence of the species at other locations given the environmental conditions at that location (i.e., they predict additional areas where an animal is likely to be found based on conditions in the areas it has been confirmed to inhabit). This approach to identifying potentially suitable habitat for the focal species often is more cost effective than conducting on-ground inventories of areas with suitable environmental conditions. In addition, this approach can be used to increase efficiency of ground surveys by directing observers to potentially suitable habitat. It is often useful as a first step in identifying suitable habitat, particularly for cryptic species or those that traverse large areas of the landscape. Migratory insects are challenging to follow, as many are too small for transponders (Fisher et al. 2020). Ecological niche models are a possible alternative for studying their migratory needs.

Monarch butterflies are a flagship species whose brilliant coloration and dramatic migration have helped mobilize generations of citizen scientists to assist in monitoring and conservation (Diffendorfer et al. 2013). They are also a well-recognized pollinator species throughout most of the North American continent (Robertson 1928, Tooker et al 2002). The Monarch’s adult migratory life cycle commonly is partitioned into three phases: 1) overwintering
in large aggregations, 2) dispersal across the breeding range in spring and summer, and 3) migration back to the overwintering grounds in fall (Urquhart 1960). There are two primary migrating populations of Monarchs in the United States - a western population that overwinters in California, and an eastern population that overwinters mostly in Mexico. The eastern population includes a population ("central") that occurs predominately in the plains and Midwest (Urquhart and Urquhart 1978), and a population that crosses over the Appalachians ("Atlantic") and travels along the eastern seaboard (Howard and Davis 2008). North American migrating Monarchs traverse three countries and dozens of U.S. States; thus, protection of this migratory phenomenon requires a cooperative effort that spans domestic and international borders, a collaboration that Canada, Mexico, and the USA are committed to (Obama et al. 2014).

Annually, Monarchs produce several generations per year, beginning with adults that leave wintering grounds in Mexico, and they produce successive generations migrating northward from March to August. The season’s final generation (whose terminus spans the U.S.-Canada border) enters reproductive diapause in late summer (Urquhart and Stegner 1966, Herman 1981) and travels south (Urquhart and Urquhart 1978). Individuals of the eastern population that start at the northern edge of the breeding range travel in excess of 3,000 km southward to reach their wintering grounds in the Oyamel Fir (Abies religiosa) forests of southern Mexico by late fall (Urquhart and Urquhart 1978). Monarchs fuel their journey by feeding at flowers, often exhibiting increased nectaring time in Texas, where they accumulate reserves for the winter (Brower et al. 2006). At the end of this migration, the butterflies reach southern Mexico, where they spend the winter and become the following spring’s first northward dispersing generation (Urquhart and Urquhart 1978).
Current niche models describe the Monarch’s ecological niche during the breeding season (Batalden et al. 2007) and the overwintering period (Oberhauser and Peterson 2003). However, similar models to describe the species’ southbound fall migration habitat have not been developed. This represents a major gap in knowledge that needs to be filled. During this phase of the Monarch’s life history, they travel diurnally, averaging 45 kilometers per day (Brower et al. 2006), and they roost on trees, shrubs, or snags in gatherings of up to thousands of individuals (Davis et al. 2012). The criteria Monarch butterflies use for selection of these roost areas are poorly characterized, although reported sites tend to have woody vegetation on which the Monarchs spend the night (Davis et al. 2012). Roost sites have been documented in much of the Monarch’s migration flyway, except for the southeastern United States. Fewer than 0.33% of monarchs tagged in the Atlantic flyway are recovered at overwintering sites (Howard and Davis 2008). Similarly, only approximately 1% of tagged individuals in the central population reach wintering grounds (Howard and Davis 2008). Climate change is one of many factors challenging successful Monarch migration in the modern era. Warming temperatures are causing many Monarchs to begin their northward migration sooner than milkweed (Asclepias), the genus they oviposit on (Taylor 2019), is available in the spring. Additionally, warmer temperatures and increasing drought events contribute to accelerated drying of nectar sources during the fall return (Taylor 2019). These changes affect the entire eastern population, however, a series of recent models suggest the central population is suffering more adverse consequences, meaning the smaller Atlantic population may be increasingly important for the species persistence (Taylor 2019).

The fall migration is a critical stage in the Monarch’s life history (Howard and Davis 2008). Although the species distribution across the United States appears stable (Howard and
the number of butterflies reaching the overwintering sites in Mexico has dropped by approximately 85% since monitoring began in 1995 (Ries et al. 2015). An initial step toward identifying causative mechanisms of this decline and developing targeted management to increase Monarch populations is to identify important habitat during all life stages, including locations and characteristics of roosting habitat used during migration. While some larger roosting areas, such as Cape May, New Jersey, are well documented (Walton et al. 2005), many areas suitable for roosting are less well known (McCord and Davis 2010). We addressed this knowledge gap with spatial models developed to predict landscape suitability for Monarch butterfly stopover habitat east of the Appalachian Mountains. Our models identify characteristics of the landscape context of known roost sites, and they predict the probability of a landscape being suitable based on environmental conditions throughout the Atlantic Flyway region. We expected to find landscapes with high probability of suitable roost areas distributed in patches across the flyway, representative of the highly dispersed nature of migrating Monarchs (Urquhart 1960). We identified areas with predicted suitable environmental conditions to target future surveys to improve knowledge about Monarch stopover habitat used during migration. Subsequently, we evaluated our models’ predictive ability with model assessment tools that engage citizen and peer scientists.

Methods

Monarch Occurrence Data

We developed a species distribution model (SDM) for Monarch stopover habitat, which required known occurrences of roost sites, and environmental variables describing relevant conditions. We sought Monarch butterfly locality data from 14 citizen science databases, excluding data from eight databases that did not report relevant information for our study or that
used collection methods that did not meet our standards for data accuracy and relevance (Table 1). Specifically, we omitted databases focused on regions outside of our study area, non-adult butterflies, and one database that had insufficient spatial precision (owing to sightings reported to the geographic center of the local zip code). The remaining six databases provided 145,292 occurrences. We pruned these records to remove reports of eggs, caterpillars, chrysalis, or individual adults nectaring or flying during the day, thereby retaining only records indicative of roosting behavior. We limited the geographic extent to only those reported in the Atlantic Flyway, which spans the area east and inclusive of the western Allegheny Plateau and the southwestern Appalachians. We excluded records from Florida, where there is a permanent, non-migratory population that could not be distinguished from those that migrate through the state. We retained sightings reported only during August 15 - December 31, the primary period for fall migration. We retained sightings with 12 or more Monarchs or that occurred between 1800 and 0800 hours. Observations of large numbers of Monarchs in the evening or early morning are indicative of roosting (Davis et al. 2012). Finally, we reviewed comments and removed records with questionable validity (e.g., captive Monarchs, individuals expressing doubt regarding their identification) (Fig. 1).

The remaining 1,052 Monarch roost site observations comprised the occurrences dataset for our SDM development. We accounted for location sampling bias found in citizen science data (Geldmann 2016) with a “bias file.” The bias file is a raster layer developed to represent sampling intensity throughout the study area (Stolar and Nielsen 2014). It interpolates a value surface given the number of total observations around a focal pixel and identifies areas with the greatest density of observations. The bias file is used to weight sightings of the target species, so that areas with fewer total observations are considered more heavily in training the model. Our
bias file contained observations of all adult Nymphalidae (the family that includes Monarchs) reported to iNaturalist, for a total of 9,394 reported observations. We assumed that if an observer reported any member of Nymphalidae, they also could have recognized and reported an observed Monarch.

**Environmental Variables**

We selected 16 environmental variables that are known to affect the Monarch or similar taxa in various life stages, or that influence Monarch behavior at reported roost sites, and that are publicly available as geospatial raster data (Table 2). Agriculture, depending on the type, can create nectaring opportunities (Smeesaert et al. 2019) or poison butterflies through overuse of pesticides (Saunders et al. 2017). Migrating Monarchs bask in the morning prior to beginning flight (Urquhart 1960), and aspect and solar radiation affect the amount of sunlight a butterfly can receive while basking. Human-created development and roads drastically changes the landscape, which can create both hazards (Phillips et al. 2019) and benefits (Lewis et al. 2019), while conservation areas are managed specifically for the protection of ecological processes (Muir 1901).

Migrating Atlantic Flyway Monarchs traverse two primary flight regions paralleling the Appalachian Mountain range (Howard and Davis 2008), suggesting that high elevation and steep slopes may create a barrier. Monarchs are known to roost on trees (Davis et al. 2012); therefore, we included land cover categories to account for dominant vegetation type. Monarchs are exothermic (Urquhart 1960), so ambient temperature has a strong effect on metabolic properties (Wong et al. 2016). They are known to delay flight during storms (Ries et al. 2018), so we included precipitation, which can slow their movement. The largest reported roost sites are along coasts (Walton et al. 2005), and roosting Monarchs are also reported near freshwater (Davis et al.
2012), so we included the distance to lakes, rivers, and the Atlantic Ocean. Because Monarchs use wind currents to facilitate flight (Gibo 1986), we included estimates of average wind speeds. We projected all data in the WGS 1984 map datum with a data grain of 35 m, the greatest precision in the available environmental rasters (ESRI, Inc., ArcMap version 10.5.1). We constructed a correlogram and discarded variables with a correlation > 0.70 (Table 2). We retained temperature (instead of precipitation), because solar radiation also was correlated with precipitation. We retained ecological integrity instead of roads to obtain a more complete estimate of habitat heterogeneity (i.e., ecological integrity is a quantitative measure of roads, buildings, light, and sound pollution). We developed a model with the remaining variables to assess the comparative predictive value of each, and we discarded any of those variables with a training gain of ≤ 0.5% (Table 2), which is an intentionally low threshold to favor inclusivity at the cost of parsimony.

Algorithm Selection

We developed habitat suitability predictions with two models: the Maximum Entropy Modeling algorithm (MaxEnt) (Phillips et al. 2006) and the Genetic Algorithm for Ruleset Prediction (GARP) (Stockwell and Peters 1999). MaxEnt assigns likelihood of suitability to pixels such that it maximizes entropy within the constraints shown by the known distribution of the species (Phillips et al. 2006). GARP creates a series of yes/no suitability rules which it stochastically cycles, retaining and developing on those rules that maximize training gain (Stockwell and Peters 1999). We selected MaxEnt and GARP from a variety of modeling algorithms (i.e., Random Forests, BIOCLIM, Artificial Neural Networks, support-vector machines) owing to the fit with our modeling needs, including demonstrated use in ecological niche modeling with occurrence data and lack of true absence records (Tarkesh and Jetschke
Citizen science data, while plentiful, commonly lack true absence data for the target species (Stolar and Nielsen 2014). Ecological niche models compare where a species is found with where it is not, necessitating an approach for addressing data absence. MaxEnt balances sensitivity versus specificity (Ashraf et al. 2017), whereas, GARP tends to over predict suitable habitat, increasing sensitivity at the cost of decreasing specificity (Ashraf et al. 2017). GARP has been used to model the spring, summer, and winter habitat of Monarch butterflies, thus, our GARP model is complementary to these previously developed distribution models (Batalden et al. 2007, Oberhauser and Peterson 2003) by targeting a different life stage (i.e., migration) and geographic location (i.e., Atlantic Flyway).

### Running Algorithms

Our final MaxEnt model included 13 variables (Table 2) with three cross validated replications, four threads (matched to number of processor cores to maximize performance), a complementary log-log output format, variable jackknife evaluations, a 25% random test size (meaning the model is trained on 75% of the data and internally validated on the remaining 25%), a convergence threshold of 0.00001, 500 maximum iterations, and allowed for partial data. We used default settings with the exceptions of increasing the number of threads to four to match our processor cores, adding jackknives to test variable importance, including test sites, and performing multiple replications. Exceeding three replications was not feasible owing to large dataset file size filling our computer’s memory, and insufficient storage available beyond this number. We used the bias file in this algorithm run. We ran the GARP model in openModeller Desktop Version 1.1.0 ((http://openmodeller.sourceforge.net/) with the same observations and variables, and we used the default settings of a 0.010 convergence limit, a maximum of 400
iterations and 50 rules, and 2500 test points. We did not use a bias file with the GARP model, as this algorithm is designed to select pseudoabsences from the background (Stockwell and Peters 1999).

Comparing Models

We identified areas of agreement and disagreement between the models by subtracting the MaxEnt output from the GARP output, where zero indicated perfect agreement and (+/-) 100% indicated maximum disagreement. We assessed the quality of the individual models with Receiver Operating Characteristic (ROC) Curves, True Skill Statistic (TSS), and the aforementioned assessment of the algorithm’s normal sensitivity and specificity levels (Ashraf et al. 2017). ROCs assess the model’s sensitivity versus specificity over the full range of probability values (Shabani et al. 2016), while TSS assesses sensitivity versus specificity at a given threshold probability value. In our comparative assessment, we favored MaxEnt over GARP, as only MaxEnt used the bias file, which suggests that GARP output likely included affects from sampling bias.

Determining Best Suitable Habitat

The MaxEnt algorithm represents the best balance between sensitivity and specificity (Ashraf et al. 2017). In developing our assessment of best suitable habitat, we used all areas with a MaxEnt predicted suitability rank of $\geq 0.70$. Since the output is a percent likelihood of suitability, bounded by 0 and 1, we selected this threshold to balance thoroughness and over reporting. We combined model predictions from MaxEnt and GARP to develop a composite suitability map. We identified areas with GARP-predicted suitable habitat $\geq 0.70$ that also scored
≥ 0.50 in the MaxEnt model, incorporating the greater sensitivity of GARP while using the greater specificity of MaxEnt model to reduce Type I errors resulting from GARP’s lower specificity.

**Model Validation**

In addition to the in-model validation provided by the 25% test size, we designed two approaches for model validation. First, we created an application for smartphones (https://umaine.edu/mainecoopunit/monarch-model-validator/) and distributed the details of this application to citizen scientists through a variety of conservation organizations and ecological NGOs, including the United States Forest Service, U.S. Fish and Wildlife Service, and National Park Service, headquarters offices of State Parks and State conservation agencies within our study area, the Sierra Club, The Nature Conservancy, the Appalachian Mountain Club, as well as numerous zoos, museums, aquariums, botanical gardens, and butterfly gardens. We provided flyers and posters to these organizations to distribute for recruiting butterfly enthusiasts to download the app and follow the instructions to complete a survey (Supplemental Material [SM] 1) about habitat conditions for roosting Monarch butterflies. We also distributed the Monarch Model Validator website link (link provided above) on the EcoLog listserve (https://www.esa.org/membership/ecolog/) to recruit professional ecologists to assist with model validation.

