University of Nevada, Reno

# Fantastic Birds and Where to Find Them

A dissertation submitted in partial fulfillment of the
requirements for the degree of Doctor of Philosophy in
Geography

by

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THE GRADUATE SCHOOL

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# ABSTRACT

I investigated avian-habitat relationships in three related study systems. In my first chapter I characterize the nonbreeding habitat of the western subspecies of Willow Flycatchers (*Empidonax traillii subspp.*), including the federally endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus)*, with a range-wide species distribution model. The three western subspecies of Willow Flycatchers migrate between the riparian landscapes in the western and southwestern United States to the riparian areas in tropical dry forests along the Pacific coast of Central America. The predictive model of potential habitat suitability will be corroborated on the ground by conservation collaborators and used to locate new long-term monitoring sites, and acquire new protected areas. Unlike the migratory western Willow Flycatchers, The Nicaraguan Grackle is a residential (non-migratory) bird that occupies more open wetlands and riparian areas around the Nicaraguan great lakes and the Caño Negro wetland complex of Costa Rica. In my second chapter, I create urgently-needed baseline maps of habitat suitability with varied levels of freshwater recurrence for the Nicaraguan Grackle (*Quiscalus nicaraguensis*). This map of predicted habitat suitability will be used as evidence to garner elevated protection status for this understudied, declining species. Finally, in my third chapter, I use unmanned aerial systems (UAS or drones) to explore methods to improve habitat variables used in nest-site selection modeling for Mojave Desert riparian songbirds, including the endangered Least Bell’s Vireo (*Vireo bellii pusillus*). I compared UAS and satellite image products of vegetation structure within first and second order resource selection functions for breeding and nesting habitat in Amargosa Canyon. The ultimate goal with this research was to determine key features of vegetation structure that influence nest-site selection to inform habitat restoration upstream on the Amargosa River.

# DEDICATION

to my family, Dennis, Susan, and Nicole Phillips, whose encouragement
and unwavering support drove me to truly achieve my dreams.

to my loving husband and best friend Sean, words cannot express my gratitude
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Something that was very important to me in choosing a PhD program was to find one in which I could have a direct impact or influence on conservation management of threatened species. My transition from Zoology to Fisheries and Wildlife for my masters made me realize that the science I was most passionate about had these direct applications to management or conservation practice. Once I became captivated by the distributions of wildlife, Geography became the obvious option for advancing my knowledge, skills, and practice. Over the past five years, I have learned innumerable lessons from the field of Geography that drove the direction of my research. My research has been guided by a group of academic and community members that grew every year as I advanced in my program. None of the studies featured in these three chapters were completed without the guidance and input of collaborators, mentors, and peers.

I want to specifically acknowledge my advisor, Tom Albright, for his support, guidance, and patience throughout this degree program. Whether I was coming up against a tight grant deadline or working through self-doubt, I could always count on him for judgement-free conversation and advise. Tom never had unreasonable expectations for me and allowed me to find my own ways of accomplishing tasks, which I really grew to appreciate. I also learned a lot from Tom as an instructor, in particular, how to engage higher levels of learning from more junior students. I also want to thank Tom’s wife, Katia Albright, who I shared so many fun lunchtime conversations with. Katia not only became an instant friend, but was an amazing resource for opportunities at the university. She always made me feel seen, heard, and valued. I will genuinely miss being a part of their lives in Reno, but hope that we will always stay connected.

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Finally, I would be remiss if I didn’t take the time to acknowledge my cohort and peers. Graduate school is a challenging time and I’m convinced that the only way to get through it is to find people who inspire your personal growth and progress. I was so fortunate to go through this journey with Jon DeBoer, Anjana Parandhaman, Steve Hromada, Ranae Sullivan, Ally Xiong, Cory Mitchell, and Danielle Miles (among others). Between all of the lab meetings, practice talks, late night coding sessions, epic dinners and weeknight hangouts—we made memories I will cherish for the rest of my life.

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# INTRODUCTION

Birds have fascinated humankind long before Darwin mused the bills of finches. Beyond their iconic status in culture, lore, and symbology, birds have adapted to make use of nearly every ecosystem *and* provide globally important ecosystem services. Birds are important to agriculture, economies, and ecosystem health (Wenny *et al*. 2011; Whelan *et al*. 2015). Birds regulate agricultural and urban pests, pollinate crops and native plants, disperse seeds, regulate carrion and carrion-vectored diseases, and have inspired countless technological advances in human civilization (Whelan *et al*. 2008). Despite birds' importance to humanity, anthropogenic environmental changes are the primary drivers of global avian decline. Habitat loss and degradation, climate change, chemical and plastic pollution, overharvesting, and other anthropogenic mortalities have contributed substantially to global declines in avifauna (Grenyer *et al*. 2006). A recent study published in *Science* estimated that nearly 3 billion birds have disappeared from North America alone in the last 50 years (Rosenberg *et al*. 2019). This monumental decline in avian abundance impacts both rare and common species, and impacts birds in nearly all biomes (Gaston and Fuller 2008, Lee et al. 2022). And while birds are indeed among the most studied taxa (Bonnet et al. 2002, Donaldson et al. 2016, Troudet et al. 2017), not all species are represented equally in the literature. With an estimated 10,000-18,000 bird species on Earth (Barrowclough *et al*. 2016), there are many that remain undescribed, data deficient, or understudied. A migratory species may be well-studied in its breeding range but not in its migratory or non-breeding range. Even species that are readily accessible with a very limited range may be virtually unrepresented in the scientific literature.

In the last 100 or so years that people have noticed birds declining, our investigative focus has shifted more heavily to where we can find these birds and how can we help them persist in our rapidly changing world. While quantifying the populations of declining birds is an essential piece of conservation management, it is only half of the puzzle. The leading threat to most declining birds is habitat loss (Lee et al. 2022), and thus, studies that focus on the quality and distribution of bird habitat play a critical, complementary role in conservation planning and management (Johnson and Gillingham 2005, Cayuela et al. 2009, Lawler et al. 2010). Habitat has been defined in a variety of ways, but at its core it is species-specific term used to describe the sum of needs required by an organism to survive, reproduce, and/or persist in the abiotic and biotic environment (Hall et al. 1997; Krausman 1999). Characterizing the suitability and availability of habitat is essential to understand the basic needs of a target species (Franklin 2010a). The creation of habitat suitability maps is especially important for species that lack a strong presence in the scientific literature (Guisan and Thuiller 2005, Elith et al. 2006), effectively establishing a baseline for contextualizing the species in space.

Modern ecology boasts a substantial collection of statistical analyses and global databases that enable wildlife investigation at continental or global scales. In this dissertation, I will use species distribution models, resource selection functions, and drone-based habitat characterization to map distributions and determine key environmental variables for several species of migratory and resident riparian songbirds.

Species distribution modeling (or habitat suitability modeling) is a widely applied methodology that ascended during the period of rapid spatial science advancement.

Specifically, species distribution modeling developed from ecological gradient analysis in in the early 1970s as biogeography and landscape ecology became more established (Franklin 2010a; Cox et al., 2016). These modeling approaches are similar in that they both attempt to define correlations between target species and features of their environment by modeling presences and absences (or random pseudo-absences). Both methods have evolved significantly alongside the expansion of open-source programming platforms and can now be customized to answer deeper questions relating to where, how, and why a species selects or uses a given habitat (Porfirio et al. 2014, Marcer et al. 2013). The habitat suitability maps and habitat usage information that result from these modeling approaches can be used to define range limits, select new survey or translocation sties, and identify key environmental features that define high-quality, marginal, or sink habitat (Franklin 2010b, Lawler et al. 2010, Marcer et al. 2013).