Second, we used images of known roost sites and habitat characteristics identified by the MaxEnt model to train four peer scientists to view Google Earth (https://www.google.com/earth/) aerial images and interpret suitability of the focal area for Monarch butterfly roosting habitat. We randomly selected 1000 locations within the modeled extent, and instructed the reviewer to evaluate and rank in 10% increments (with respect to
habitat suitability for roosting Monarchs) the area in a 100 m radius circle centered on the random location. We provided Google Earth aerial imagery captured at reference locations as a guide for interpreting habitat suitability. The reviewers also approximated the amount (%) of the area enclosed in the 100-meter radius circle in each of four land cover categories: Urban/Suburban contained a large amount of buildings; Agriculture contained evidence of row crops or tillage; Forest contained large woody vegetation; and Pasture contained short or non-woody vegetation.

The reviewer’s assessment of the focal area included only the conditions immediately (within the 100 m radius) around the given site, whereas the model variables also estimated the Euclidean distance from the focal cell to water. Therefore, we instructed reviewers to measure the Euclidean distance from the focal point to the nearest fresh water source and to the Atlantic coast. We created linear models of the variable response curves from MaxEnt for distance to freshwater and distance to coast, with the suitability value at 0 distance as the X-Intercept and a slope down to the minimum suitability value at the model’s greatest distance, such that distance to freshwater was estimated as

\[ Y = (-2.1875 \times 10^{-6}) \times X + 0.65000 \]

and the equation for distance to the coast was

\[ Y = (-1.2857 \times 10^{-6}) \times X + 0.90000 \]

such that Y equals the approximate suitability value at a given distance. We assigned a fresh water and coast suitability rating to the validation points with these linear models. We scaled these estimated suitability ratings to the importance assigned to these variables by MaxEnt, scaled the peer scientist reviewer ratings to the value of the remaining variables, and then
summed the reviewer assessed suitability (R), the Euclidean distance to freshwater (F), and the Euclidean distance to coast (C), for the final scaled reviewer assessed suitability score (S):

\[ S = (R \times 0.40) + (F \times 0.15) + (C \times 0.45) \]

We compared the scaled suitability (S) to only the MaxEnt output (i.e., exclusive of the GARP output), as both the S and the MaxEnt output provided a predicted suitability value as a percent, whereas the combined MaxEnt and GARP model represents only Boolean values of “meets” or “does not meet” the threshold value of \( \geq 0.70 \). We compared the S to the MaxEnt model predicted suitability value by subtracting the model prediction from the S at each evaluation point and tabulating the frequencies of differences. We also performed linear regressions of the S versus MaxEnt predictions for each of the primary land cover types used for classification by our peer scientist reviewers to evaluate differences between the interpretations and the reference land cover type suitability.

**Results**

**MaxEnt and GARP Models**

Model performance of the GARP and MaxEnt models was similar. The GARP model exceeded the MaxEnt model in AUC (0.775 GARP versus 0.667 MaxEnt), however, with a TSS threshold of 0.70, the MaxEnt model (0.049) outperformed GARP (0.024) (Fig. 2). The larger AUC for GARP reflected a more rapid increase in sensitivity at smaller values of 1-specificity (i.e., fractional area). The MaxEnt model predicted a narrow (generally \( \leq 1 \) km) area of suitable land (defined as suitability \( \geq 0.70 \)) parallel to the Atlantic coast, with scattered patches of habitat distributed inland adjacent to the ridges and valleys of the Appalachian Mountains (Fig. 3). The GARP model predicted a wider band of suitable land along the coast (generally \( > 10 \) km), and in
patches around major urban centers (Fig. 4). Both models predicted more suitable habitat in the northern portion of the Atlantic Flyway. The greatest differences in model predictions occurred in the coastal plains, where GARP predicted more suitable habitat, and along the Appalachian Mountain ridges, where MaxEnt predicted greater habitat suitability (Fig. 5, Table 3). Overall, MaxEnt predicted more areas in greater suitability than GARP, however, the prediction values for both models were within 25% for the majority (77.3%) of cells (Fig. 6). GARP had a large drop off in the amount of land for each suitability value beyond 0.4, while MaxEnt had a more gradual decrease in amount of land per suitability value (Fig. 6). Although there was wide disparity in predicted suitability among states (Table 4), most of the Atlantic Flyway region was predicted unsuitable (<0.70) for roosting habitat, including 97.5% for MaxEnt and 99.3% for GARP. For example, in Maine MaxEnt predicted that 5.4% of the land area has 61-70% probability of being suitable, whereas GARP predicted 2.6% in this suitability range. In total, we identified 2.6 million hectares (2.9% of the study area) of land area predicted to be suitable for Monarch stop over and roosting during migration in the Atlantic Flyway (Fig. 7). The predicted suitable habitat along the coast curves westward in Georgia, and in the Appalachians it curves westward in the Tennessee River Valley (Fig. 8).

Model Variables

Proximity to coastal habitats accounted for 44.8% contribution to the MaxEnt model with a permutation importance of 27.7%. Other important variables included the proximity to other surface water (e.g., lakes and rivers; 13.6% contribution, 18.7% permutation importance), elevation above mean sea level (8.5% contribution, 10.3% permutation), and presence and type of agriculture (e.g., corn and wheat ranked low, while orchards and clover ranked high; 7.8% contribution, 8.4% permutation) (Table 2). Areas adjacent to the Atlantic coastline were rated as
suitable (approximately 0.90, with other variables at median values along the coast), with a marked decline in suitability immediately away from the coast and followed by a more gradual decline moving inland (Fig. 9A). Areas closer to lakes and rivers were ranked as more suitable (approximately 0.65, with other variables at median values) (Fig. 9B), however, freshwater wetlands showed greater suitability at greater distances from the wetland edge. There was a peak in elevation suitability at approximately 1000 meters above mean sea level (Fig. 9D). Land cover types such as fields of crops, particularly orchards, clover, and alfalfa, showed peaks in contribution to the model (Fig. 9C), whereas other land cover types contributed less. Areas with human influence on the landscape had greater suitability for Monarchs (Supplemental Material 1), as did areas managed for conservation (SM2). Areas with moderate to strong prevailing winds (>6.5 m/s), low annual solar radiation (< 1750 kWh/kWp), and moderate to high air temperature (>10° C) were also more suitable (SM2). South facing slopes were more suitable than north facing ones, with a similar but less pronounced divergence that favored west facing slopes over those that are east facing (SM2).

Model Validation

Approximately 1/3 of the contacted organizations indicated interest in assisting with distribution of information about the validation application (app), and we distributed over 100 posters and 3,000 tri-fold brochures. We received approximately 200 requests for more information about use of the app, and we received invitations from local media, schools, libraries, and NGO meetings to present the app. Despite the widespread interest, we received an insufficient number of completed surveys to inform validation with this method.

In the Google Image-based visual evaluation of roost habitat suitability, the peer scientist reviewers rated land suitability slightly less than the model predictions. The average likelihood
for evaluator predictions of suitability across all points was 32.6%, compared with 34.9%
predicted by the MaxEnt model and 28.6% for the GARP model. Since the MaxEnt model was
our primary model and we used the GARP model only to round out areas that the MaxEnt model
may have missed, we performed all comparisons to the MaxEnt model. The scalers for distance
to freshwater and coast adjusted the evaluator ratings to an average likelihood of suitability
predictions of 51%. The scaled evaluator predictions fell within 30% of the model likelihood of
suitability predictions 75% of the time, and within 50% of the model likelihood of suitability
predictions 96% of the time (Fig. 10). Only approximately 2.38% of the rater assessments were
predicted by the raster scores, however for every primary land cover type except agriculture
there was a statistically significant (p<0.05) relationship between the two (Fig. 11). We visually
compared the data and found little variation among evaluators.

Discussion

Our spatial predictive models, developed with citizen scientist reported observations of
roosting Monarchs, estimate the probability of suitable Monarch butterfly roosting habitat
occurring throughout the Atlantic migratory flyway to inform habitat conservation planning for
Monarch butterflies. The predicted suitable habitat is clustered along the coast and through the
Appalachian Mountains. This suggests there may be two migration routes flown by the
Monarchs in the Atlantic Flyway, a study that tracks individual Monarchs could determine if this
is true or if there are individuals moving back and forth between the coast and the ridges.
Migratory species require a variety of habitats distributed and connected across large extents to
fulfill their needs through all life stages (Gurarie et al. 2017), as well as suitable stop over habitat
for resting and refueling during migration (Schaub et al. 2008). Identifying where stop over
habitat occurs requires accurate and current spatial data spanning the breadth of migration, and at
a sufficient spatial resolution to detect the environmental stimuli to which individuals respond. Our models predict that most (>97.5% of the region, per MaxEnt) of the Atlantic Flyway is not suitable for use as stop over habitat, highlighting the importance of strategic conservation planning that facilitates Monarch butterfly access to suitable habitat as they navigate through the Flyway during their southward migration.

**Model Output**

Our model predicted that habitat suitable for Monarch roosts fell within two primary areas, one that encompasses the Atlantic coastal plains and the other along the ridges of the Appalachian Mountains. These areas are nearly adjacent in and around New York and Pennsylvania, and they diverge southward. Our model does not reflect temporal changes in predicted roost habitat suitability during the migratory season, so it is unclear whether these areas represent temporally distinct flyways. Additional study to track movements of individual Monarchs may reveal whether they move between these areas and how use changes over time (Fisher et al. 2020). Reported sightings have associated dates, however they are not tied to specific Monarchs and were therefore are not suitable for this purpose. The well-documented pattern of fewer reported roost sites in the southern regions of the Atlantic Flyway (Howard and Davis 2008) may be explained in part by our model prediction of a narrowing of suitable roost habitat to a navigation corridor through the Tennessee River Valley (Fig. 8), which offers an important area for further study.

The MaxEnt model identified more land with greater predicted suitability compared to the GARP model, contrary to our expectations given that GARP is known to over-predict (Ashraf et al. 2017). This may reflect differences in how the models process data. MaxEnt directly assigns likelihoods of suitability to the pixels based on the range of conditions present at
those locations such that it maximizes entropy within the constraints shown by the known distribution of the species (Phillips et al. 2006). The GARP process creates a series of rules with binary yes/no suitability values and then stochastically cycles rules and retains those that maximize training gain. After each run a binary grid is created, and the average of these grids is the likelihood of suitability (Stockwell and Peters 1999). In discarding rules, GARP is selectively retaining those that affect the largest areas and stretching the area around these locations to capture the edge of the range (Tarkesh and Jetschke 2012). Other factors contributing to differences in the model predictions are related to the scale of individual Monarch roost sites, which is much smaller than the scale describing the criteria that identify ideal habitat conditions for the species, as well as the transient use of much of the habitat (Davis and Howard 2012). For example, GARP did not identify the Appalachian ridgeline area predicted by MaxEnt to be highly suitable habitat.

There are small areas separated from the coastal plains, where the majority of suitable land predicted by GARP is found. Additionally, a larger AUC value indicates a model is better at predicting true positives and true negatives, suggesting that GARP produced a better model (Norton and Uryasev 2018). However, the GARP model building process does not incorporate a bias file, which would reduce the influence of over-sampled locations (e.g., near populated areas with abundant citizen scientist reports). In fact, densely populated areas are discernable in the GARP model map (Fig. 4), suggesting that the improved predictive power reflects modeling sampling bias rather than reliable relationship of Monarch observations and habitat variables. Finally, in areas where GARP did find likely suitable habitat, it predicted wider regions (e.g., 10 times as broad a swath along the coast), suggesting less precision. This is further shown by the way in which lakes and rivers were ranked by the models. Areas near freshwater were ranked
highly, although monarchs are not an aquatic insect. MaxEnt recognized this, and ranked lakes and rivers as low suitability. GARP confounded the high suitability of areas near freshwater with the water itself and ranked lakes and rivers as high suitability. In contrast, the slightly larger TSS score for the model produced with MaxEnt, and the ability of the software to use data at a finer scale, indicates a more conservative prediction resulting in less area of suitable habitat in the flyway. In species distribution modelling, both MaxEnt and GARP are used primarily to identify 1st order habitat usage (Ashraf et al. 2017), while our roost model focuses on 3rd order habitat usage (Johnson 1980). The functionality of the models is based around recognizing patterns in areas around the input occurrence. As long as the input data are limited to only the relevant habitat usage, the output suitability will be limited to the same. Our study is not the first to use species distribution models specifically to find roost sites (Fuller et al. 2018), but this usage is rare enough that no studies exist to compare model performance at this level. Our application implies MaxEnt may offer greater precision in analyzing this inherently finer scale.

Despite differences in the algorithmic approaches and differences from the regional perspective, however, the models generally predict similar Monarch roosting habitat suitability on a cell-by-cell basis across the study area. Given the small proportion of the region that is predicted to be suitable by both modeling approaches (2.5% for MaxEnt and 0.7% for GARP), agreement at the pixel scale is noteworthy, and it provides actionable information to aid resource managers in prioritizing roosting habitat conservation at the local scale.

**Characteristics of Migration Habitat**

Animals respond to habitat across many scales. They may view wide-scale landscape features available to them in selecting movement corridors, and decide to stop based on preference for more specific conditions they encounter along the migratory route (Pickens et al.
21). Many migrating animals follow along major landmass features, such as a coastline, which may provide navigation reference (Read 2007) and create thermal air currents to facilitate flight (Bohrer et al. 2012). Atlantic Flyway Monarchs appear to also follow the coast in their southward flight path. In some instances, they may be carried to the coast by strong winds, which potentially creates a hazard if they are blown out to sea, as they are unlikely to survive traveling over the open ocean (Alerstam and Pettersson 1977). Mountain land masses can aid and also obstruct movement of migratory animals (Aschwanden et al. 2020, Ainslie et al. 2014). For example, the peak in roosting habitat suitability for migrating Monarchs at 1000 meters above mean sea level may indicate that Monarchs following along the Appalachian Mountain ridgelines benefit from thermals as well as the navigational aid provided by the mountain range. Monarchs, however, are not believed to cross back and forth across the mountain chain (Howard and Davis 2008). Therefore, it is likely something is preventing them from flying over the tops of the mountains. Although Monarchs are capable of flying as high as 4 km, their normal top altitude during migration is approximately 1 km (Gibo and Pallett 1978). This matches the peak in elevation for the ridgelines Monarchs follow, implying that the maximum elevations may limit crossing the range. Our model prediction of a band of suitable roosting habitat along the Appalachian Mountains at 500-1000 m AMSL matches anecdotal observations of Monarch butterflies migrating along ridgelines (Journey North 2019).

Our models predicted greater habitat suitability near open bodies of fresh water, but interestingly not in proximity to palustrine wetlands. This result mirrors previous studies of Monarch roosting behavior (Davis and Nibbelink 2012). Monarchs are believed to use polarized light to assist in navigation, so the high polarity of light which reflects off the surface of the water may attract them (Reppert et al. 2010). There may also be more nectar sources near water,
and open riparian habitats may facilitate movement along the shore. In contrast, forested and scrub-shrub palustrine wetlands may offer poor roosting habitat owing to dense vegetation that obstructs flight. Our models identified land near conservation areas to have a greater likelihood of suitability than the land actually within these areas. The peak in suitability was adjacent to these managed lands, potentially suggesting that easy accessibility to both managed and unmanaged areas provides a balance in forage and roosting habitats. Agricultural lands such as orchards, alfalfa, and clover fields and developed land with horticultural plantings offer nectar sources in addition to a navigable landscape for a butterfly. Although this habitat association mirrors findings for butterfly species worldwide (Tam and Bonebrake 2016), it may also reflect the citizen science dataset sampling bias of opportunistic sightings. More people live in areas that are developed, and therefore more sightings are reported in those areas. Including a bias file, as we did with development of our MaxEnt model, is intended to minimize this effect (Stolar and Nielsen 2014), and our model validation process also examined effects of spatial sampling bias in the model. Additional scientifically rigorous sampling, particularly in areas that are poorly represented in citizen scientist databases, will improve our understanding of Monarch habitat use during migration.

The greater suitability of south facing slopes may reflect the Monarch’s need to bask before beginning morning flight (Urquhart 1960), as well as provide areas where longer daily flight periods are possible. Additionally, warmer air increases evaporation, and the greater suitability at higher temperatures may be related to decreased relative humidity. Monarchs usually avoid the hazard of flying during storms (Ries et al. 2018), and thus they are likely to roost longer in areas with low solar radiation as this is often an indication that there is more
cloud cover. The greater suitability of areas experiencing greater average wind speeds suggests that Monarchs are efficient migrators that can conserve energy by riding southward on the wind (Chapman et al. 2010).

Our models predict conditions that are likely to be suitable based on conditions at known occurrences, however, they do not demonstrate causality. Furthermore, these models are static. They do not incorporate adaptability as a function of physiological processes. Additional study to increase our understanding of habitat requirements during migration and effects of habitat condition on survival as Monarchs navigate to the overwintering sites in Mexico will enhance effectiveness of conservation actions for the species. Additionally, Monarch sensitivity to seasonally changing habitat conditions during the southward migration is poorly studied.

**Model Validation**

Initial responses from conservation organizations solicited to distribute our Monarch Model Validator App suggested there would be widespread interest in the app, however, we received few submissions with usable data. We attribute this problem to two issues. First, we received inquiries indicating that users were not accessing the web-available instructional material prior to using this application as they were directed. Engagement may have been greater if instructions had been accessible within the App. Second, users may have been discouraged by the length of the survey. Effective engagement of citizen scientists requires a simple survey of reasonable length with clearly understandable questions (Bonney et al. 2009). Most responses to our survey were incomplete or reported observations that were not relevant to the model validation (e.g., caterpillar or chrysalis observations). Nevertheless, we are encouraged that there was interest in the citizen science community to assist with model validation broadly. Evaluating model performance is an important part of model development (Mouton et al. 2010). Although
successful models are useful, none are perfect (Box 1976), and relying on untested models can lead to mistakes and wasted resources (Cohen et al. 2019). With model validation, a more accurate model increases the likelihood that actions based on the model’s predictions will be correct (Eddy et al. 2012). Although many models developed from citizen science data have been validated (Nagy et al. 2012) and archived citizen science data have been used to validate models (Spellman and Mulder 2016), there are few examples of engaging citizen scientists in model validation, directly. Citizen scientist interest in Monarch conservation reflects recent trends in pollinator conservation (Senepathi et al. 2015) and the growth of citizen science opportunities (Kullenberg and Kasperowski 2016). Modifications to the App to improve usability in this and other similar applications will likely broaden its use in model validation (Malthus et al. 2020).

We validated our model with peer review of web-available imagery. While on-the-ground surveys may be ideal, the broad geographic extent of our study made on-site validation untenable. Photo based model validation is an appropriate alternative to site visits, as long as potential errors attributable to content and image resolution are addressed (Fischer et al. 2017). Despite a small spread in evaluation scores reported by individual reviewers, when scaled among reviewers the scores indicated similar trends: locations predicted with greater suitability by the model were also ranked more suitable by the reviewer, albeit with a small slope and much variability. Interpretations of agricultural habitats were more variable, reflecting uncertainty in distinguishing between fallow and planted agricultural fields in the Google Earth aerial imagery. Land cover and land use can be dynamic; interpretation error may be introduced in model validation when there is a temporal mismatch between data used in model validation and those used in model creation (McRoberts et al. 2018). The observations of Monarch roost sites used in model development came from a nearly 20-year time period (1998-2017), whereas the images
reviewed to validate the model were more recent (2010-2019). Spatial data context also can introduce differences in model predictions, which are pixel-focused, versus human visual assessments, which incorporate the pixel setting into the interpretation. This difference in scale between the operation of model variables and what reviewers can see influences the comparative findings (Fensham and Fairfax 2007). For example, the evaluators identified more surface water compared to the model predictions, likely because the reviewers could zoom into images at a finer scale (e.g., sub meter pixels) than available in the spatial data that informed the models (e.g., 35 m pixels), and the reviewer could interpret the imagery in the viewable context. Additionally, the model included data layers for lakes and rivers, however, the evaluators also identified other water features that were too small for inclusion in the layers for environmental data such as vernal pools, septic ponds, and swimming pools. Proximity to open bodies of fresh water was an important variable in our models, and greater amount of freshwater area resulted in greater suitability, explaining the higher suitability average from the reviewers as compared to the model. Monarchs are known to roost near water (Davis and Howard 2012), and many other species of butterfly are also found near lakes and rivers (Fernandez 2017). Incorporating finer resolution hydrography data into model development may have resulted in additional predictions of suitable habitat that were not detected with the currently available spatial hydrography data.

The land cover classes we used were not classified for their value to pollinators specifically. Land cover classifications are created for a particular purpose and geographic extent. Categorizing land cover types into classes contributes to omission and commission errors (Sokal 1974). Ideally, we would develop a land cover map that is partitioned into types valued by migrating Monarch butterflies and similar species, and that map would inform the model.
Our validation methods, while falling short of true on-the-ground surveys, do lend credence to the capability of the model to differentiate between areas of greater and lesser suitability. They also reveal shortcomings of the available spatial land cover data for habitat conservation planning for pollinators. Our model suggests a framework for guiding conservation planning for Monarchs migrating southward in the Atlantic Flyway, however, our work is limited by temporal and spatial resolution of the available data resolution and an understanding of the causality of the environmental factors predicted to be important to these insects. Further, our model predictions span only a portion of the total geographic range of these insects (Urquhart 1960). Expanding the model to the Midwestern U.S., Canada, and Mexico may reveal additional suitable Monarch roosting habitat, and contribute to range-wide habitat conservation planning for the species as they migrate to the wintering grounds of Michoacán. With so little land area in the Atlantic Flyway identified as suitable, conservation of those areas may be critical to the species’ persistence.

CHAPTER 2
VULNERABILITY AND CONSERVATION VALUE OF MONARCH BUTTERFLY
(DANAUS PLEXIPPUS L.) ROOSTING HABITAT EAST OF THE APPALACHIAN MOUNTAINS, U.S.A.

The Monarch butterfly is a flagship species and pollinator that is declining across its geographic range. The largest Monarch population overwinters in Mexico, following a southward fall migration from spring and summer breeding grounds in the eastern United States and Canada. During migration along flyways spanning the central United States and Atlantic Coast, Monarch Butterflies fly during the day and roost at night in aggregations. Roosting habitat is essential to the continuation of the Monarch migration, however, threats such as anthropogenic habitat
disturbance and climate change potentially endanger these habitats. We conducted a vulnerability assessment of predicted suitable roost habitat, evaluated the connectivity of the habitat with Morphological Spatial Pattern Analysis, used Zonation software to create a relative value ranking of the Atlantic flyway region for Monarch roost site conservation, and mapped areas of with a high Zonation ranking in regards to their current predicted vulnerability. Predicted suitable roost habitats occurring in coastal areas (1 million ha) were more vulnerable than those further inland (1.6 million ha), where they mostly parallel the Appalachian Mountains chain. The majority (73%) of roosting habitat occurs within non-fragmented core patches, and many of these patches are within the average daily flight distance (45 km) of migrating Monarchs. Although the flyway contains 18.5 million hectares of lands in conservation management, there was little overlap between the areas of high predicted conservation value for migrating Monarchs and current managed lands, with only 7% of predicted suitable roost habitat currently in management areas. These findings suggest that preservation of the Monarch migratory phenomenon along the Atlantic flyway may benefit from targeted outreach and management actions on mostly private land.

**Introduction**

Effective spatial conservation planning requires knowledge of a species’ resource and habitat needs (Gunton et al. 2016), understanding of the distribution of those needs (Kukkala and Moilanen 2012), and of how both needs and their distribution change over time (Lemes and Loyola 2013). Additionally, conservation planning requires knowledge of law, policy, and cultural norms (Gil et al. 2019). With this information, conservation practitioners can balance competing priorities to develop a network of lands managed to provide suitable habitat. For migrating species, habitat needs may differ at different times and locations in migration
(Johnston et al. 2019), and the distribution will shift dramatically on a seasonal basis (Dingle and Drake 2007). Additionally, as human borders are crossed, divergent laws, policies, and cultural norms require consideration (Dickman et al. 2015).

All of these challenges are further compounded by increased urban and agricultural sprawl that further fragments habitats (Gunton et al. 2016), and by ongoing changes to global climate (Lemes and Loyola 2013). Habitats vary in their resiliency towards these hazards. Many factors influence the sensitivity and adaptive capacity of a given area (Zurlini et al. 2006). Planning and implementation of a robust conservation network often requires a triage of potential sites. The decision of the conservation focus represents a balance of the comparative importance with the cost and likelihood of success in attempting protection (Kukkala and Moilanen 2012).

Understanding a species’ niche, and the geographic distribution of that niche, can be addressed with species distribution modeling, which accounts for both deterministic and stochastic factors that affect a species’ use of its environment (Chase and Myers 2011). These models are algorithms that relate environmental conditions at a species occurrence location to predict additional areas where an organism is likely to be found based on conditions in the areas that are known to be occupied. This approach to identifying potentially suitable habitat for a focal species is often more cost effective than conducting extensive ground inventories, and may also increase efficiency of ground surveys by directing observers to potentially suitable habitat. Maximum Entropy Modeling (MaxEnt) (Ashraf et al. 2017) is one such algorithm that has been applied to pollinators broadly (Polce et al. 2013), and to Monarch butterflies (Danaus Plexippus) specifically (Chapter 1).
Assessing risks to a species population persistence requires an understanding of threats to the species and to its habitat suitability. These threats may differentially affect life stages of a given species (Brown et al. 2018). For example, younger individuals may be more susceptible to poisonous substances (e.g., pesticides) (Moser 2011) or predation (Marescot et al. 2015). These life-stage dependent effects often become even more pronounced in species that undergo metamorphosis (Calsbeek and Kuchta 2011) or migration (Melnychuk and Welch 2018). Native pollinators are an important component of the world’s economy and food supply (Morandin and Winston 2006), however, most are in steep decline owing to exposure to a multitude of threats (Potts et al. 2010) including habitat loss (Weiner et al. 2014) and climate change (Vanbergen 2013), among others. The effect of habitat loss may be compounded when remaining habitat is scattered or fragmented with little connectivity, because dispersed habitat can make it challenging for a species to exploit all available resources (Krauss et al. 2010). Highly mobile species capable of navigating the matrix between patches often do not show this same effect (MacDonald et al. 2018). Overall, understanding the connectivity of available habitat is a crucial factor in conservation planning.

Landscapes with abundant flowering plants provide valuable forage for pollinators. Historically, these landscapes have been available in natural areas (Spiesman and Inouye 2013) and low intensity agriculture (Smessaert et al. 2019). However, the United States is urbanizing, with a current population growth rate of 1,750,000 people per year (Census Bureau 2017), and this growing population is expanding along the urban fringe, with >1,000 km² of natural and agricultural land lost annually to encroachment by cities (Nechyba and Walsh 2004). Much of this urban land expansion is due to suburban development, as new suburbs often radiate outwards as they become more densely developed and urbanized (Radeloff et al. 2005).
Although high-density urban development may provide less pollinator habitat than land in low intensity agriculture, suburban development can provide abundant forage and nesting resources in gardens and green space that are increasingly unavailable in intensely farmed landscapes (Geslin et al. 2013). Urban sprawl modeling provides a method to determine the extent that the outer edges of a cityscape are likely to expand in a given time period. For example, the Theobald Human Modification model predicts the spatial distribution of current and future (to 2030) sprawl and density of development, predicting areas that are likely to be converted to urban use over the next decade (Theobald 2016). This model differentiates suburban areas that may provide potential habitat for many species (Burghardt et al. 2008) from urban areas that may contain more hazards (Wilson and Jamieson 2019).

In addition to habitat loss to urbanization, pollinators are susceptible to changes in ambient temperatures and weather patterns (Hannah et al. 2017). The concentration of greenhouse gases in the atmosphere is increasing (Callendar 1938, Keeling et al. 1976), currently at a rate of approximately 2.5 parts per million per year (Lindsey 2020). This has triggered an increase of the average global temperature of approximately 1° C since the Industrial Revolution (Arrhenius 1896, Callendar 1938, Manabe and Wetherald 1967, NASA 2019) and an increase in the frequency and intensity of severe weather events (Held and Soden 2006). The intensity of storms in the Atlantic Basin is expected to increase by 3.5% per degree of Celsius increase (Moore et al. 2015). Conditions created by these stressors are dangerous to many pollinators (Hannah et al. 2017). Additionally, rising sea levels are changing the coastline by submerging low lying areas near the ocean, destroying habitat that was previously available to pollinators (Cazenave and Llovel 2010). There are many competing climate change models that differentially predict the extent and severity of changes anticipated with increasing concentration
of greenhouse gases. For example, the community climate system model (CCSM), developed by the University Corporation for Atmospheric Research integrates five different geophysical models (atmosphere, ocean, sea ice, land ice, and land) to model trajectories based on four different representative concentration pathways (RCP), 2.6, 4.5, 6, and 8.5, representing possible atmospheric CO2 concentrations in parts per million (McClean et al. 2011). Other models, such as zones of inundation based on sea level rise (Lindsey, 2019) can be combined with the CCSM to forecast climate-driven environmental change. Collectively, these models provide a powerful tool for conservation planners by providing a glimpse at probable future environmental conditions.