Beyond these fundamental methods for characterizing habitat usage and species distributions, it is also important to build upon these processes with new sources of information. A recurring challenge in conservation biogeography is our ability to obtain environmental data at a broad enough extent or fine enough scale to draw biologically relevant conclusions for our target species (Richardson and Whitaker 2010, Franklin 2013). Since the 1970s, biogeographers have relied on satellite-derived imagery products to represent environmental and climate variables in these models (Goodchild 2010, Franklin 2013). Satellite-derived imagery products continue to improve, often offering global extents and finer grains. Grains of 1 km are nearly standard for global imagery products, and it is not uncommon to see products offered at grains of 100 m or less (Guisan et al. 2007). Environmental habitat variables at finer grains can be used for more precise targeting of future survey sites or range limit estimates. However, some investigations seek answers to study questions for areas that don’t exceed a 1-km plot. The advancement of drone technology has enabled scientists to create ultra-fine grain (sub 10-cm) maps of habitat imagery. Ultra-fine habitat imagery products may offer an opportunity to produce models that provide more nuanced answers to questions about nest-site selection and breeding habitat use.

In my dissertation, I investigate avian-habitat relationships in three separate but related study systems. Each chapter of my dissertation is set within a unique geography of space, place, and even time. I characterize nonbreeding, residential, or breeding habitat in riparian areas of the Pacific tropical dry forests of Central America, the Pacific tropical wetlands of Nicaragua, and the Mojave Desert in the southwestern United States. The scale of investigation also tightens with each chapter, from the broad extent of Central America to 1-km study sites in the Mojave Desert.

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## **Chapter 1:** Where Western WIFL Winter: A species distribution model for non-breeding Willow Flycatchers (*Empidonax traillii sp.)*

### ABSTRACT

Full life-cycle wildlife management has become the gold standard for the conservation of migratory birds, but many species still lack sufficient study in their non-breeding, wintering grounds. The Willow Flycatcher (*Empidonax traillii*, WIFL) is a small tyrant flycatcher that consists of four subspecies; three of which breed in wetlands of the western US and Canada. Like many neotropical migrants, WIFL migrate from nations with well-funded conservation initiatives and protected areas to regions where formal protections or enforcement may be lacking. While breeding populations of WIFL have been the focus of many scientific investigations and conservation efforts, less has been published about their non-breeding habitat in the neotropics. Conservation practitioners now recognize the importance of studying birds across their full life cycle to better inform management and prevent population declines. I model winter habitat suitability for western subspecies of WIFL from Nayarit, Mexico to northwestern Columbia. Wintering areas are human-dominated landscapes that continue to undergo rampant deforestation and destruction of wetlands, representing a major threat to migratory birds. For this investigation, I ask: what habitat characteristics are best suited to support wintering WIFL and where are they concentrated?  I hypothesize that willow flycatchers are associated with riparian shrub cover, flooded vegetation, and freshwater. I used WIFL survey data collected from 1999 to 2019 and characterized the region with publicly available climate and remote sensing data from CHELSA, Copernicus, and

Global Surface Water Explorer. I modeled relative habitat suitability using general additive models, and random forest algorithms. Results indicate that WIFL are positively associated with complex vegetation cover, warmer climate conditions, and proximity to freshwater. These models identify key suitable wintering habitat, which will be used by our collaborators for the acquisition of new protected areas and land management partnerships for wintering populations of WIFL.

## INTRODUCTION

Migratory birds transcend political boundaries, creating the need for collaboration between countries with sometimes vast differences in management practices. Full life-cycle wildlife management has become the gold standard for the conservation of migratory birds, but many species still lack sufficient study in their non-breeding wintering grounds. The full life-cycle conservation framework highlights the importance of conservation across breeding, migratory, and wintering habitat. The breeding habits and habitat of many threatened and endangered neotropical migrants in the United States are generally well-studied and many are protected. Migratory birds that overwinter in the neotropics face rampant habitat loss and degradation in a landscape that changes with every migration (Hansen et al. 2013), representing a significant potential population sink in their life cycles. In addition, wide-spread poverty and a lack of access to water infrastructure makes riparian areas a prime target for invasion by cattle ranching and subsequent degradation (Betts et al. 2022), with serious effects for species inhabiting them.

The Willow Flycatcher (*Empidonax traillii*) is a small, tyrant flycatcher that breeds in the United States and migrates to the neotropics during the winter months of the northern hemisphere (Finch et al. 2002). Like many neotropical migrants, WIFL migrate from nations with established protections and conservation initiatives to those with limited protections and a rapidly changing landscape. While breeding populations of WIFL have been the focus of many scientific investigations and conservation efforts (see Finch et al. 2000, Hatten 2016, Paxton et aal. 2007, Sogge et al. 2010, Stumpf et al. 2012 and others), less has been published about their non-breeding habitat (though see Paxton et al. 2011), and this study represents the first to attempt to predict habitat suitability across the entire non-breeding range of the western subspecies.

Willow flycatchers have been divided into four subspecies that breed across the United States. The Eastern Willow Flycatcher (*Empidonax traillii traillii*), Little Willow Flycatcher (*E. t. brewsteri*), Great Basin Willow Flycatcher (*E. t. adastus*), and Southwestern Willow Flycatcher (*E. t. extimus*). This study combines non-breeding observation data for the three western subspecies of Willow Flycatcher due to their striking visual similarity and overlapping wintering ranges. The western subspecies of Willow Flycatchers winter from the state of Nayarit, Mexico through Panama, while the more common Eastern Willow Flycatcher overwinters in South America (Paxton et al 2011).

WIFL are a generally riparian-dependent species that use perches like trees and shrubs to watch for insects to hunt (Finch et al. 2002, Stumpf et al. 2012). Willow Flycatchers are important regulators of insects that emerge from riparian ecosystems (Finch et al. 2002). Insect population regulation is an ecosystem service that benefits both people and riparian communities. While preferences for certain plant species have been documented in both breeding and wintering habitats (Sedgwick 2020), this species is not considered a host-plant specialist (Paxton et al. 2007). The Southwestern subspecies of the WIFL is federally listed as endangered in the United States affording it significant breeding habitat protection. Organizations like Paso Pacifico, a non-government organization that does conservation work in Central America have put considerable effort into establishing long-term monitoring sites for SWFL and other threatened neotropical migrants throughout their non-breeding range. Unlike the Least Bell's Vireo (*Vireo bellii pusillis*), another migrant riparian insectivore that breeds in the western united states, the SWFL has not rebounded in response management actions throughout its breeding range (Pottinger and Kus 2019), suggesting a need to focus management actions more heavily in its migratory or nonbreeding range.

I answer important questions about western WIFL subspecies and their non-breeding habitat. For this investigation, I ask: what habitat characteristics are best suited to support wintering WIFL and where are they concentrated? I hypothesized that WIFL were highly associated with riparian shrub cover and proximity to freshwater and expected habitat to be similar to that in their breeding range. My primary objective was to create a species distribution model to direct targeted conservation initiatives for survey design and potential land acquisition of critical habitat areas for wintering WIFL. By modeling wintering habitat suitability, I also aimed to determine which protected areas, territories and areas conserved by indigenous peoples and local communities, and other effective area-based conservation measures may play a key role in promoting non-breeding habitat for this species.

## Study Area:

The Central American neotropics support an incredible diversity of ecosystems and species. The tropical wet and dry forests are a part of a largely human-dominated landscape that is rapidly changing. Central America is experiencing rampant deforestation in response to lack of economic opportunity and pressure to produce inexpensive protein for export (López-Carr et al. 2022). Poor farmers try to make a living by clearing forest for subsistence farming and cattle ranching further and further from the cities (Casillas et al., 2010, López-Carr and Burgdorfer 2013), relying heavily on riparian areas to provide water to cattle. A weak land tenure system and lack of enforcement mean that almost all natural areas are at risk of deforestation (Broegaard, 2005; Finley-Brook & Offen, 2009).

## METHODS

Species distribution models are used to explore and predict the associations between species occurrences and environmental conditions. Open-source programming platforms like R have greatly expanded the applications of species distribution models in conservation, moving beyond the limitations of presence-only modeling with “black box” software. In this study, I primarily use open-source software and publicly available datasets to maintain an open-access modeling framework that can be adapted and expanded upon by future collaborators.

WIFL occurrence data were provided by collaborator Mary J. Whitfield (Southern Sierra Research Station) and Cornell Lab of Ornithology eBird records (Levatich and Ligocki 2019). Field research by MJW took place from 1999 to 2018 and eBird records were retrieved in mid-2019. To characterize the region, I retrieved publicly available gridded climate and remote sensing products from CHELSA, EarthEnv, and the Global Surface Water Explorer (**Table 1.1**). Previous research indicated that WIFL are positively associated with fresh water, complex vegetation structure, and emergent vegetation (Hatten 2016, Paxton et al. 2011), leading me to consider a wide variety of candidate land cover variables (**Table 1.1**). All environmental variable rasters were resampled using bilinear interpolation to a common 100-m grain and cropped to the extent of the study area using the *terra* package. Each model included eight candidate variables: two climatic, one proximity to water, and five fractional land cover variables (**Table 1.1**).

To augment the dataset and achieve a more uniform sampling of the study area, I requested data from the eBird observation database. This dataset did not separate observations by subspecies, and required substantial filtering based on the country, date, and verification status of the observation. The combined dataset numbering 3,722 records exhibited significant spatial autocorrelation and required spatial thinning (**Fig. 1.1**). Both the field records and eBird records are spatially-biased. The field records rely on a survey regime that prioritized recapture of color banded birds, necessitating multiple trips to known habitat rather than systematic sampling of potential habitat. EBird allows community scientists to report an observation anywhere, but it is common for eBird “hotspots” to attract higher numbers of observers wishing to increase their chances of seeing a wide variety of species. For the eBird records, there appears to be a significant sampling bias towards Costa Rica, no doubt due to its status as a global birding hotspot (**Fig. 1.1**). Thus, spatial thinning was carried out in Costa Rica prior to modeling. I spatially thinned records from eBird using a per-pixel approach by creating a 100-m grid and reducing the number of observations per grid cell to 3. I determined grid size and the final number of observations per cell by examining the range of spatial autocorrelation in semivariograms of the observation data. 3,190 records remained after thinning.

Because the WIFL records were not evenly distributed across Central America, I buffered the occurrence data to restrict the spatial extent of future background points and suitability predictions. I chose a 500-km buffer because the occurrences on the Atlantic coasts were approximately 500 km from the Pacific coast. I masked all candidate environmental variables with the 500-km buffer shape file in R to prepare them for modeling.

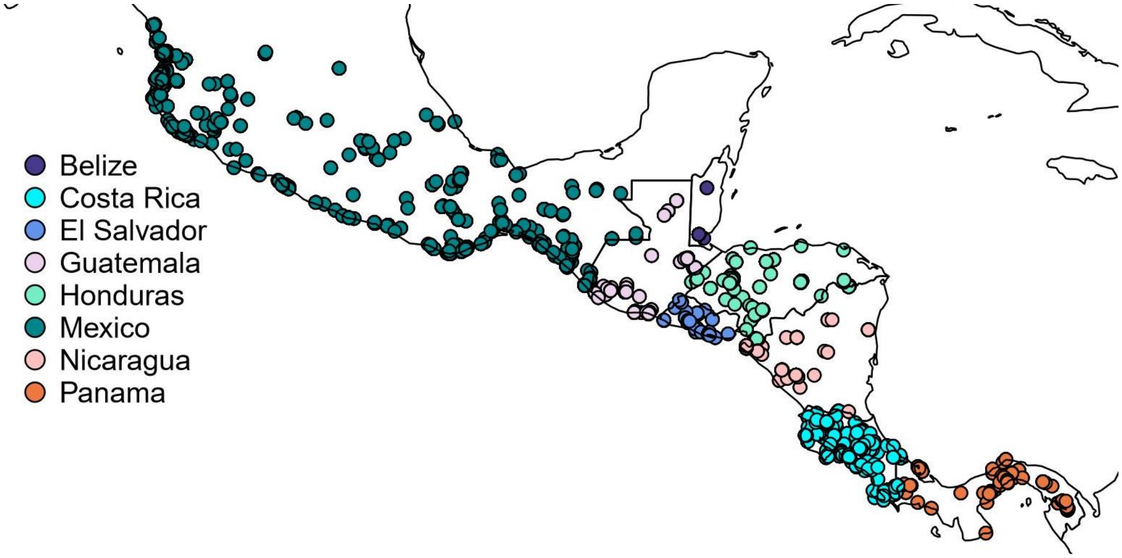

**Figure 1.1: Willow Flycatcher Occurrences** – Occurrence data consist of 532 field records and 3,722 eBird records across nine countries. Note the disproportionately high number of observations in Costa Rica.

**Table 1.1: Environmental Variables** – The initial model included eight candidate environmental variables (two climate variables and eight land cover variables.

| Variable Name | Source | Resolution | Description |
|---|---|---|---|
| Average precipitation | CHELSA Bioclimatology Dataset[1] | 1-km | Average of monthly precipitation Nov – March |
| Average maximum temperature | CHELSA Bioclimatology Dataset[1] | 1-km | Average of monthly max temperatures; Nov – March |
| Distance to Freshwater | JRC Global Surface Water Dataset[2] | 30-m | Percent of the year a pixel is water |
| Herbaceous cover | Copernicus Global Landcover[3] | 100-m | Fractional land cover prevalence per pixel (%) |
| Tree cover | Copernicus Global Landcover[3] | 100-m | Fractional land cover prevalence per pixel (%) |
| Crop cover | Copernicus Global Landcover[3] | 100-m | Fractional land cover prevalence per pixel (%) |
| Shrub Cover | Copernicus Global Landcover[3] | 100-m | Fractional land cover prevalence per pixel (%) |
| Seasonal water cover | Copernicus Global Landcover[3] | 100-m | Fractional land cover prevalence per pixel (%) |

1. Karger et al. 2017, 2. Pekel et al. 2016, 3. Buchhorn et al. 2020

## Analysis:

I used the *biomod2* package in the R programming platform to build and fit the species distribution models (R Core Team 2023, version 4.2.3). Each candidate model was fit with either a generalized additive model (GAM) or random forest (RF) algorithm. I used the *biomod2* package to produce pseudo-absences equal in number to the occurrences using the ‘random’ strategy. Once I combined the occurrences, absences, and pseudo-absences into a common dataset. I ran 20 iterations of each candidate model (RF or GAM) with an 80% data split for model calibration and cross validation and 10 permutations for variable importance estimation. I selected the true skill statistic (TSS), receiver operating characteristic (ROC), and accuracy (ACCURACY) methods to evaluate each model and compare their performance. Each of these performance metrics represents a threshold-dependent, threshold-independent, and basic strategy for evaluating model performance. I plotted the averaged response curves with confidence intervals for each environmental variable. Finally, I used a ‘TSS’ binary transformation method to forecast the prediction surfaces for the 20 iterations of the reduced model, and created an averaged surface for each algorithm.

## RESULTS

The random forest model produced a map of predicted WIFL habitat suitability for their nonbreeding range across Central America (**Figs. 1.2 and 1.3**)**.** Predicted habitat suitability index values ranged from 0 to 1, with 1 indicating higher suitability. The random forest model scored higher than the GAM model in all performance metrics (TSS, ROC, ACC), and thus, only results from the random forest model are presented (**Table 1.2**). Estimates of variable importance indicated that the variables contributing the most to suitability predictions were distance to freshwater, mean precipitation, mean temperature, and percent shrub cover (**Table 1.3**). A subset of the prediction surface is included as an additional figure to improve interpretation of the prediction surface and compare it to the occurrence data (**Fig. 1.3**). The subset map focuses on Nicaragua, which is one location where the endangered SWFL subspecies is believed to be concentrated (**Fig. 1.3**). The mean suitability index for WIFL occurrences based on the predicted habitat suitability is 0.87 (median =0.97).