The Monarch butterfly is a flagship species (Diffendorfer et al. 2013) and pollinator (Robertson 1928, Tooker et al 2002) with populations currently in decline (Brower et al. 2012, Vidal and Rendon-Salinas 2014, Inamine et. al 2016). There are two main migrating populations of Monarchs in the United States - a western population that overwinters in California, and an eastern population that overwinters in Mexico. The eastern population can be further subdivided into two groups: one that occurs predominately in the plains and Midwest (Urquhart and Urquhart 1978), hereafter referred to as the central population, and one that crosses over the Appalachians and flies along the eastern seaboard (Howard and Davis 2008), hereafter referred to as the Atlantic population.

Despite being a charismatic and ecologically important species, however, the Monarch butterfly currently faces a multitude of threats. The amount of habitat available to Monarchs is declining and becoming increasingly fragmented, owing largely to urbanization and changing agricultural practices in the breeding zone (Brower et al. 2002, Flockhart et al. 2015) and illegal forest harvesting in the overwintering area (Brower et al. 2002). The amount of milkweed
(Asclepias spp), upon which Monarchs are entirely dependent for reproduction, is decreasing, attributed in large part to the spread of chemical resistant crops and subsequent overuse of herbicides (Pleasants and Oberhauser 2012) and pesticides (Stanley-Horn et al. 2001). Additional stress on Monarch populations comes from their susceptibility to numerous diseases, parasites, and parasitoids, which drastically decrease survival (McCoshum et al. 2016). Finally, all life stages potentially are threatened by environmental changes attributable to the changing climate (Batalden et al 2007, Oberhauser and Peterson 2003). There are a variety of threats to Monarch roosting habitat along the Atlantic flyway (Chapter 1), with three increasingly urgent stressors including changing land use, rising temperatures, and rising sea levels.

The eastern Monarch butterfly overwintering population is currently in decline (Forest Service 2015). Although the Oyamel (Abies religiosa) forest available to Monarchs for overwintering habitat declined by only 10% during 2001-2009 (Brower et al. 2012), the area used by the overwintering population declined by 97% during 1997-2014 (Brower et al. 2012, Vidal and Rendon-Salinas 2014). The numbers of Monarchs passing through known migratory funnel points, however, are not mirroring this precipitous drop (Walton et al. 2005). Although there is high annual variability, there is minimal evidence for a consistent decline in migrating numbers. For example, the largest known concentration of migrating Monarchs along the eastern seaboard is at Cape May, New Jersey. Although large year-to-year fluctuations, from 452 to 15,751, were documented over 13 years, there were insufficient data to detect trends (Walton et al. 2005). Nevertheless, there is up to a 62% chance of the Monarch’s eastern population reaching quasi-extinction, a level too low from which to recover, within the next 20 years, according to some estimated (Semmens et al. 2016). The central population is relatively well-studied compared to the Atlantic, however, the fall migratory period is less studied than the
breeding season or the overwintering period (Saunders et al. 2018). Survival of fall migrants is essential for providing sufficient numbers of spring-breeding Monarchs to replenish both populations (Howard and Davis 2008), and recent models suggest that climate change may have a more adverse effect on the Central flyway than on the Atlantic flyway (Taylor 2019).

Conservation planning that anticipates changing environmental conditions may contribute to a species’ long-term persistence and resilience (Magness et al. 2011). Pollinators are dependent on the plants they pollinate, and both the pollinators and host plant species may be forced to new locations as local conditions change (Malcolm et al. 2002). Climate predictions combined with species distribution models can be used to suggest where a species’ geographic range may shift with climate change. These models may also be coupled with a vulnerability assessment, a tool that predicts the risk level of a given area (Magness et al. 2011) to loss attributed to climate change or development. By combining vulnerability assessments with niche models, conservation planners can identify areas that are currently facing threats and develop a prioritization plan for conserving target species or habitats.

We evaluated habitat vulnerability and conservation value of areas predicted to be highly suitable for use by roosting Monarch butterflies during their southward migration in the Atlantic Flyway. We assessed predicted Monarch roosting habitat suitability with respect to its function as areas of high quality core or connecting habitat, the vulnerability of those areas to development or climate-driven change, and identified predicted suitable habitat that may have greater conservation value owing to proximity to currently conserved lands. We expected that areas along the Atlantic coastline and the ridges of the Appalachians would have high conservation value, as these areas are most suitable for use by Monarchs (Chapter 1). We further
expected these areas would be highly vulnerable, owing to high exposure to sea level rise and human development along the U.S. coast, and owing to low adaptive capacity resulting from the fragmented distribution in the Appalachians.

**Methods**

**Model Development**

We identified pixel-scale high quality roosting habitat with our previously created species distribution models spanning the US Atlantic seaboard from the western Allegheny Plateau and the southwestern Appalachians and east, inclusive (Chapter 1). Our model was developed with 1,052 sightings of Monarch roost sites reported to six citizen scientist databases and publicly available spatial data layers for 13 environmental variables representing conditions that affect the Monarch butterfly (Chapter 1). Roost habitat for Monarchs is characterized by freestanding vegetation, usually trees or snags, and is often surrounded by open land nectar sources (Howard and Davis 2008). We combined output from two algorithms, including both MaxEnt and the Genetic Algorithm for Ruleset Prediction (GARP) to identify 2.6 million hectares (2.9% of the study area) predicted to be suitable habitat for Monarch roosting during the southward migration in the Atlantic flyway. We used this habitat suitability layer to represent suitable habitat for roosting Monarchs in our vulnerability and conservation assessments.

**Distribution and Vulnerability of Potentially Suitable Habitat**

We assessed the Vulnerability of the model-predicted best suitable habitat (pixel value ≥ 0.70; Chapter 1) with estimates of Sensitivity (i.e., how sensitive an area is to changing conditions), Adaptive Capacity (i.e., how well an area can adapt to changing conditions), and Exposure (i.e., the threats which cause changing conditions) (Table 5) following methods of Magness et. al (2011). We formatted all data sources included in this analysis in the WGS 1984...
map datum with a data grain of 35 m (ESRI, Inc., ArcMap version 10.5.1). We estimated two factors that reflect Sensitivity of the focal pixel habitat suitability to change. Current predicted suitability represented the habitat quality of a focal cell compared to the ideal habitat suitability (i.e., predicted by the ecological niche model). The second factor compared the suitability of the pixels immediately surrounding and adjacent to that of the focal cell to identify where suitable habitat occurs in the landscape context of the focal pixel (Figure 12). Adaptive Capacity was estimated from four spatial data layers representing distribution of protected lands, ecoregions, anthropogenic development, and climate-driven conditions. We represented land conservation status with the Protected Areas Database – United States (https://www.usgs.gov/core-science-systems/science-analytics-and-synthesis/gap/science/protected-areas), assuming that protected areas will continue to be managed as such. The PAD-US provides a consolidated database of all conserved lands in this study area, broken into four categories reflecting conservation purpose: (1) managed for biodiversity – disturbance events proceed or are mimicked; (2) managed for biodiversity – disturbance events suppressed; (3) managed for multiple uses – subject to extractive or Off Highway Vehicle (OHV) use; (4) no known mandate for protection (USGS 2018). These categories represent a diverse set of management strategies with potentially different implications for Monarch butterflies (e.g., suppression of disturbance events in category 2 may mean less open areas than in category 1). The remaining three factors were chosen to represent potential for response to changes that may cause ideal conditions to shift spatially or disappear altogether. Proximity to ecoregion boundary, represented by EPA Level III ecoregions (https://www.epa.gov/eco-research/ecoregions), represented how centrally located the focal pixel was within a given climatic and vegetative region. The third factor contributing to Adaptive Capacity was range in elevation, calculated from the National Map (https://www.usgs.gov/core-
science-systems/ngp/tnm-delivery/) with a moving window analysis in a 100x100 meter window around the focal pixel. This variable represented the amount changing climatic conditions could be compensated for by moving to higher elevation areas. The fourth variable contributing to Adaptive Capacity was proximity to the closest suitable habitat. We calculated this as the Euclidean distance between suitable habitats. The final component of Vulnerability was Exposure, represented by three criteria. Urban sprawl was estimated with the Theobald Ecological Integrity Index 2030 predictions (Theobald 2016). We subtracted each pixel’s current average temperature during the migratory season (August-November) from the average temperature predicted under the CCSM RCP 4.5 climate change model to approximate temperature increase. Finally, we used the NOAA sea level rise two feet prediction (https://www.fisheries.noaa.gov/inport/item/48106) to identify pixels predicted to be threatened with partial or total submersion in the next 50 years.

We scaled pixels in all spatial data layers from 1 to 100 using natural breaks in the data over the extent of the study area. We averaged the scaled scores in each pixel for each of the three primary categories (Sensitivity, Adaptive Capacity, and Exposure) to create an estimated value of each Vulnerability factor resulting in one raster scaled from 1 to 100 for each factor (Figure 13a) (Sutton et al. 2015). We next subtracted Sensitivity from Adaptive Capacity and again scaled the result from 1 to 100, giving us a Resiliency layer. We subtracted this layer from the Exposure layer, and scaled the results from 1 to 100, creating a map of the Vulnerability of pixels in the eastern seaboard (Figure 13b) (Magness et. al 2011). We extracted the values from this map in the areas that our previous SDM predicted to have a high probability (≥ 0.70) of containing suitable habitat for roosting Monarchs, thus creating a map of predicted Vulnerability of these areas.
There were several assumptions inherent in this method. Chief amongst them was that we assumed each of the factors value and risk had a consistent linear increase as its value changed, and we did not perform line fitting or assign cutoff values. Additionally, owing to the lack of weighting, each of the three primary categories was equally important to the overall vulnerability, and each component of each category to be equally important. Finally, by adding the scores instead of multiplying them, we prevented any one factor from being an absolute limit. The strength of this method comes from its ability to combine multiple factors together rather than to rely solely on one. While it is possible a single factor (i.e., sea level rise) may make it impossible for monarchs to roost, we assumed that it is always possible for them to adapt (i.e., by flying a short distance inland).

**Morphological Spatial Pattern Analysis**

We used Morphological Spatial Pattern Analysis (European Commission Joint Research Centre) to evaluate the function each pixel serves (e.g., core, connector, etc.) in the landscape (Soille and Vogt 2009). We created a binary raster layer from the most suitable (value ≥ 0.70) areas predicted in our SDM set as foreground (raster value = 1) to be evaluated in a matrix of the background (raster value = 2) surrounding the suitable habitat. We partitioned the dataset into 26 tiles (approximately 300 kilometers by 400 kilometers) to process in a batch analysis owing to the extent of the study area. We used the default program settings for foreground connectivity (8), edge width (1), and using transition pixels and intext (allows classification inside of perforations) turned on. The program evaluates the connectivity of each foreground pixel with bordering pixels and places each pixel into one of eight primary category types (core, edge, perforations, bridges, loops, branches, islets, and background) (Figure 14). We mosaicked the processed tiles and determined the area of predicted suitable habitat in each type. We combined
the eight types into two that represented the basic functions they provide: 1) Core/Edge (core and edge) provides large core patches, and 2) Fragmentation (islets, loops, bridges, perforations, branches) provides stepping stones across the landscape.

**Zonation**

The conservation benefit an area provides to butterflies is raised when it can be connected to other protected lands (Schultz and Crone 2005). Zonation (version 4.0.0; https://github.com/cbig/zonation-core) is a systematic conservation planning software designed for use with MaxENT ecological niche modelling (Lehtomaki and Moilanen 2013) to assess the predicted suitability and connectivity between focal pixels to estimate its value in conserving connected habitat for the species. Each cell is ranked (scaled 0-100) with respect to the value of conserving that cell to create high quality habitat connected with other quality habitat (Lehtomaki and Moilanen 2013, Wan et al. 2014). This analysis provides conservation practitioners a visualization of the relative value of given areas, and enables more effective prioritization of habitat for conservation when combined with knowledge about the vulnerability of a site owing to threats such as climate and land use change.

We used Zonation to identify areas with potentially high conservation value owing to the predicted suitability and connectivity of the local habitat (Figure 15). Zonation identifies these areas by iteratively removing the lowest valued cells based on suitability and connectivity to other suitable cells (Lehtomaki and Moilanen 2013). We ran Zonation state-by-state, which provided an assessment of the value of the focal cell with respect to other cells in that state. We ran each state twice. First, we used only the Monarch SDM as input so that each cell is assigned a prioritization value based exclusively on the benefit it provides to Monarch butterflies, representing the “biologically optimum solution.” The second application automatically scores
locations within conservation areas as greater value than those outside of conservation areas. Owing to the way the application evaluates each pixel relative to adjacent pixels, this approach scores pixels adjacent to conservation lands (represented in the PAD-US layer; https://www.usgs.gov/core-science-systems/science-analytics-and-synthesis/gap/science/protected-areas) with a larger value. We created a mask of this layer, which instructed Zonation to remove all pixels outside of the conservation zones before removing any pixels that fell within these areas (Lehtomaki and Moilanen 2013). In doing so, the Zonation procedure prioritized habitat that borders or overlaps conservation lands. While this land may have a lower predicted suitability and therefore provide less biological value to the Monarch (Lehtomaki and Moilanen 2013), acquisition and/or management of Monarch habitat in or adjacent to existing conservation areas is likely more feasible than founding a new conservation area (Adams et al. 2011). We used Core Area Zonation (designed to recognize areas valuable to a single species of concern) without a boundary length penalty (which does not penalize the model for sinuosity of edges), with edge removal (which prioritizes removal along edges, increasing value of aggregation) and a warp factor of 100 (which allows removal of up to 100 cells at a time). Zonation operates with the assumption that connectivity of high suitability land is an important factor in the value of that land.

**Areas of Greatest Concern and Opportunity**

We combined the output from the Vulnerability assessment and Zonation to identify areas of greatest conservation concern and opportunity. We ranked the vulnerability scores in bins of 10 within areas ranked ≥ 91% biologically optimum by Zonation to compare threat levels within those areas. These high vulnerability scores therefore represent the most important (i.e., highest conservation concern) Monarch stop-over habitat areas expected to be lost in the absence
of conservation. Conversely, low vulnerability scores represent areas of greatest conservation value that will require the least active land management to protect, and therefore these are areas of greatest opportunity.

**Results**

**Vulnerability Assessment**

We identified 2.6 million hectares of predicted suitable habitat (≥ 0.70%) representing 2.9% of the available land in the study region, with greatest amount of suitable habitat in New York (963,923 ha, 6.8% of state) and least in Alabama (1,082 ha, 0.008% of state) (Chapter 1). The Northeastern Highlands ecoregion contains the greatest amount (4,782,209 ha), and the Interior Plateau ecoregion contains the least amount (61,455 ha) of suitable area (Chapter 1). Nearly 37% of the habitat predicted suitable for roosting had a vulnerability score > 50, with the most vulnerable Monarch habitat occurring along the coast from Maine to North Carolina, and throughout southern parts of the flyway (e.g., South Carolina, Georgia, Alabama) (Figure 16). The southern shores of the Great Lakes in Western New York through Ohio also are vulnerable (97% of suitable habitat in Ohio score > 60 Vulnerability) (Figure 16). The suitable habitat in the Appalachian Mountains is predicted to be less vulnerable (67% of suitable habitat in West Virginia scored < 40 Vulnerability), as is habitat in the northern extent of the flyway from Maine through Virginia (86% of suitable habitat in Maine scored < 40 Vulnerability) (Figure 16). Vulnerability of coastal land is attributed to increased exposure to land use change and sea level rise, whereas in the southern part of the flyway vulnerability reflects the scarcity of suitable habitat (Figure 17). The lower vulnerability in the Appalachians can be attributed to the abundant suitable habitat currently available (Chapter 1), which provides alternative nearby locations as conditions in the landscape change (Figure 17). The majority (70%) of suitable habitat had
vulnerability scores of 31 to 60, with virtually no land (0.3%) predicted to be highly suitable (>0.70) and also highly vulnerable (> 0.70) (Table 6). The majority of suitable habitat was not currently in land managed for conservation (Figure 18), with a large range from approximately 0% conserved in Ohio, Kentucky, and Tennessee to 31% conserved in Delaware (Table 7). Our study area included approximately half of the area of Tennessee, Ohio, and Kentucky, where only seven hectares of habitat predicted to be suitable for roosting Monarch butterflies occurs. Overall, the northern Mid-Atlantic states contain the largest proportion of suitable habitat in conserved lands, ranging from 9,733 ha in Delaware (31% of state) to 16,226 ha in Maryland (9% of state) (Table 7, Figure 19). The majority of suitable land that was in conservation areas was found in PAD-US categories 1 (90,705 ha) and 3 (74,568 ha) (Table 7).

**Morphological Spatial Pattern Analysis**

The majority (56%) of predicted suitable Monarch habitat fell into core areas, with edges (17%) and islets (11%) ranking a distant second and third. The core and edge combination accounted for 73% of suitable habitat, with all other categories representing 27%. The proportion of suitable habitat falling into different MSPA designated connectivity categories is generally evenly distributed across the study area (Figures 20 and 21). The Ridge and Valley ecoregion contains the most suitable habitat at 511,400 ha, with 78% in core or edge types. The coastal region with the most suitable habitat was the Northeastern Coastal Zone at 478,617 ha, with 72% of this found in core or edge types.

**Zonation**

Habitat areas in ecoregions with coastline (including parts of the Northeastern Coastal Zone, Atlantic Coastal Pine Barrens, and Middle Atlantic Coastal Plains ecoregions) and the Appalachian Mountains (including parts of the Blue Ridge, Ridge and Valley, Southwestern
Appalachians, and Central Appalachians ecoregions) were scored by Zonation as having the highest combination of suitability and connectivity, and as such were the most valuable land for Monarch roosting habitat conservation (Figure 22). There is wide variation in Zonation rankings of suitability for conservation lands among states, with the majority (63%) of currently conserved habitat ranked by Zonation to be less valuable for Monarchs (Table 8 and Figure 23). The same pattern holds across ecoregions (Table 9 and Figure 24), with most lands currently in conservation ranked less valuable for Monarchs. Cumulative curves show the amount of conservation land at or below a given Zonation ranking, with a more gradual slope indicating the states and ecoregions where Zonation ranked the land in conservation zones as being more valuable, which may facilitate management to directly benefit migrating Monarchs. The Appalachian ecoregions contain greater amounts of highly ranked land in conservation status than the coastal ecoregions. When the mask for conservation lands was added, the highest ranked areas shifted to cluster near the largest conserved areas (Figure 25), reflecting how Zonation prioritizes areas with high connectivity. The result is that habitat in or adjacent to conservation lands is ranked higher than habitat not in or near conservation lands, regardless of the predicted habitat quality, providing an opportunity to visualize distribution of lands most available for management to directly benefit Monarchs compared to distribution of land that is not in conservation management

**Areas of Greatest Concern and Opportunity**

The areas of greatest concern (where land Zonation ranked as highly valuable for Monarch roost-site conservation is highly vulnerable) occurred in southern and coastal areas, and near cities. The areas of greatest opportunity (where land Zonation ranked as highly valuable for Monarch roost-site conservation is minimally vulnerable) occurred in the Appalachian
Mountains and the northern part of the flyway (Figure 26). For example, northern Georgia primarily contains land ranked as highly valuable by Zonation and highly vulnerable (red shades in Figure 26), whereas northern Maine primarily contains land ranked as highly valuable by Zonation but with low vulnerability (shades of blue, Figure 26).

**Discussion**

Our findings suggest that areas of suitable Monarch roosting habitat that are most at risk occur mostly on private land in coastal areas, owing to rising sea levels and urban sprawl. Roosting habitat for Monarch butterflies migrating in the Appalachian Mountains region of the flyway is less threatened by these factors, and although scattered in distribution, it is potentially more easily conserved due to the comparatively greater adaptive capacity. The greatest amount of suitable habitat for roosting Monarchs is in New York and Pennsylvania, where Monarchs gathering across this large area early in the migratory period may congregate and find suitable sites to rest as they begin the southward journey. Monarchs leave the northern part of the flyway early in migration, however, and as they travel southward they will encounter less suitable habitat that is distributed in smaller and more sparsely distributed patches that are less accessible. Sparse habitat in South Carolina and Georgia, through which the entire Atlantic Flyway population must travel, may be particularly important for sustaining migrating Monarchs as they move southwestward towards Mexico. Sparse roosting occurrences in the southern part of the flyway are a documented issue, although the reason is unknown (Howard and Davis 2008).

Much of the focus for conservation action has centered around managed lands, where conservation practitioners have the most direct control over land management actions (Keiter 2018). These areas are managed to provide habitat for many species (Clements and Cumming 2016), however, this management approach may not create habitat that meets the Monarchs’
needs, such as disturbed conditions created by low-intensity agriculture (Chapter 1). Additionally, Monarchs must migrate southward to survive winter and produce the next generation in the subsequent spring migration. Given the patchy, disconnected distribution of conservation lands, it is important to consider their landscape context across the land ownership boundaries traversed by migrating Monarchs. An effective management plan would provide habitat for roosting and nectaring regardless of ownership status.

Migratory species need to find suitable habitat throughout the migratory path (Gurarie et al. 2017). Where geographic features constrict their movements and densities increase, individuals may become more vulnerable to pathogens and disease (Davis et al. 2017), predation (Hossie and Murray 2010), and insufficient food and water (Lamb et al. 2017), particularly where suitable habitat is limited. These areas also have increased importance for conservation (Hilgerloh 2009). Roosting habitat for migrating Monarch butterflies in the southern extent of the Atlantic flyway is apparently rare. This causes it to have heightened sensitivity, and by extension vulnerability, compared with habitat elsewhere in the region (Chapter 1). This rarity contributes to greater sensitivity to disturbance, because loss of any roost habitat has a disproportionate effect on what is available. This rarity also decreases the adaptive capacity for Monarchs, because when roosting areas are lost there is less likely to be an alternative accessible within the normal 45 km distance travelled daily by migrating Monarchs (Brower et al. 2006). Monarchs are capable of flying significantly farther than 45 km a day (Dockx 2007), so they may be able to accommodate this change by flying farther. However, being forced to do so consistently may take its toll on their energy reserves. All Monarchs from the Atlantic flyway that reach the wintering grounds in Mexico traverse this vulnerable area at the southern end of the flyway (Howard and Davis 2008), highlighting its potential out-sized role
for the Atlantic flyway population. Coastal habitat, where Monarchs travel and roost as they move southward (McCord and Davis 2010), also was ranked as highly vulnerable. This habitat is threatened by sea level rise (Gutierrez et al. 2011) and development (Terando et al. 2014). Although the Great Lakes shoreline, which was also identified as highly suitable for migrating Monarch butterflies, is not threatened by sea level rise, it shares the Atlantic Coasts susceptibility to increasing development (Pijanowski et al. 2002).

We did not identify large areas of suitable roosting habitat that also are highly vulnerable. This reflects the analysis assumption that high quality habitat is more resilient, and therefore less sensitive, which may be an unsupported assumption. The method developed by Magness et al. (2011) to evaluate habitat vulnerability by identifying potential threats is a useful tool for proactive management of conservation lands (Beever et al. 2015, Aplet and McKinley 2017, Magness et al. 2018). Only 0.203% of the study region contains conserved suitable habitat, and 93% of the predicted suitable Monarch roosting habitat occurs on land that is not formally protected. Our species distribution modeling approach identified low intensity agriculture and suburban (e.g., low to moderate density development) areas as important habitats for Monarch roost habitat (Chapter 1). These conditions are not typically included in conservation lands (Seppelt et al. 2016). Recent promotion of pollinator gardens for insect conservation (Majewska et al 2018), including those promoted by conservation organizations (USFWS 2018) may benefit migrating Monarchs, provided the gardens include fall blooming flowers for nectaring and nearby roosting habitat such as large trees. A more thorough understanding of the vulnerability of roosting habitat could be gained with additional research into how well exploited these pollinator gardens are, identifying those that may provide quality roosting habitat, and an inventory of where the gardens are positioned along the migration corridor. Similarly, use of
crop types and flowers in suburban gardens, how many of these gardens also contain large trees and snags suitable for Monarch roosting, and the availability and value of these habitats for sustaining Monarchs as they migrate are not well-studied.

Where suitable habitat falls within the migration corridor is often as important as how much is available (Collingham and Huntley 2000). To survive, an individual requires patches of sufficient area to meet its individual and population’s needs, however, there also must be accessible corridors for travel between these patches (Xu et al. 2019). The abundance (73%) of suitable habitat occurring as core and edge (compared with islets, loops, bridges, perforations, and branches) suggests Monarchs may have choices of roost habitat when they stop to rest during migration. This suggests adaptability in the landscape to accommodate land use or land cover changes, when the destruction of some habitat may still leave suitable, accessible areas untouched (Gittman et al. 2018). This may explain why our vulnerability analysis assessed these areas of core habitat to be less vulnerable (i.e., they have higher Adaptive Capacity and lower Sensitivity). Having a patch that is sufficiently large to support stop-over behavior is integral (Xu et al. 2019), however, the Monarch roost structures tend to be small (Davis and Howard 2012), and the butterflies’ ability to fly at heights in excess of 1 km (Gibo and Pallett 1978) allows them to bypass most hazards and reach isolated or fragmented patches that are within 45 km, their average daily flight distance (Kang et al. 2017). Therefore, while habitat occurring in islets comprises much less total space in the region, these areas may still be important, particularly if they can increase landscape permeability by serving as “stepping stones” to larger patches where more Monarchs can congregate. Since only 27% of the study area is comprised of these stepping stones, they may represent a limiting factor in the ability of Monarchs to migrate. It is unclear how conditions at these sites may contribute to a Monarch’s ability to sustain flight for the
duration of migration; small areas with roosting structures but without forage will only partially meet a migrating Monarch butterfly’s daily needs. Determining if these islets may fulfill the butterflies’ needs while providing integral connectivity across the migratory corridor (Collingham and Huntley 2000) is an area for additional study.

Our analysis with Zonation ranked the most valuable lands for conservation of Monarch roosting habitat to be along the Atlantic coast and in the Appalachian Mountains, similar to where the most suitable land for roosting was identified by our species distribution model (Chapter 1). Monarch roosting habitat is poorly represented in current conservation lands, with only 7% of the best Monarch roosting habitat currently predicted to be in protected status. Field and disturbed habitat provides forage for Monarchs (Coulin et al. 2019), and reported roost sites occur frequently in or near this habitat type. During migration, Monarchs are attracted to low intensity agriculture and development where nectar sources may be abundant (Chapter 1), however, this land use type is not well represented in the conservation system (Gunton et al. 2016). Monarchs use large trees, as individuals or in groves, for roosting (Davis et al. 2012). These structures occupy little space, and where they occur in partially developed land, the landscape may be ideal open space for flying with plentiful flowers and trees for nectaring and resting (Lewis et al. 2019). A biologically optimum approach (i.e., conserving the best habitat) shows the areas to protect that will be most valuable to aid survival of Monarchs (Lehtomaki and Moilanen 2013), however, acquisition of new land can be expensive, difficult, or even impossible (Kukkala and Moilanen 2012). Our Zonation analysis suggests that even with compromising the biologically optimum solution (i.e., best habitat conserved) and considering the habitat conservation costs and opportunities, there is high quality Monarch roosting habitat available along the margins of currently conserved land. Prioritizing potentially suitable habitat
in areas proximal to land already managed for conservation acknowledges the value of location and connectivity to these lands (Lehtomaki and Moilanen 2013).

The Zonation analysis serves to inform conservationists who may have flexibility in management strategies where the greatest gains can be optimized (Lehtomaki and Moilanen 2013), while also providing guidance for expanding the footprint at the perimeter of current holdings. Our analysis suggests that patches of land currently in conservation management are within the Monarch’s daily flying distance of 45 km (Brower et al. 2006), throughout the Atlantic Flyway, potentially providing accessible habitat for roosting in stepping stones during migration. Zonation favors suitable habitat patches in close proximity to other suitable patches, and when a mask of conservation areas was included, lands surrounding large conservation areas provided greater connectivity than lands surrounding small patches of conserved land, and they were therefore ranked higher. This approach amplifies the prioritization of lands in close proximity, which may be poorer quality habitat, at the cost of not conserving higher quality habitat that is more dispersed. Ignoring habitat connectivity in assessing habitat quality potentially increases the risk that Monarchs may not find suitable roosting areas after a day of flight through the network of conservation lands, particularly if management of those lands does not create or maintain roosting trees and sources of nectar.