The variable response plots highlight the effects of each environmental variable on predicted habitat suitability (**Fig. 1.4**). Each environmental variable was plotted against predicted habitat suitability (0-1) across its full range of values within the study area while all other variables were fixed at their median value. The fractional land cover values range from 0–100%, with 0 representing no presence in the pixel and 100 representing complete coverage of the pixel. Therefore, a single 100x100-m pixel may have a mixture of land cover types. Predicted habitat suitability (PHS) was most heavily influenced by *distance to freshwater* (**Fig. 1.4h**), with PHS dropping from 0.70 to 0.45 as distance to freshwater increases. *Mean temperature* was the second most influential environmental variable, with PHS increasing from 0.20 to as high as 0.87 as mean temperature increases (**Fig. 1.4f**). The effects of *mean precipitation* on PHS are more variable, with PHS dropping slightly at lower levels precipitation. Other than *percent seasonal water (*described subsequently), the four remaining fractional land cover variables all had a negative effect on PHS. PHS dropped steeply (0.60 to 0.10) as the *percent shrub cover* per pixel exceeded 20%. *Percent herbaceous cover* per pixel showed a more gradual drop in PHS (0.60 to 0.35) over 20-50% cover. PHS peaked slightly between 25 and 60% *tree cover* per pixel, dropping slightly after 60% cover. PHS was highest for *percent crop cover* between 25 and 40% per pixel, dropping gradually to 0.50 as % cover increased. *Percent seasonal water* only had a slight effect on PHS, increasing quickly and leveling out at low percentages of cover.

In order to draw more concrete conclusions about the concentration of suitable habitat for non-breeding western WIFL, predicted habitat suitability was thresholded at the averaged optimized cutoff value for the model based on all three performance metrics. This value minimizes the absolute difference between sensitivity (correctly predicted percentage of presences) and specificity (correctly predicted the percentage of absences). The predicted habitat suitability surface was thresholded at 0.38, with all values at or above considered “suitable”. This cutoff value is appropriate given the range of riparian habitat preferences exhibited by non-breeding WIFL.

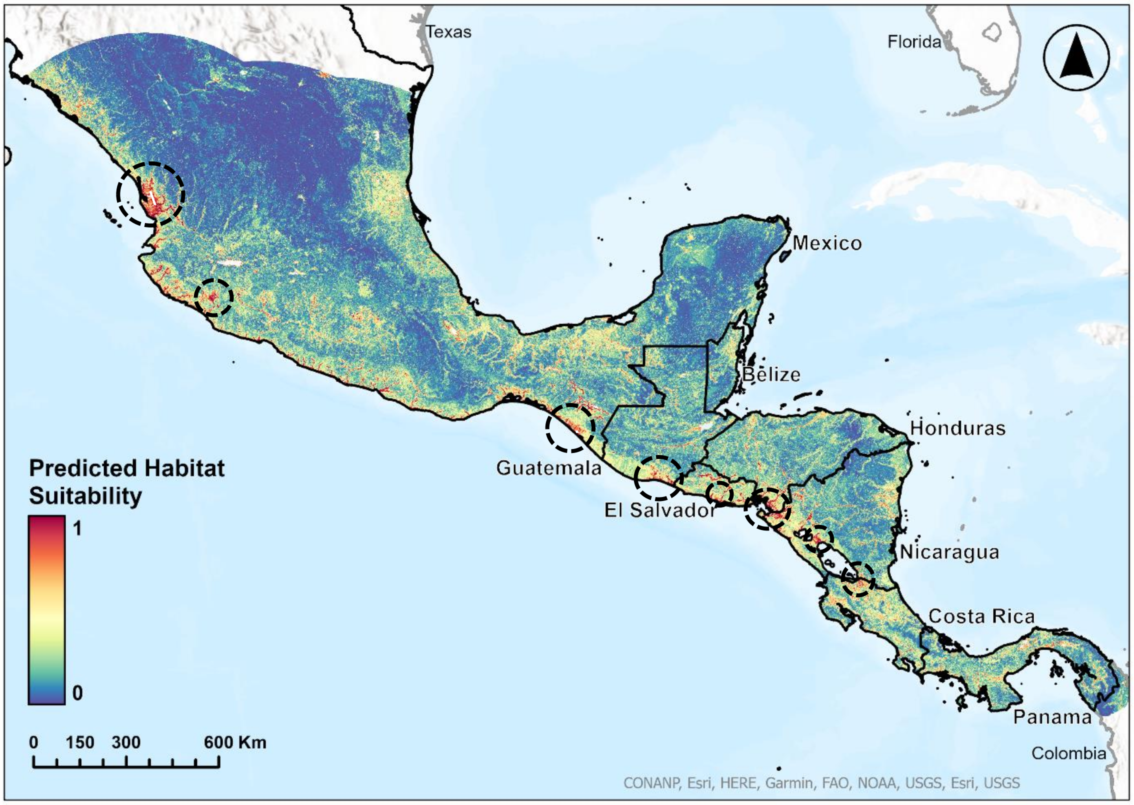

**Figure 1.2: Predicted Habitat Suitability for Non-breeding WIFL** – The random forest model included eight environmental variables. High predicted habitat suitability values are red, and low predicted habitat suitability values are blue. The final prediction surface above is an average of 20 iterations of the random forest model. Suitability hotspots are indicated by black dashed circles.

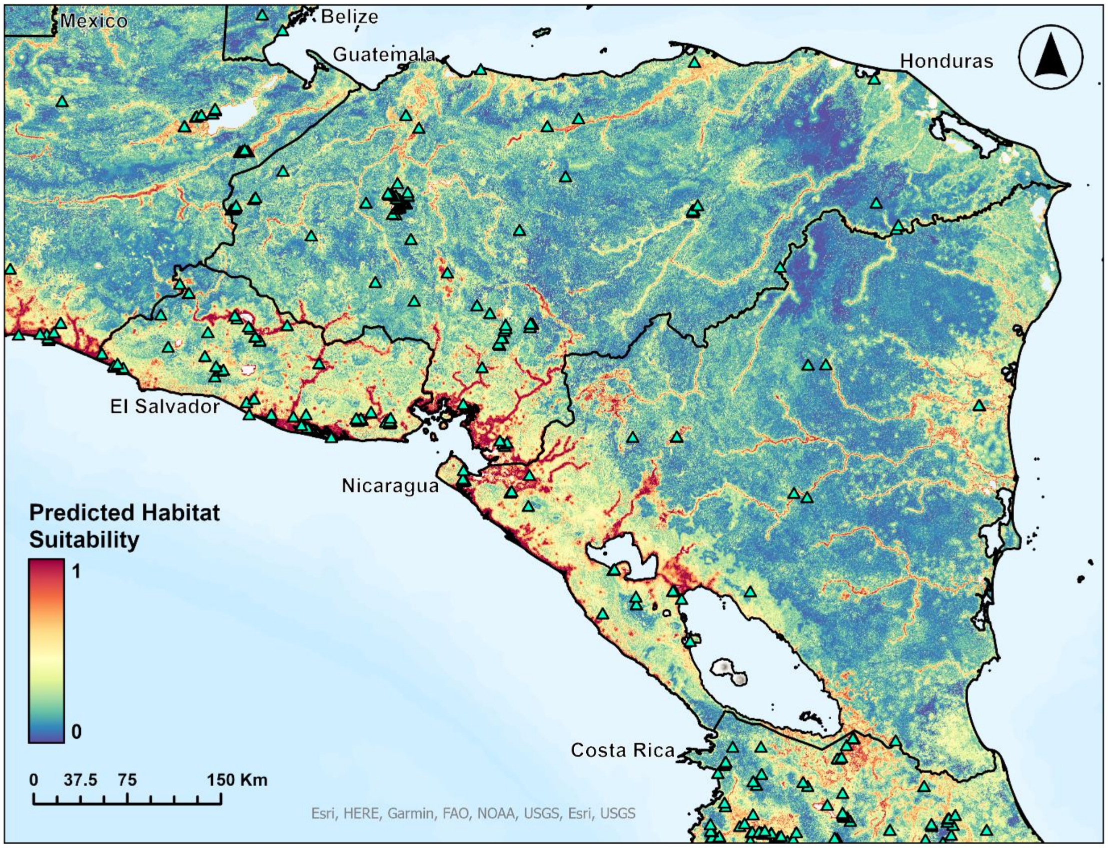

**Figure 1.3: Predicted Habitat Suitability with Observations –** A closer look at the final random forest model predictions with an observation overlay. The prediction surface produced suitable habitat apart from the occurrences, demonstrating the model's ability to predict habitat in places that have not been surveyed.

**Table 1.2: Model Performance** – True Skill Statistic (TSS), Receiver Operating Characteristic (ROC), and accuracy results for both the GAM and random forest models. Results are broken down further by the divisions in data: calibration data (used to train models), and validation data (used to cross-validate models), The values below have been averaged across 20 iterations.

| Model | Metric | Sensitivity | Specificity | Calibration | Validation |
|---|---|---|---|---|---|
| RF | TSS | 98.94 | 98.65 | 0.98 | 0.82 |
|  | ROC | 98.96 | 98.67 | 0.99 | 0.96 |
|  | Accuracy | 98.86 | 98.70 | 0.99 | 0.90 |
| GAM | TSS | 78.90 | 86.50 | 0.65 | 0.64 |
|  | ROC | 79.10 | 86.49 | 0.90 | 0.89 |
|  | Accuracy | 78.70 | 86.72 | 0.83 | 0.82 |

**Table 1.3: Variable Importance Values** – Importance values range from 0 to 1, with a higher value indicating a greater contribution to model predictions. Importance values may not sum to 100 due to averaging across model runs.

| **Variable** | **Importance** |
|---|---|
| Distance to Freshwater | 26.1 |
| Mean Temperature | 18.0 |
| Mean Precipitation | 15.0 |
| Shrub cover | 9.4 |
| Tree cover | 4.3 |
| Herbaceous cover | 3.4 |
| Crop cover | 3.4 |
| Seasonal water cover | 1.0 |

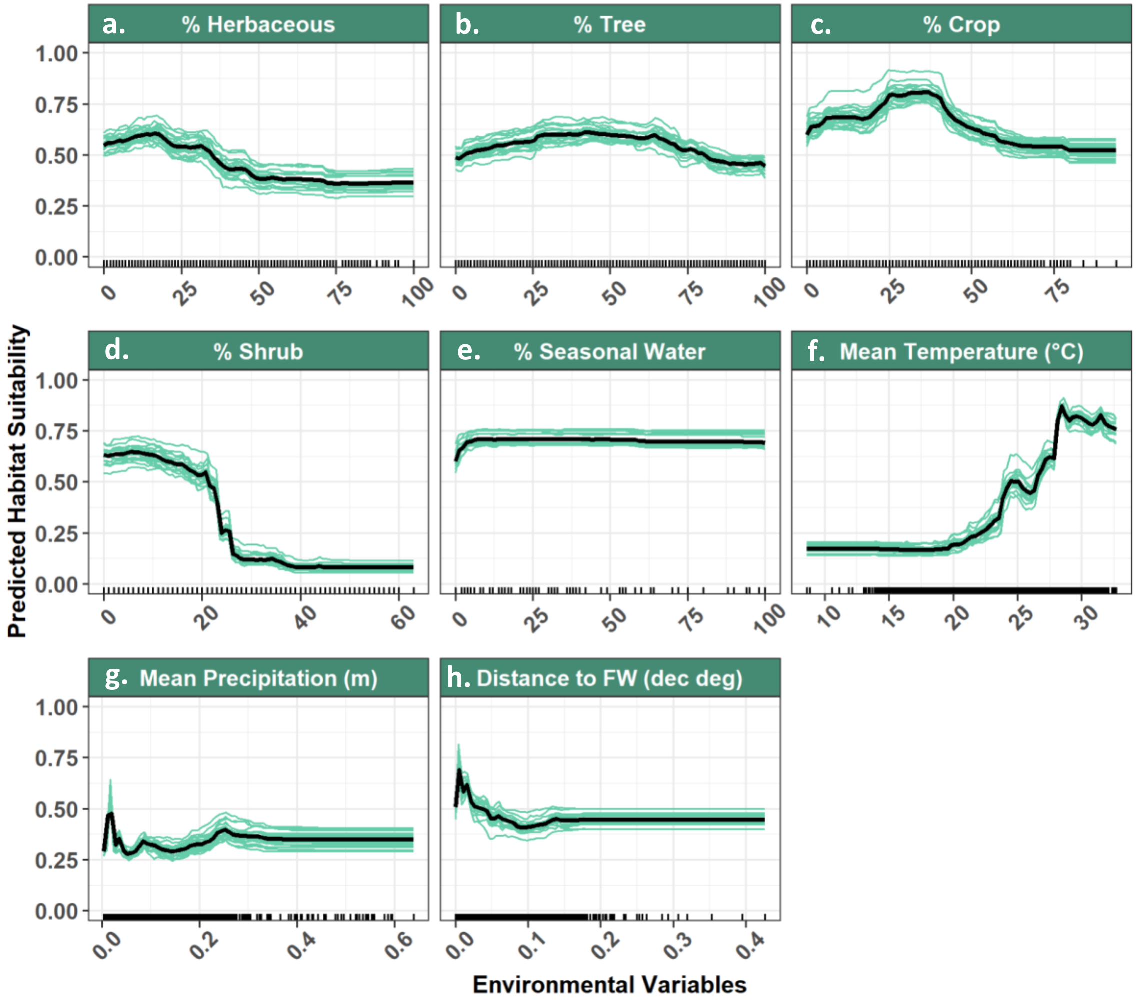

**Figure 1.4: Response Plots for the Random Forest Model –** Response plots were generated with the *biomod2* package in R. Teal lines represent each of 20 individual model runs. Black lines represent the average response curve across all 20 model runs. Tick marks along the x-axis represent the frequency of pixels with that value within the study area.