Ecological conservation is conducted in a resource constrained environment (Kukkala and Moilanen 2012). Conservation practitioners simply cannot acquire all land of value for a species, and so they identify priority areas to focus on using the best available science and usually including the needs of many species at multiple scales (Gunton et al. 2016). Zonation is a powerful tool for this purpose, resulting in a rank ordered listing of the relative value of each cell in a potential management zone (Lehtomaki and Moilanen 2013). Our analysis is a novel
expansion of this approach. By also considering the relative vulnerability of high quality habitat, we have provided information about the threats these areas face, which is useful for assessing the feasibility of conserving them. The areas of greatest concern, where high conservation value areas are the most vulnerable, and greatest opportunity, where high conservation value areas are the least vulnerable, represent opportunities for conservation practitioners to focus efforts on areas our models identify as being particularly valuable based on their own assessment of reasonable prioritization. For example, a conservation practitioner who is interested in areas where their efforts are most likely to conserve the greatest area at the least cost could focus on the areas of greatest opportunity, as these are predicted valuable habitat for the Monarchs that are either not exposed to many threats or have high resilience. Fewer resources dedicated to secure these areas may provide a disproportionately important benefit of ensuring their continued suitability for Monarchs. In contrast, conservation may be directed at high quality areas with greater risk of loss, at the expense of requiring more resources or conserving less total area. Other practitioners may strike a balance of approaches: their conservation goals may be determined by the cost of management actions (Kukkala and Moilanen 2012) instead of for achieving the biological optimum.

Our vulnerability analysis identified both the distribution of at risk habitat and the conditions contributing to that risk. Lands along the coastline provide important roosting habitat that potentially is vulnerable to sea level rise attributed to global climate change. Preventing coastal flooding caused by rising sea level can be prohibitively expensive (Lenk et al. 2017), and therefore is unlikely as a habitat conservation focus for migrating Monarchs. Areas identified as suitable habitat around cities are vulnerable owing to urban sprawl. Land acquisition is difficult in these areas, as real estate often is expensive close to urban centers (Espey et al. 2007).
However, there may be opportunities to engage citizen conservationists to create or maintain Monarch habitat in their suburban properties (Lewis et al. 2019). The low adaptive capacity in the southern region of the Atlantic Flyway may be attributed to the lack of suitable habitat, a particular concern given that Monarchs migrating southward in the flyway must pass through this largely unsuitable area (Howard and Davis 2008). It is also possible that there is less roosting habitat in the southern flyway because the majority of Monarchs turn west before reaching this area, or because they increase speed when flying through this area and roost less, or because the area is more conducive to roosting as individuals rather than in congregation and therefore decreases likelihood of detecting a roost site. A study that follows tagged individual Monarchs throughout migration would be a valuable contribution to their conservation. Inland areas of the flyway, such as habitat along the Appalachian Mountains and northern interior had higher adaptive capacity and were therefore less vulnerable, suggesting that it may be strategic to conserve habitat for migrating Monarchs traversing this region of the flyway.

Ensuring there are adequate roost sites available to migrating Monarchs will help to conserve this iconic species for future generations. The butterflies must reach Mexico to survive winter months (Urquhart and Urquhart 1978), and they require roosting habitat to rest and refuel on the journey (Brower et al. 2006). Although areas predicted to contain greater quality roost habitat are primarily outside of lands currently in conservation, a more comprehensive understanding of how the factors that make a roost area suitable to benefit the Monarch would inform management. Although we did not address the expansion and intensification of forested landscape in the Northeast in our study, this may be a threat to Monarchs as they do not often roost in dense forests. This is an understudied topic in developing Monarch conservation strategies. The threat of sea level rise to roosting areas along the coast creates an urgency to
identify accessible habitat in nearby areas not prone to flooding. Improved understanding of the Monarch’s use of agricultural and suburban (low to moderate density development) land in the flyway may provide opportunity to strengthen partnerships with private land owners to create conservation benefits for Monarchs as well as natural resources more broadly. Combining this knowledge with management action has the potential to protect the Monarch migratory phenomenon for generations to come. Our spatially explicit roost habitat model and vulnerability assessment provide valuable information to use in prioritizing these efforts.
**Table 1.** Species occurrence databases and number of records evaluated and used to develop the models of suitable Monarch roost habitat in the Atlantic Flyway. Shaded rows represent datasets used in the models, and rationale for omitting datasets is indicated for excluded datasets

<table>
<thead>
<tr>
<th>Dataset</th>
<th>Number</th>
<th>URL</th>
<th>Rationale for exclusion</th>
</tr>
</thead>
<tbody>
<tr>
<td>BAMONA</td>
<td>9,115</td>
<td><a href="https://www.butterfliesandmoths.org/">https://www.butterfliesandmoths.org/</a></td>
<td>n/a</td>
</tr>
<tr>
<td>BISON</td>
<td>52,889</td>
<td><a href="https://bison.usgs.gov/#home">https://bison.usgs.gov/#home</a></td>
<td>n/a</td>
</tr>
<tr>
<td>eButterfly</td>
<td>11,766</td>
<td><a href="http://www.e-butterfly.org/#/">http://www.e-butterfly.org/#/</a></td>
<td>n/a</td>
</tr>
<tr>
<td>GBIF</td>
<td>51,782</td>
<td><a href="https://www.gbif.org/">https://www.gbif.org/</a></td>
<td>n/a</td>
</tr>
<tr>
<td>iNaturalist</td>
<td>18,786</td>
<td><a href="https://www.inaturalist.org/">https://www.inaturalist.org/</a></td>
<td>n/a</td>
</tr>
<tr>
<td>Journey North</td>
<td>n/a</td>
<td><a href="https://journynorth.org/">https://journynorth.org/</a></td>
<td>Observations centered on observer zip code, limits spatial accuracy</td>
</tr>
<tr>
<td>Mission Monarch</td>
<td>954</td>
<td><a href="https://www.mission-monarch.org/">https://www.mission-monarch.org/</a></td>
<td>n/a</td>
</tr>
<tr>
<td>Monarch Joint Venture</td>
<td>n/a</td>
<td><a href="https://www.monarchjointventure.com/">https://www.monarchjointventure.com/</a></td>
<td>Tracks monarch conservation projects, not individual monarch occurrences</td>
</tr>
<tr>
<td>Monarch Lab</td>
<td>n/a</td>
<td><a href="https://monarchlab.org/">https://monarchlab.org/</a></td>
<td>Tracks larvae, which are non-migratory</td>
</tr>
<tr>
<td>Monarch Monitoring Project</td>
<td>n/a</td>
<td><a href="http://www.monarchmonitoringproject.com/">http://www.monarchmonitoringproject.com/</a></td>
<td>Conducts road censuses only at Cape May, N.J. USA</td>
</tr>
<tr>
<td>Monarch Net</td>
<td>n/a</td>
<td><a href="https://www.monarchnet.org/">https://www.monarchnet.org/</a></td>
<td>Portal links to other reporting sites, but does not have its own data</td>
</tr>
<tr>
<td>Monarch Watch</td>
<td>n/a</td>
<td><a href="https://www.monarchwatch.org/">https://www.monarchwatch.org/</a></td>
<td>Focus is on tagging, mark / recapture studies</td>
</tr>
<tr>
<td>NABA</td>
<td>n/a</td>
<td><a href="https://www.naba.org/">https://www.naba.org/</a></td>
<td>Sightings are also included in iNaturalist’s database</td>
</tr>
<tr>
<td>Texas Monarch Watch</td>
<td>n/a</td>
<td><a href="http://texasono.net/dplex.htm">http://texasono.net/dplex.htm</a></td>
<td>Area of focus is outside of study area</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>145,292</strong></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2. Percent contribution and permutation importance of environmental variables evaluated for inclusion in the Maximum Entropy (MaxEnt) model of Monarch migratory roost site suitability in the Atlantic Flyway. Percent contribution represents the increase in regularized training gain from the corresponding variable, and Permutation Importance represents the drop in AUC* when the corresponding variable is randomly removed from the model. For both values, a larger number represents greater importance for the variable.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Source</th>
<th>% Contribution</th>
<th>Permutation Importance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agriculture</td>
<td><a href="https://nassgeodata.gmu.edu/CropScape/">https://nassgeodata.gmu.edu/CropScape/</a></td>
<td>7.8</td>
<td>8.4</td>
</tr>
<tr>
<td>Aspect</td>
<td><a href="https://www.usgs.gov/core-science-systems/ngp/tnm-delivery/">https://www.usgs.gov/core-science-systems/ngp/tnm-delivery/</a></td>
<td>0.9</td>
<td>0.7</td>
</tr>
<tr>
<td>Ecological Integrity</td>
<td><a href="https://databasin.org/datasets/110a8b7e238444e2ad95b7c17e889b66">https://databasin.org/datasets/110a8b7e238444e2ad95b7c17e889b66</a></td>
<td>3</td>
<td>4.1</td>
</tr>
<tr>
<td>Land Cover</td>
<td><a href="https://www.mrlc.gov/">https://www.mrlc.gov/</a></td>
<td>4.9</td>
<td>4.5</td>
</tr>
<tr>
<td>Precipitation(^a)</td>
<td><a href="https://climatedataguide.ucar.edu/climate-data/">https://climatedataguide.ucar.edu/climate-data/</a></td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>Proximity to Coast</td>
<td><a href="https://www.ngdc.noaa.gov/mgg/shorelines/shorelines.html">https://www.ngdc.noaa.gov/mgg/shorelines/shorelines.html</a></td>
<td>44.8</td>
<td>27.7</td>
</tr>
<tr>
<td>Proximity to Lakes</td>
<td><a href="https://www.usgs.gov/core-science-systems-ngp/tnm-delivery/">https://www.usgs.gov/core-science-systems-ngp/tnm-delivery/</a></td>
<td>10</td>
<td>5.2</td>
</tr>
<tr>
<td>Proximity to Roads(^b)</td>
<td><a href="https://www.gis.fhwa.dot.gov/">https://www.gis.fhwa.dot.gov/</a></td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>Proximity to Wetlands</td>
<td><a href="https://www.fws.gov/wetlands/data/Data-Download.html">https://www.fws.gov/wetlands/data/Data-Download.html</a></td>
<td>2.1</td>
<td>3</td>
</tr>
<tr>
<td>Slope(^c)</td>
<td><a href="https://www.usgs.gov/core-science-systems-ngp/tnm-delivery/">https://www.usgs.gov/core-science-systems-ngp/tnm-delivery/</a></td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>Solar Radiation</td>
<td><a href="https://globalsolaratlas.info/">https://globalsolaratlas.info/</a></td>
<td>4.7</td>
<td>5.5</td>
</tr>
<tr>
<td>Temperature</td>
<td><a href="https://climatedataguide.ucar.edu/climate-data/">https://climatedataguide.ucar.edu/climate-data/</a></td>
<td>3</td>
<td>8.6</td>
</tr>
<tr>
<td>Wind</td>
<td><a href="https://globalwindatlas.info/">https://globalwindatlas.info/</a></td>
<td>2.9</td>
<td>2.4</td>
</tr>
</tbody>
</table>

\(^a\) Discarded owing to high covariance (0.99998) with temperature.
\(^b\) Discarded owing to high covariance (0.99843) with ecological integrity.
\(^c\) Discarded owing to lack of model contribution (Percent Contribution = 0.5)
Table 3. Percentage of land area in bins representing amount of agreement between the Maximum Entropy (MaxEnt) and Genetic Algorithm for Ruleset Prediction (GARP) outputs by EPA Ecoregion (Ecoregions available at https://www.epa.gov/eco-research/ecoregions). For each model type, the five columns report the range of pixels exceeding the suitability predicted by the other algorithm. The middle column represents the percentage of pixels in which the model suitability predictions agreed within 5%.

<table>
<thead>
<tr>
<th>Ecoregion</th>
<th>% MaxEnt Higher</th>
<th>Within 5%</th>
<th>% GARP Higher</th>
</tr>
</thead>
<tbody>
<tr>
<td>45+</td>
<td>35-44</td>
<td>25-34</td>
<td>15-24</td>
</tr>
<tr>
<td>Acadian Plains and Hills</td>
<td>1.7</td>
<td>5.1</td>
<td>12.3</td>
</tr>
<tr>
<td>Atlantic Coastal Pine Barrens</td>
<td>0.2</td>
<td>0.8</td>
<td>1.6</td>
</tr>
<tr>
<td>Blue Ridge</td>
<td>2.8</td>
<td>8.8</td>
<td>22.6</td>
</tr>
<tr>
<td>Central Appalachians</td>
<td>5.5</td>
<td>14.2</td>
<td>26.3</td>
</tr>
<tr>
<td>Eastern Great Lakes Lowlands</td>
<td>2.4</td>
<td>6.2</td>
<td>13.3</td>
</tr>
<tr>
<td>Interior Plateau</td>
<td>0.0</td>
<td>0.1</td>
<td>2.4</td>
</tr>
<tr>
<td>Middle Atlantic Coastal Plain</td>
<td>0.2</td>
<td>0.6</td>
<td>1.6</td>
</tr>
<tr>
<td>North Central Appalachians</td>
<td>5.0</td>
<td>14.2</td>
<td>30.5</td>
</tr>
<tr>
<td>Northeastern Coastal Zone</td>
<td>0.4</td>
<td>2.3</td>
<td>11.1</td>
</tr>
<tr>
<td>Northeastern Highlands</td>
<td>1.7</td>
<td>6.9</td>
<td>15.5</td>
</tr>
<tr>
<td>Northern Allegheny Plateau</td>
<td>11.9</td>
<td>21.8</td>
<td>27.8</td>
</tr>
<tr>
<td>Northern Piedmont</td>
<td>0.1</td>
<td>1.0</td>
<td>5.8</td>
</tr>
<tr>
<td>Piedmont</td>
<td>0.2</td>
<td>1.1</td>
<td>5.8</td>
</tr>
<tr>
<td>Ridge and Valley</td>
<td>3.4</td>
<td>9.6</td>
<td>21.5</td>
</tr>
<tr>
<td>Southeastern Plains</td>
<td>0.2</td>
<td>0.5</td>
<td>0.7</td>
</tr>
<tr>
<td>Southern Coastal Plain</td>
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<td>0.8</td>
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* For example, in the Acadian Plains and Hills Ecoregion, 19.4% of the land area was rated within 5% suitability by both algorithms, whereas 20.6% of the land area was rated 15-24% more likely to be suitable by MaxEnt, and 4.2% of the land area was rated to be 15-24% more likely to be suitable by GARP.
Table 4. Percentage of land in each state predicted with Maximum Entropy (MaxEnt) and Genetic Algorithm for Ruleset Prediction (GARP) models, partitioned into bins for probability of suitability. Rows sum to 100% of the land area in each state. Columns partition each algorithm’s predicted suitability values into bins.