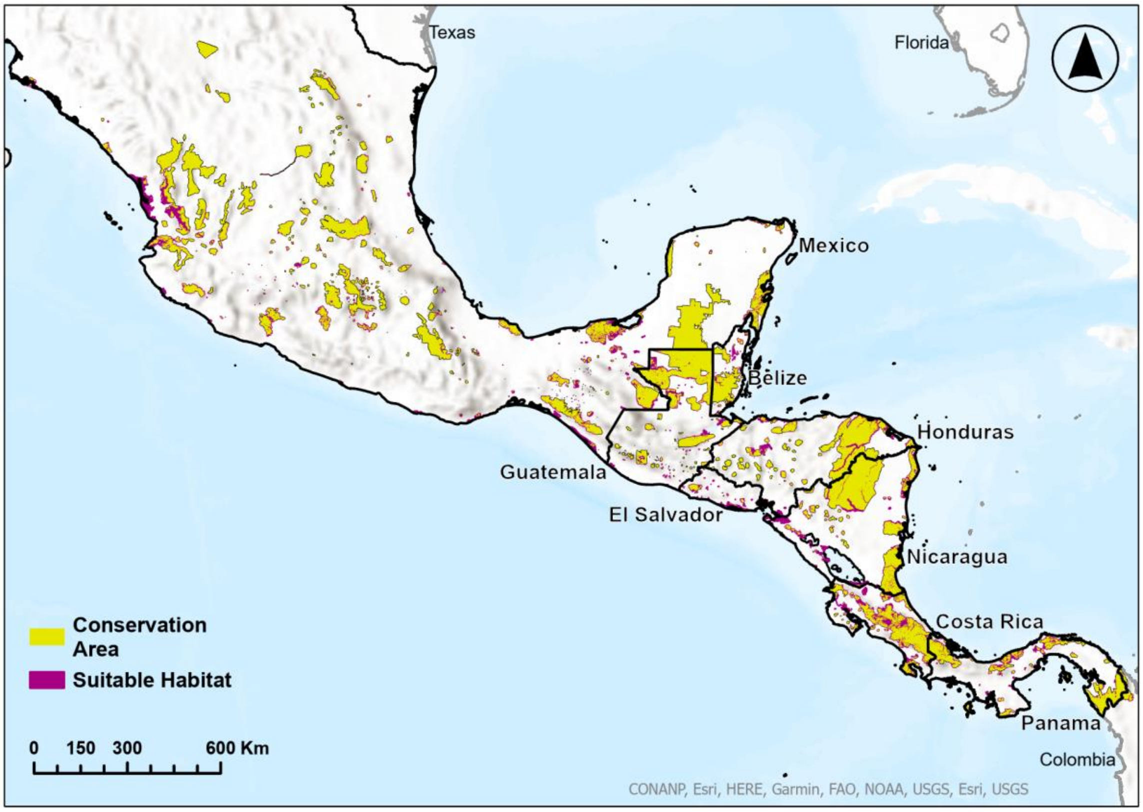

**Figure 1.5: Predicted Suitable Habitat within Protected Areas –** Suitable habitat thresholded at a 0.38 suitability index made up less than 11% of conservation areas. Conservation areas cover 264,197 km$^2$ of the study area. Suitable habitat outside of conservation areas is not shown on the map.

## DISCUSSION

Predicted habitat suitability for western subspecies of Willow Flycatcher was mapped at a 100-m across the entirely of their non-breeding range to target future survey efforts and prioritize land partnerships or acquisition. Areas with higher predicted habitat suitability remain largely outside of protected areas and indigenous conservation areas (**Fig. 1.5**). Higher habitat suitability is driven by proximity to freshwater, the warmer temperatures on the pacific dry slope, and complex vegetation structure (**Fig. 1.4**). The results of our model confirm that western subspecies of Willow Flycatcher are associated with similar habitat features between their breeding and non-breeding range. The positive influence of proximity to freshwater is expected as WIFL are a well-known inhabitant of riparian ecosystems in their breeding range (Finch et al. 2002, Paxton et al. 2007, Sogge 2010, Hatten 2016). While some sources suggested that WIFL may venture further from riparian areas in their non-breeding range (Sedgwick 2020), our observations place WIFL within 1 km of freshwater on average, with most observations occurring within 350 m of water. It is also possible however that this may be due to survey strategies that prioritize sampling of WIFL at riparian sites to maximize recaptures, or just that birders aren't looking for them beyond the willows. Articles focusing on non-breeding territoriality and fecundity though, suggest that riparian areas may still be the prime target for non-breeding WIFL (Koronkiewicz et al. 2006, Sogge et al. 2006). Areas with a higher maximum temperature were also a strong driver of high habitat suitability, perhaps suggesting that the western subspecies of WIFL prefer non-breeding habitat with semiarid climates similar to those in their breeding range (Howell and Webb 1995). Predicted habitat suitability had a parabolic or negative relationship with the four fractional land cover variables of vegetation types (herbaceous, shrub, tree, and crop), indicating a distinct preference for 100 x 100 m areas with complex or varied vegetation types or structure. When any one variable exceeded 25-50% cover, predicted habitat suitability decreased. As expected, fractional shrub cover had the strongest influence on PHS of any vegetation cover variable, but the strong association with fractional shrub cover below 25% was unexpected. While WIFL are well-documented in highly "shrubby" riparian areas in their breeding range, this may be due to an increased need to provide cover for nesting during the breeding season (Finch et al. 2000, Hatten and Paradzick 2003). A preference for more open, edge, or mixed-height areas may be indicated for improved arthropod foraging via hawking or hover-gleaning during the non-breeding period (Sedgwick et al. 2020). It may also be possible that larger shrubs have been grouped within the fractional tree cover variable, or that WIFL have a preference towards smaller trees in their non-breeding range. The variable effects of precipitation observed in the response curves may be explained by the lack of consistent precipitation on the Pacific dry slope during the months that WIFL reside there. WIFL overwinter in Central America during the dry season (Yong and Finch 1997, Finch and Kelly 1999), and WIFL have likely evolved to select non-breeding habitat with similar climatic conditions to that of their breeding habitat. This could also explain why predicted habitat suitability was higher for areas with higher average maximum temperature during the winter months.

The largest concentration of suitable areas is along the Pacific Coast, but those areas are characterized by a low fraction of protected areas. Areas that may be especially important for migratory and non-breeding habitat in Mexico include the wetlands between the Grande de Santiago and Acaponeta Rivers in Nyarit, the riparian forest east of Colima where Rio Salado intersects Rio Naranjo, and the coastal riparian habitat between Laguna de le Joya and Laguna Chontuto west of Pijijiapan (**Fig. 1.4**). Most of the pacific coast between Rio Achiguate and Rio Paz in Guatemala is also a suitability hotspot. El Salvador’s hotspots include the area surrounding Bahia de Jiquilisco, continuing north around the Rio Lempa. The coastal wetlands surrounding Golfa Fonseca in Hondurus and Nicaragua represent an expansive suitability hotspot. Laguna de Tisma in Nicaragua, and the area between Los Guatuzos wetlands and Cano Negro Reserve in Costa Rica also represent potential hotpots. This reclassified surface was then used to calculate the area covered by suitable habitat within protected areas (**Fig. 1.5**). Suitable habitat makes up less than 11% of conservation areas, despite covering 203,566 km$^2$ of the study area.

Potential limitations of this study are primarily related to issues of sampling bias that have been discussed at length with regards to eBird data (see Steen et al. 2019, Steen et al. 2021, Tang et al. 2021). Prioritizing repeated observations at the same locations or non-random survey sites to increase detection probability may have biased this dataset to have a stronger correlation with *distance to freshwater*. To determine whether or not WIFL truly occupy areas further than 1 km from freshwater, a follow-up study with stratified or random sampling at greater distances from freshwater would be required. The predictive capacity of the habitat suitability map is also limited by pooling observations for the three western subspecies of WIFL. If these subspecies were able to be more reliably differentiated, I could focus modeling efforts on the endangered Southwestern subspecies. However, combining the prediction surface with the gene-based geographic sorting in Paxton et al (2011), we can further prioritize survey efforts and land-based conservation initiatives.

## CONCLUSIONS

Overall, I found that the environmental variables that drive WIFL habitat suitability in their non-breeding range resembles that of their breeding range, with a strong correlation for riparian areas, more arid climate, and complex vegetation structure. This 100-m SDM can be used to improve survey site selection and to prioritize areas for land acquisition or conservation partnerships. Areas with high predicted habitat suitability are more concentrated along the Pacific coast of Central America, with hot spots of suitability present in most countries. There is a significant gap in protected area coverage where predicted habitat suitability is highest on the west coast, suggesting a need to prioritize conservation initiatives in that area. My hope is that others will take this information and continue to improve upon it for a more focused approach to the conservation of this species in its non-breeding range.

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## **Chapter 2:** Evidence Indicates a Critical Need to Reassess Conservation Status of the Nicaraguan Grackle *(Quiscalus nicaraguensis)*

### ABSTRACT

The Nicaraguan Grackle (*Quiscalus nicaraguensis*) is a passerine bird endemic to the great lakes of Nicaragua and neighboring wetlands in Nicaragua and Costa Rica. Nicaraguan ornithologists and birders have noticed a stark decline in this species throughout its range over the past decade. Major threats to the persistence of their habitat include cattle grazing, agricultural encroachment, and prolonged drought. In this research I estimated the current and potential distribution of this understudied species. Intensive field surveys were combined with recent data from eBird to determine the presence of the Nicaraguan Grackle throughout its range. I estimated the current distribution for the Nicaraguan Grackle via species distribution modeling (SDM) with varied levels of inter-annual freshwater. Results from the SDM suggest a very limited inhabited distribution within the current BirdLife International range map (<15%; 0.55 probability threshold). Few records document the presence of this species at distances beyond 250 m from permanent or recurrent fresh water. The importance of proximity to freshwater was confirmed in the random forest SDM analysis with additional strong association to wetland vegetation. Based on these findings and reports of continued declines, I suggest a revised distribution map and an update to their current IUCN status. This will allow more accurate evaluation of their protection status and generate urgency for more directed surveys of this species.

# INTRODUCTION

The Nicaraguan Grackle (hereafter “NICGRA”; *Quiscalus nicaraguensis*), is an icterid (Family Icteridae: “Blackbirds and Allies”) considered endemic to the Pacific arid slope of Nicaragua and Costa Rica. Nicaragua encompasses 75% of the species’ global distribution, most of which is around Lakes Nicaragua and Managua (L. Xolotlán and L. Cocibolca respectively; BLI 2016). NICGRA also inhabit the adjacent wetlands southeast of the lakes and the north central lowlands of Costa Rica (BirdLife International & Handbook of the Birds of the World, 2016; Jaramillo & Burke, 1999; Stattersfield et al., 1998; Stotz, Fitzpatrick, Parker, & Moskovits, 1996).

Despite its near-endemic and emblematic status to Nicaragua, this species is virtually unrepresented in the scientific literature. Publicly available knowledge of this species is limited to field guides, a book on new world blackbirds (Jaramillo and Burke 1999), and unpublished bird surveys. Surveys and observations by local birders suggest an unstable population requiring immediate conservation action. Articles in the Nicaraguan press also warn that the species is rapidly declining due to human-induced habitat loss and climate change (Gonzalez, El Nuevo Diario 2019). Historical and contemporary data suggest that the species’ research priority is low (Stotz et al., 1996), possibly owing to the erroneous perception that flooded pasture for cattle-raising would favor a range expansion (Jaramillo & Burke, 1999; Martínez-Sánchez & Will, 2010). Unpublished manuscripts and recently published field guides provide some insight on their life history. One of the earliest descriptions of their distribution stated the species was historically abundant on the shores of Lakes Managua in Nicaragua, occurring wherever shorelines were shallow or marshy with dense growth of cattails and bushes in which the species nested (Miller and Griscom 1922, unpub.). They added that NICGRA associated with the larger Great-tailed Grackle; however, it was never seen to leave the vicinity of the water or enter towns like its synanthropic relative. This last statement was corroborated by Howell (1964) and highlights the species' specialization on freshwater wetland habitat and their tendency to avoid human settlements. More recent descriptions of their habitat align with the historic documentation of a freshwater wetland specialist (Chavarría-Duriaux et al. 2018). Freshwater occurrence in the Pacific dry region of Nicaragua varies seasonally and between years. Water may recur (ebb and return) across years due to prolonged dry periods or consistently abundant water years. The recurrence of freshwater on the landscape directly impacts the presence of seasonal wetlands which in turn alters the availability of habitat for freshwater wetland specialists like the Nicaraguan Grackle. Global satellite-based freshwater recurrence products provide opportunities to analyze habitat relationships as they relate to different levels of freshwater recurrence in the recent past (Pekel et al. 2016).

The Nicaraguan Grackle is currently designated as "Least Concern" by the IUCN (IUCN, 2012). The justification is made primarily upon their estimated area of occupancy, which is stated to be near 20,000 km$^2$, a sufficiently large area to avoid designation as 'Vulnerable'. Given that this species appears to be a freshwater wetland specialist its range is likely considerably smaller than what was estimated by the IUCN. In addition to the range criterion, the IUCN has categorized the population as "stable, unfragmented, and not experiencing extreme fluctuations" (Birdlife International, 2016). However, no formal study has been published to document a stable, unfragmented population. I believe the designation of “Least Concern” is not appropriate or well justified.

In this research, I sought to study a species that is virtually unrepresented in the scientific literature, provide empirical and quantifiable data to support future management decisions, and update knowledge on the distribution of NICGRA. I documented the species’ contemporary distribution within Nicaragua and Costa Rica using a combination of existing unpublished field surveys and more recently collected eBird data. I mapped the likely distribution and identified important environmental habitat variables using species distribution modeling (SDM) approaches with varied levels of freshwater recurrence on the landscape. I believe this work provides support for reclassification of the global conservation status of NICGRA from that of “Least Concern” to one of higher conservation concern, contingent upon the results of an additional population study following the IUCN Red List classification criteria (IUCN Red List, 2018).

## METHODS

### Data Collection:

Data from audio-visual surveys and online repositories were collected and combined across five sources from 2007 to 2022 (**Fig. 2.1**). Collecting accurate data on the Nicaraguan Grackle is challenging because it is similar in appearance to the ubiquitous Great-tailed Grackle (*Quiscalus mexicanus*). The Nicaraguan Grackle and Great-tailed Grackle differ in size, song, and plumage, but not -visual surveys were conducted from the shoreline to the interior for up to 3 kmenough to rely on observations reported by inexperienced persons. Audio-visual survey detections performed by authors

LC, WA, MT, OJ, and TA were recorded from 2016 to 2018 at several sites in the Southern Dry Pacific ecoregion of Nicaragua and the eastern portion of Lake Nicaragua. Audio. Records from surveys conducted by MT and OJ during the proposed Gran Canal Environmental Impact Assessment were completed during November–December 2013 and April–May 2014 (Environmental Resources Management, 2015). WA, MT, and OJ, conducted bird surveys with local partner NGO Paso Pacifico at "Sierra Serena" and "Isla Vista" within the range of NICGRA for the Conservation and Sustainable Tourism in Critical Watersheds project (Bauer & Arendt 2007). Finally, LC recorded additional observations of NICGRA while conducting intensive bird surveys across Nicaragua to increase the knowledge of local birds and fill in gaps of information related to rare bird distributions for the 2018 Nicaragua Bird Guide.

Many of the audio-visual surveys were point counts in which abundance data was collected at a single georeferenced location. The focus of this investigation was spatial habitat prediction, which relies solely on the georeferenced locations of each survey. Thus, to increase the number of georeferenced records for the analysis I obtained observations from the eBird Data Repository (Sullivan et al., 2009; ebird, 2012). Observations by novice birders were not considered research grade and records were heavily filtered by the authors prior to inclusion in the dataset. To maintain the accuracy of the species' identity, I only included observations accompanied by audio recordings, photos, or detailed and extensive descriptions.

### **Modeling Distribution**:

In this study, I created SDMs to determine the overall distribution of the NICGRA as it relates to fractional land cover classes and distance to freshwater at various levels of historical recurrence. SDMs work by determining the correlational relationship between habitat-relevant environmental variables and species presence/absence (Guisan and Thuiller 2005, Elith et al. 2006). Given that NICGRA has a documented dependence on a specific habitat type (freshwater wetlands), I felt that this method was well suited for this task. The extent of the study area was determined by creating a 50-km buffer around the current BLI-IUCN range map. This buffer captures the narrow historical range of the species, as well as more recent observations that marginally extend their range (**Fig 2.1**). Prior to modeling, I spatially thinned records from eBird using a per-pixel approach because of the disproportionate observational effort caused by birding tourism in Costa Rica (Echeverri et al. 2022). Thinning was carried out by creating a 1-km grid and reducing the number of observations per grid cell to 3. I determined grid size and the final number of observations per cell by examining the range of spatial autocorrelation in semivariograms of the observation data. The initial data aggregation of 304 records were spatially thinned to 217 records, with all thinning occurring in Costa Rica at the southern edge of NICGRA's range.