<table>
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<tr>
<th>State</th>
<th>0-10</th>
<th>11-20</th>
<th>21-30</th>
<th>31-40</th>
<th>41-50</th>
<th>51-60</th>
<th>61-70</th>
<th>71-80</th>
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<td>GARP</td>
<td>MaxEnt</td>
<td>GARP</td>
<td>MaxEnt</td>
<td>GARP</td>
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<td>30.5</td>
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</tbody>
</table>

* For example, in Maine, MaxEnt predicted that 5.4% of the land area has 61-70% probability of being suitable, whereas GARP predicted 2.6% of the state’s land area in this suitability range.
Table 5. Variables used for the vulnerability assessment (Magness et al. 2011) of the suitable habitat for monarch butterfly roost sites along the Atlantic Coast, U.S.A.

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<tr>
<th>Category</th>
<th>Variable</th>
<th>Source</th>
<th>URL</th>
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<td><a href="https://coast.noaa.gov/slrdata/">https://coast.noaa.gov/slrdata/</a></td>
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<tr>
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<td>Temperature Increase</td>
<td>Community Climate System Model</td>
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<td>Land Use Change</td>
<td>Theobald 2030 Projections</td>
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<td>EPA Ecoregions</td>
<td><a href="https://www.epa.gov/eco-research/ecoregions">https://www.epa.gov/eco-research/ecoregions</a></td>
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<td>Current Predicted Suitability Rating</td>
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<td></td>
<td>Landscape Context</td>
<td>Chapter 1</td>
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Table 6. Hectares of model-predicted suitable monarch roost habitat (suitability value >0.70) in predicted vulnerability bins by state. Bins represent scaled vulnerability index values in a 10-point range. Predominant vulnerability bin for each state is highlighted in gray. For example, in Alabama, 452 ha (>40%) of predicted suitable habitat has a vulnerability score of 31-40.

<table>
<thead>
<tr>
<th>State</th>
<th>State Land Area</th>
<th>0-10</th>
<th>11-20</th>
<th>21-30</th>
<th>31-40</th>
<th>41-50</th>
<th>51-60</th>
<th>61-70</th>
<th>71-80</th>
<th>81-90</th>
<th>91-100</th>
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<td>555</td>
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<td>5,650</td>
<td>10,761</td>
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<td>314</td>
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</table>
Table 7: Hectares of model predicted suitable (≥ 0.70) monarch roost habitat in conservation lands by state. PAD-US conservation categories are (1) managed for biodiversity - disturbance events proceed or are mimicked; (2) managed for biodiversity - disturbance events suppressed; (3) managed for multiple uses - subject to extractive or OHV use; (4) no known mandate for protection. Shaded cells show PAD-US categories with the most area.

<table>
<thead>
<tr>
<th>State</th>
<th>Amount of Conservation Land in State (ha)</th>
<th>% of Monarch Habitat in Conservation Land</th>
<th>Non-Conserved</th>
<th>Suitable Monarch Habitat (ha)</th>
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Table 8. Percentage of conservation lands in Zonation priority bins by state. Columns represent all conservation land in the given state, and rows represent Zonation recommended prioritization partitioned by PAD-US category.

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a. For example, in Maine conservation lands, 2.25% are PAD-US Category 1 with a recommended Zonation prioritization between 61 and 80%; 3.65% are PAD-US Category 2 with a recommended Zonation prioritization between 61 and 80%; 4.74% are PAD-US Category 3 with a recommended Zonation prioritization between 61 and 80%; and 0.01% are PAD-US Category 4 with a recommended Zonation prioritization between 61 and 80%.
Table 9. Percentage of conservation lands in Zonation priority bins by EPA Level III ecoregion. Columns represent all conservation land in the given ecoregion, and rows represent the Zonation recommended prioritization partitioned by PAD-US category.

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<th>Blue Ridge</th>
<th>Central Appalachian</th>
<th>Eastern Great Lakes Lowlands</th>
<th>Interior Plateau</th>
<th>Middle Atlantic Coastal Plain</th>
<th>North Central Appalachian</th>
<th>NE Coastal Zone</th>
<th>NE Highlands</th>
<th>Northern Allegheny Plateau</th>
<th>Northern Piedmont</th>
<th>Piedmont</th>
<th>Ridge and Valley</th>
<th>SE Plains</th>
<th>Southern Coastal Plain</th>
<th>SW Appalachian</th>
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a. For example, of conservation lands within the Acadian Plains and Hills, 3.97% are PAD-US Category 1 with a recommended Zonation prioritization between 61 and 80%; 5.61% are PAD-US Category 2 with a recommended Zonation prioritization between 61 and 80%; 12.40% are PAD-US Category 3 with a recommended Zonation prioritization between 61 and 80%; and 0.01% are PAD-US Category 4 with a recommended Zonation prioritization between 61 and 80%.
Figure 1. Decision process for review of citizen scientist databases to identify records of reported Monarch occurrences to include in model development.
Figure 2. Receiver Operating Characteristic (ROC) Curve for Maximum Entropy (A) and GARP (B) models of Monarch migratory roost site suitability in the Atlantic Flyway. MaxEnt algorithm conducted 3 replicates, black line represents average value, gray area represents +/- one standard deviation. Sensitivity is 1 - the Omission Rate, 1 - Specificity is the Fractional Predicted Area. The AUC indicates predictive capability of the model where 1 equals a perfect model and 0.5 equals random chance. The True Skill Statistic (TSS) shows the predictive power at a given threshold (0.7) where 0 is no better than random and 1 is a perfect model.
Figure 3. Maximum Entropy predicted habitat suitability for Monarch migratory roost habitat in the Atlantic Flyway. Boxes represent areas enlarged to provide viewing detail. Maps are presented for each state in the Supplemental Material. Boxes represent areas enlarged to provide viewing detail.
Figure 4. Genetic Algorithm for Ruleset Prediction (GARP) predicted habitat suitability for Monarch migratory roost habitat in the Atlantic Flyway. Boxes represent areas enlarged to provide viewing detail. Maps are presented for each state in the Supplemental Material.
Figure 5. Relative differences between Maximum Entropy (MaxEnt) and Genetic Algorithm for Ruleset Prediction (GARP) predicted habitat suitability for Monarch migratory roost sites in the Atlantic Flyway. In model comparisons, GARP + represents areas where the GARP algorithm predicted greater suitability, and MaxEnt + represents areas MaxEnt predicted greater suitability. Even indicates agreement between the algorithms. Boxes represent areas enlarged to provide viewing detail. Maps are presented for each state in the Supplemental Material.
Figure 6. Relative differences in suitability prediction between the MaxEnt and GARP algorithms. Bars represent the percent of total land area in the study region each model rated as more suitable than the other, in 10% increments. Inset shows the hectares of land ranked in each bin of suitability by each model.
Figure 7. Areas predicted to contain suitable habitat (≥ 0.70) for Monarch migratory roost sites in the Atlantic Flyway as identified by the combined model output from Maximum Entropy (MaxEnt) and Genetic Algorithm for Ruleset Prediction (GARP) models. Boxes represent areas enlarged to provide viewing detail. Maps are presented for each state in the Supplemental Material.
Figure 8. Tennessee River Valley with reported observations of Monarch roost sites by month and model predicted suitable habitat. There is a westward shift of suitable habitat within the river valley, with later observations generally in the western side of the valley. Data from this area are limited, and additional surveys in this area may determine distribution of migrating Monarchs navigating through the Appalachian Mountains via the Tennessee River Valley.
Figure 9. Environmental variable response curves for the four variables (Distance to Coast, Distance to Rivers, Predominant Crop Cover, Elevation) explaining the most variation in the Maximum Entropy model of roost site suitability for migrating Monarchs in the Atlantic Flyway. Black represents mean and gray represents +/- 1 standard deviation. Response curves for other variables are presented in Supplementary Material. USDA Crop Codes a for the Predominant Crop Cover are available at https://nassgeodata.gmu.edu/CropScape/.
Figure 10. Difference between model predicted suitability and evaluator assessed suitability of Monarch migratory roost habitat in the Atlantic Flyway by four reviewers each evaluating 250 test point locations and 50 control point locations.
Figure 11. Evaluator assessed suitability versus Maximum Entropy model predicted suitability for dominant land cover types within a 100-meter radius of random points throughout the model’s area of coverage. All (A) includes all training points. Pasture (B) is areas appearing to be covered by short non-woody vegetation. Forest (C) is areas covered by woody vegetation. Agriculture (D) is areas showing row crops or evidence of tilling. Urban (E) represented areas with buildings. No majority (F) is areas where no single category comprised > 50% of the 100-meter radius area. The thick line is a 1:1 slope, while the thin line is the slope of the linear regression model comparing the evaluator and model prediction.
Figure 12. Schematic of sensitivity factors for vulnerability analysis. The numbers represent the Maximum Entropy Model predicted likelihood of suitability. The focal cell (green) value represents the current predicted probability of being suitable, in this case 0.82. The average of the surrounding cells represents the probability of being suitable habitat in the landscape context for that focal cell, in this case 0.55 \((0.78+0.61+0.42+0.67+0.33+0.55+0.15+0.91)/8\). This calculation was repeated for every cell in the study area.

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Figure 13. Schematic diagram of variable combinations to identify regional vulnerability of monarch roosting habitat, based on Magness et al. 2011. Blue areas are high value for the factor considered, while yellow is low value.

\[
\begin{align*}
\text{a. } & \left( \frac{\text{Sea Level Rise} + \text{Temperature Change} + \text{Land Use Change}}{3} \right) = \text{Exposure} \\
\text{b. } & \left( \frac{\text{Conservation Status} + \text{Proximity to Ecoregion Boundary} + \text{Regional Changes in Elevation} + \text{Proximity to Suitable Habitat}}{4} \right) = \text{Adaptive Capacity} \\
\text{c. } & \left( \frac{\text{Current Precipitation Stability} + \text{Landscape Context}}{2} \right) = \text{Sensitivity}
\end{align*}
\]
Figure 14. Morphological Spatial Pattern Analysis class designations. Figure taken from MSPA Online documentation, https://forest.jrc.ec.europa.eu/en/activities/lpa/mspa/. For visibility and interpretability, we compressed our outputs into two categories. Core/Edge contained core and edge, while Fragmentation combined all other types (Islets, Loops, Bridges, Perforations, and Branches).
Figure 15. Conceptual diagram of Zonation decision making process, showing the results of the same area with and without a conservation mask (see Zonation methods), with areas receiving high, medium, and low ranking scores. Numbers represent simplified MaxEnt output cell scores for probability of suitable habitat. Darkened cells represent areas with a score sufficient to qualify under our good habitat criteria (Suitability ≥ 0.70). Green cells represent theoretical conservation areas. In high scoring areas there are frequent high scores clustered together. In medium scoring areas there are still many high suitability cells but less conglomeration, and in low scoring areas there are few high suitability cells and they are spread apart.
Figure 16. Predicted vulnerability of areas with high probability (≥ 0.70) of being suitable for monarch roosting habitat (identified with MaxEnt and GARP models, Chapter 1). Boxes represent areas enlarged to provide viewing detail. Maps are presented for each state in the Supplemental Material.
Figure 17. Example regions showing how Adaptive Capacity, Sensitivity, and Exposure affect the Vulnerability rating of areas throughout the Atlantic Flyway. Blue areas are high for the factor considered, while yellow is low.
Figure 18. Proportions of conservation lands, lands that are suitable habitat for monarch roost sites, and that are both in conservation status and suitable for monarch roost sites. Table 3 contains corresponding area estimates.
Figure 19. Predicted suitable habitat overlaid on PAD-US Conservation Land Categories with EPA level III ecoregions. Boxes represent areas enlarged to provide viewing detail. Maps are presented for each state in the Supplemental Material.
Figure 20. Morphological Spatial Pattern Analysis of predicted suitable habitat as defined by spatial patterns. See Figure 2 for how pattern classes are combined to indicated core/edge and fragmentation types. Boxes represent areas enlarged to provide viewing detail. Maps are presented for each state in the Supplemental Material.
Figure 21. Hectares of predicted suitable habitat in categories for each EPA Level III Ecoregion as defined by Morphological Spatial Pattern Analysis. Core is defined as an area that is entirely surrounded by suitable habitat, edge is defined as the cells that make up the boundary of core areas. Category descriptions available in Figure 3 and Soille and Vogt (2008).
Figure 22. Zonation-defined protection priorities based on predicted suitability and connectivity in the Atlantic Flyway. Boxes represent areas enlarged to provide viewing detail. Maps are presented for each state in the Supplemental Material.
Figure 23. Cumulative proportion of conservation lands by Zonation prioritization of value for monarch roosting habitat. Lines represent states. The top row of the X axis represents range of zonation prioritization, and the bottom row represents the PAD-US category. Gridlines designate Zonation prioritization level bins. West Virginia, North Carolina, and New Hampshire are bolded to show States with a large, moderate, and small proportion of high quality lands in conservation areas, respectively.
Figure 24. Cumulative proportion of conservation lands by Zonation prioritization of value for monarch roosting habitat. Lines represent EPA Level III ecoregions, with the top row of the X axis representing ranges of zonation prioritization, and the bottom row representing PAD-US categories. Gridlines designate cutoffs between Zonation prioritization levels. The North Central Appalachians, Northern Allegheny Plateau, and Atlantic Coastal Pine Barrens are bolded to show examples of ecoregions where there is a large, moderate, and small proportion of high quality Zonation lands in conservation areas, respectively.
Figure 25. Zonation identified suitable roosting sites of the Atlantic Flyway showing Zonation indicated protection priorities based on predicted suitability, connectivity, and current conservation status. While Figure 9 shows the prioritized map based off of purely biological considerations, this figure is weighted to show preference towards current conservation zones and the lands immediately around them. Boxes represent areas enlarged to provide viewing detail. Maps are presented for each state in the Supplemental Material.
Figure 26. Map of the top 10% Zonation ranking using the biologically optimum model colored by vulnerability rating. Blues represent the bottom 50 vulnerability rankings (areas of least risk) while reds represent the top 50 vulnerability rankings (areas of greatest risk). Lighter colors represent more extreme vulnerability scores.
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APPENDIX A: SURVEY USED IN VALIDATION SMARTPHONE APPLICATION

Site Evaluation Survey Questions

I acknowledge that I have read the Disclosure and Access Information [https://umaine.edu/mainecoopunit/monarch-validator-disclosure/](https://umaine.edu/mainecoopunit/monarch-validator-disclosure/). Indicate that you fully understand and agree with the terms listed on this webpage by providing the Username revealed by selecting the “YES” button at the bottom of the Disclosure and Access Information page. Username is ____________. We can not use your responses without your acceptance of these terms and conditions.

When completed, please e-mail your survey responses and photos to monarch-model-group@maine.edu if you do not complete the survey on a smartphone or desktop computer.

1) The ID of this (or closest) point is _______________.

2) I would describe myself as a (select one):
   - Field biologist
   - Professional entomologist
   - Hobbyist with little experience
   - Hobbyist with lots of experience.

3) What % of the landscape is grassland/agriculture?
   - Provide a % from 0-100%, in 10% increments ______

4) What type of grassland/agriculture is visible? (Select one)
   - Pasture/Meadow
   - Cultivated Crop
   - Mix--even split
   - Mix--mostly pasture/meadow
   - Mix--mostly cultivated crop

5) What % is development?
   - Provide a % from 0-100%, in 10% increments ______

6) What type of development is visible? (Select one)
   - Residences and lawns
   - Heavy pavement
   - Mix--even split
   - Mix--mostly residences and lawns
   - Mix--mostly heavy pavement

7) What % is forest with mid- or understory?
   - Provide a % from 0-100%, in 10% increments ______

8) What type of forest with mid- or understory is visible? (Select one)
   - Evergreen
   - Deciduous
   - Mix--even split
   - Mix--mostly evergreen
   - Mix--mostly deciduous
9) What % is forest without mid- or understory?
   Provide a % from 0-100%, in 10% increments _______

10) What type of forest without mid- or understory is visible? (Select one)
    Evergreen
    Deciduous
    Mix--even split
    Mix--mostly evergreen
    Mix--mostly deciduous

11) What % scrub/shrub?
    Provide a % from 0-100%, in 10% increments _______

12) What % is wetland?
    Provide a % from 0-100%, in 10% increments _______

13) What type of wetland is visible? (Select one)
    Open water
    Emergent wetland
    Shrub/woody
    Mix--even split
    Mix--mostly open water
    Mix--mostly emergent wetland
    Mix--mostly shrub/woody

14) I have a location lat/long or UTM coordinates tagged on my photos. YES or NO
    If NO, Latitude (or UTM Y) _______________ Longitude (or UTM X) ________________

    If reporting location coordinates in UTM, the zone # is _____________

15) What is the local suitability (at your feet)? (Select one)
    Totally unsuitable
    Minimally suitable (1-25%)
    Moderately suitable (26-50%)
    Generally suitable (51-75%)
    Highly suitable (76-100%)

16) What is the landscape suitability (out to the horizon)? (Select one)
    (Totally unsuitable
    Minimally suitable (1-25%)
    Moderately suitable (26-50%)
    Generally suitable (51-75%)
    Highly suitable (76-100%)

17) Are monarchs visible at the site? (Select one)
    Yes, 1-5 monarchs
    Yes, >5 monarchs
    No monarchs are visible
APPENDIX B: MAXENT ENVIRONMENTAL VARIABLE RESPONSE CURVES.

Figure B-1. Aspect

Aspect Categories – 1: Northeast, 2: Southeast, 3: Southwest, 4: Northwest
Figure B-2. Crop Cover

1=Corn, 24=Winter Wheat, 36=Alfalfa, 59=Sod Grass/Grass Seed, 68=Apples 74=Pecans, 111=Open Water, 131=Barren, 152=Shrubland, 176=Grassland/Pasture, 195=Herbaceous Wetland, 229=Pumpkins

Full list of codes available at https://nassgeodata.gmu.edu/CropScape/
Figure B-3. Elevation
Figure B-4. Distance to Coast

![Graph showing the relationship between distance to coast and estimated suitability. The x-axis represents distance to coast in decimal degrees, ranging from 0 to 5. The y-axis represents estimated suitability, ranging from 0.0 to 1.0. The graph shows a decreasing trend in estimated suitability as distance to coast increases.]

The graph illustrates the decline in estimated suitability as the distance to the coast increases, indicating a possible negative correlation between the two variables.
Figure B-5. Distance to Conservation Land
Figure B-6. Distance to Lake
Figure B-7. Distance to River
Figure B-8. Distance to Wetland
Figure B-9. Human Influence

Estimated Suitability

Human Influence (Development Level)
Figure B-10. Land-Cover Classification

21-24=Developed, 41-43=Forest, 71=Grassland, 81-82=Cropland

Figure B-11. Solar Radiation
Figure B-12. Temperature

Estimated Suitability vs. Average Temperature (Celsius X 10)
Figure B-13. Wind Speed
APPENDIX C: STATE LEVEL MAPS OF MAXENT PREDICTIONS (CORRESPONDS TO FIGURE 3)

Figure C-1. Alabama
Figure C-2. Connecticut
Figure C-4. Georgia
Figure C-5. Kentucky
Figure C-6. Maine
Figure C-7. Maryland
Figure C-8. Massachusetts
Figure C-9. New Hampshire
Figure C-10. New Jersey
Figure C-11. New York
Figure C-12. North Carolina
Figure C-13. Ohio
Figure C-14. Pennsylvania
Figure C-15. Rhode Island
Figure C-16. South Carolina
Figure C-17. Tennessee
Figure C-18. Vermont
Figure C-19. Virginia
Figure C-20. West Virginia
APPENDIX D: STATE LEVEL MAPS OF GARP PREDICTIONS (CORRESPONDS TO FIGURE 4)

Figure D-1. Alabama
Figure D-2. Connecticut
Figure D-3. Delaware
Figure D-4. Georgia
Figure D-5. Kentucky
Figure D-6. Maine
Figure D-7. Maryland
Figure D-8. Massachusetts
Figure D-9. New Hampshire
Figure D-10. New Jersey
Figure D-11. New York
Figure D-12. North Carolina
Figure D-13. Ohio
Figure D-14. Pennsylvania
Figure D-15. Rhode Island
Figure D-16. South Carolina
Figure D-17. Tennessee
Figure D-18. Vermont
Figure D-19. Virginia
Figure D-20. West Virginia
APPENDIX E: STATE LEVEL MAPS OF MAXENT AND GARP PREDICTIONS COMPARATIVE SUITABILITY (CORRESPONDS TO FIGURE 5)

Figure E-1. Alabama
Figure E-2. Connecticut
Figure E-3. Delaware
Figure E-4. Georgia
Figure E-5. Kentucky
Figure E-6. Maine
Figure E-7. Maryland
Figure E-8. Massachusetts
Figure E-9. New Hampshire
Figure E-10. New Jersey
Figure E-11. New York
Figure E-12. North Carolina
Figure E-13. Ohio
Figure E-14. Pennsylvania
Figure E-15. Rhode Island
Figure E-16. South Carolina
Figure E-17. Tennessee
Figure E-19. Virginia
Figure E-20. West Virginia
APPENDIX F: STATE LEVEL MAPS OF PREDICTED SUITABLE HABITAT
(CORRESPONDS TO FIGURE 7)

Figure F-1. Alabama
Figure F-2. Connecticut
Figure F-3. Delaware
Figure F-4. Georgia
Figure F-5. Kentucky
Figure F-6. Maine
Figure F-7. Maryland
Figure F-8. Massachusetts
Figure F-9. New Hampshire
Figure F-10. New Jersey
Figure F-11. New York
Figure F-12. North Carolina
Figure F-13. Ohio
Figure F-14. Pennsylvania
Figure F-15. Rhode Island
Figure F-16. South Carolina
Figure F-17. Tennessee
Figure F-18. Vermont
Figure F-19. Virginia
Figure F-20. West Virginia
APPENDIX G: STATE LEVEL MAPS OF VULNERABILITY PREDICTIONS (CORRESPONDS TO Figure 5). SMALLER MAPS REPRESENT THE AVERAGED VALUES FOR EACH OF THE PRIMARY CATEGORIES

Figure G-1. Alabama
Figure G-2. Connecticut
Figure G-3. Delaware
Figure G-4. Georgia
Figure G-5. Kentucky
Figure G-6. Maine
Figure G-7. Maryland
Figure G-8. Massachusetts
Figure G-10. New Jersey
Figure G-11. New York
Figure G-12. North Carolina
Figure G-13. Ohio
Figure G-14. Pennsylvania
Figure G-15. Rhode Island
Figure G-16. South Carolina
Figure G-17. Tennessee
Figure G-18. Vermont
Figure G-19. Virginia
Figure G-20. West Virginia

Habitat Vulnerability
Rating
- 0 - 20
- 20 - 40
- 40 - 60
- 60 - 80
- 80 - 100

Adaptive Capacity, Sensitivity, and Exposure
- High : 100
- Low : 1

Adaptive Capacity
Sensitivity
Exposure
Figure H-1. Alabama
Figure H-2. Connecticut
Figure H-3. Delaware
Figure H-4. Georgia
Figure H-5. Kentucky
Figure H-6. Maine
Figure H-7. Maryland
Figure H-8. Massachusetts
Figure H-9. New Hampshire
Figure H-10. New Jersey
Figure H-11. New York
Figure H-12. North Carolina
Figure H-13. Ohio
Figure H-14. Pennsylvania
Figure H-15. Rhode Island
Figure H-16. South Carolina
Figure H-17. Tennessee
Figure H-18. Vermont
Figure H-19. Virginia
Figure H-20. West Virginia
APPENDIX I: STATE LEVEL MAPS OF MORPHOLOGICAL SPATIAL PATTERN ANALYSIS OF PREDICTED SUITABLE HABITAT (CORRESPONDS TO FIGURE 9)

Figure I-1. Alabama
Figure I-2. Connecticut
Figure I-3. Delaware
Figure I-4. Georgia
Figure I-5. Kentucky
Figure I-6. Maine
Figure I-8. Massachusetts
Figure I-9. New Hampshire
Figure I-10. New Jersey
Figure I-11. New York
Figure I-12. North Carolina
Figure I-13. Ohio
Figure I-14. Pennsylvania
Figure I-15. Rhode Island
Figure I-16. South Carolina
Figure I-17. Tennessee
Figure I-18. Vermont
Figure I-19. Virginia
Figure I-20. West Virginia
APPENDIX J: STATE LEVEL MAPS OF ZONATION-DEFINED PROTECTION PRIORITIES BASED ON PREDICTED SUITABILITY AND CONNECTIVITY (CORRESPONDS TO FIGURE 11)

Figure J-1. Alabama
Figure J-2. Connecticut
Figure J-3. Delaware
Figure J-4. Georgia
Figure J-5. Kentucky
Figure J-6. Maine
Figure J-7. Maryland
Figure J-8. Massachusetts
Figure J-9. New Hampshire
Figure J-10. New Jersey
Figure J-11. New York
Figure J-12. North Carolina
Figure J-13. Ohio
Figure J-14. Pennsylvania
Figure J-15. Rhode Island
Figure J-16. South Carolina
Figure J-17. Tennessee
Figure J-18. Vermont
Figure J-19. Virginia
Figure J-20. West Virginia
APPENDIX K: STATE LEVEL MAPS OF ZONATION-DEFINED PROTECTION PRIORITIES BASED ON PREDICTED SUITABILITY, CONNECTIVITY, AND CURRENT CONSERVATION STATUS (CORRESPONDS TO FIGURE 14)

Figure K-1. Alabama
Figure K-2. Connecticut
Figure K-3. Delaware
Figure K-4. Georgia
Figure K-5. Kentucky
Figure K-6. Maine
Figure K-7. Maryland
Figure K-8. Massachusetts
Figure K-9. New Hampshire
Figure K-10. New Jersey
Figure K-11. New York
Figure K-12. North Carolina
Figure K-13. Ohio
Figure K-14. Pennsylvania
Figure K-15. Rhode Island
Figure K-16. South Carolina
Figure K-17. Tennessee
Figure K-18. Vermont
Figure K-19. Virginia
Figure K-20. West Virginia
APPENDIX L: STATE LEVEL MAPS OF THE TOP 10% ZONATION RANKING USING THE BIOLOGICALLY OPTIMUM MODEL COLORED BY VULNERABILITY RATING (CORRESPONDS TO FIGURE 15)

Figure L-1. Alabama
Figure L-2. Connecticut
Figure L-3. Delaware
Figure L-4. Georgia
Figure L-5. Kentucky
Figure L-6. Maine
Figure L-7. Maryland
Figure L-8. Massachusetts
Figure L-9. New Hampshire
Figure L-10. New Jersey
Figure L-11. New York
Figure L-12. North Carolina
Figure L-13. Ohio
Figure L-14. Pennsylvania
Figure L-15. Rhode Island
Figure L-16. South Carolina
Figure L-17. Tennessee
Figure L-18. Vermont
Figure L-19. Virginia
Figure L-20. West Virginia
BIOGRAPHY OF THE AUTHOR

Brandon Boxler was born in North Kansas City, Missouri on June 17, 1987. His childhood was split between five states, ending in Minnesota where he received a High School diploma from the School of Environmental Studies in 2006. He attended the United States Military Academy at West Point and graduated in 2010 with a Bachelor’s degree in Environmental Sciences and Geospatial Information Sciences. He commissioned into the United States Army as a Military Police Officer and served in multiple roles including as a Platoon Leader, Rear Detachment Commander, Battalion Training Officer, and Battalion Headquarters and Headquarters Detachment Officer in Charge. He left the Army in 2017 and entered the Ecology and Environmental Sciences graduate program at The University of Maine. Brandon has a wife, Beth, and two children, Marian and Teddy. He is currently working for the United States Forest Service as a GIS Specialist at the Chugach National Forest based out of Anchorage, Alaska. Brandon is a candidate for the Master of Science degree in Ecology and Environmental Sciences from the University of Maine in December 2020.