I prepared seven candidate environmental variables at a 100-m resolution for use in the SDM (**Table 2.1**): four *distance to fresh wate*r or *distance to herbaceous wetland* variables, and six land cover variables. The *distance to recurrent fresh water* variables were derived from the Joint Resource Commission's global surface water "Recurrence" data product (Pekel et al. 2016), which captures the percentage of time over the past 38 years that a given pixel has recurred as surface water. The *distance to herbaceous wetland* variable was derived from the Copernicus discrete land cover classification product (Buckhorn et al. 2020). Land cover classes based on spatial fraction of pixels were obtained from the 2019 Copernicus fractional land cover dataset and included: *permanent water, seasonal water, built-up, shrub, herbaceous,* and *tree* (Buckhorn et al. 2019; **Table 2.1**). The four *distance to fresh water* layers were resampled to the 100-m resolution of the fractional land cover classes using a bilinear interpolation approach. All environmental variables were masked to the study area extent with uninhabitable large open bodies of permanent freshwater removed.

To build and fit the models, I used the *biomod2* package in the R programming environment (Thuiller et al. 2023; R Core Team 2023, version 4.2.3). Because I did not have “absence” data, I used the biomod2 to randomly generate pseudoabsences equal to the number of occurrences. With support from the *randomForest* and *mgcv* packages in R, I selected the Random Forest and General Additive Model (GAM) algorithms to fit the candidate models (Brieman 2001, Liaw and Weiner 2002, and Wood 2011). I cross-validated the model by dividing the data into 80% calibration sets (used for model training) and 20% validation sets (used for testing) in a 20-fold manner. The model was evaluated using three metrics: the true skill statistic (TSS; Allouche et al. 2006), receiver operating characteristic (ROC; Elith et al. 2006), and accuracy (ACC). Each of these performance metrics represents a threshold-dependent, threshold-independent, and basic strategy for evaluating model performance. Variable importance measures were derived using 10 permutations for each environmental variable.

After reviewing the response plots, evaluation metrics, and variable importance results for the initial models with all seven variables, I removed the only variable below a 1% model contribution based on the variable importance measures and repeated the modeling process with the reduced set of environmental variables (**Table 2.2**).

Furthermore, all SDMs fitted with the GAM algorithm were dropped from the analysis due to poor model performance. Finally, I used *biomod2* to forecast the prediction surfaces for each of 20 iterations of the reduced random forest models, and created an averaged habitat suitability map for each of the final four models.

**Table 2.1: Candidate Environmental Variables** – The four initial models included seven candidate environmental variables. Each model contained **one** of the four "proximity to fresh water or wetland" variables and **all** six fractional land cover variables). Variables removed from the four revised models are listed in italics. All JRC water variables were resampled to 100-m resolution prior to calculating the distance rasters used in the analysis.

| Name | Source layer | Initial Grain | Description |
|---|---|---|---|
| Distance to ≥ 25% recurring fresh water | JRC Global Surface Water Dataset[1] | 30-m | Distance to pixels that recurred as water in at least 25% of the past 38 years |
| Distance to ≥ 50% recurring fresh water | JRC Global Surface Water Dataset[1] | 30-m | Distance to pixels that recurred as water in at least 50% of the past 38 years |
| Distance to ≥ 75% recurring fresh water | JRC Global Surface Water Dataset[1] | 30-m | Distance to pixels that recurred as water in at least 75% of the past 38 years |
| Distance to Herbaceous wetland | Copernicus Global Dataset[2] | 100-m | Distance to discrete herbaceous wetland pixels |
| Shrub | Copernicus Global Dataset[2] | 100-m | Fractional land cover prevalence in percentage |
| Tree | Copernicus Global Dataset[2] | 100-m | Fractional land cover prevalence in percentage |
| Herbaceous | Copernicus Global Dataset[2] | 100-m | Fractional land cover prevalence in percentage |
| Built-up | Copernicus Global Dataset[2] | 100-m | Fractional land cover prevalence in percentage |
| Seasonal water | Copernicus Global Dataset[2] | 100-m | Fractional land cover prevalence in percentage |
| *Permanent water* | *Copernicus Global Dataset*[2] | *100-m* | *Fractional land cover prevalence in percentage* |

1. Pekel et al. 2016, 2. Buchhorn et al. 2020

**Table 2.2: Revised Models** – The four revised models were fitted with the random forest algorithm and six environmental variables. Each model differed by the inclusion of a unique "proximity to freshwater or wetland" variable.

| **Model Name** | **Environmental Variables** |
|---|---|
| Low Recurrence | Distance to freshwater recurring at least 25% of the last 38 years, Shrub, Tree, Herbaceous, Built-Up, Seasonal Water |
| Moderate Recurrence | Distance to freshwater recurring at least 50% of the last 38 years, Shrub, Tree, Herbaceous, Built-Up, Seasonal Water |
| High Recurrence | Distance to freshwater recurring at least 75% of the last 38 years, Shrub, Tree, Herbaceous, Built-Up, Seasonal Water, |
| Herbaceous Wetland | Distance to discretely classified herbaceous wetland cover, Shrub, Tree, Herbaceous, Built-Up, Seasonal Water |

**Figure 2.1: NICGRA Occurrences, Range and Wetlands** – The majority of occurrences fell within the BLI-defined range (orange). The study area for the species distribution model (black) was made with a 50-km buffer around the BLI-IUCN range to account for potential range expansion and unreported occurrences. Referenced wetlands are indicated by blue place markers. Tisma Lagoon, San Miguelito wetlands, Caño Negro Wildlife Refuge, and Los Guatuzos wetland complex are RAMSAR-designated important wetland sites.

## RESULTS

This analysis used 217 locations and a suite of environmental variables to predict habitat suitability within and around the BLI-IUCN range of NICGRA. Performance metrics and cross-validation indicated good predictive power for all four models (**Table 2.3**). Results for relative model importance for all models suggested that the most critical predictor of NICGRA distribution is distance to recurring fresh water or herbaceous wetland (**Table 2.4**). The relative importance for these variables on a scale from 0 to 1 ranged from 0.61–0.67. The remaining relative importance values of all other variables in each model were lower (≤0.06) but still had a noticeable impact on habitat predictions.

I examined the response plots from the top two models to highlight the effects of individual variables (**Figs. 2.4 and 2.5**). Each environmental variable was plotted against predicted habitat suitability (0-1) across their full range of values within the study area while all other variables were fixed at their median value. Each of the five fractional land cover values range from 0–100%, with 0 representing no presence in the pixel and 100 representing complete coverage of the pixel. Thus, a single 100x100-m pixel may have a mixture of land cover types. For both models, percent seasonal water per pixel (**Figs. 2.4a and 2.5a**) and percent built-up per pixel (**Figs. 2.4b and 2.5b**) had only slight effects on predicted habitat suitability (hereby referred to as PHS or suitability), with suitability remaining relatively high across the range of values for both variables. The effects of percent herbaceous per pixel (**Figs. 2.4c and 2.5c**) were notable but varied between models. The Moderate Recurrence model showed a gradual, very significant increase between 0 and 30% herbaceous cover with PHS remaining high beyond 30%. In contrast, the Herbaceous Wetland model indicates higher PHS from 10–50% with PHS dropping somewhat after 50%. The effects of percent tree (**Figs. 2.4d and 2.5d**) and percent shrub per pixel (**Figs. 2.4e and 2.5e**) were more pronounced in the Moderate Recurrence Model. PHS significantly decreased and remained low as shrub and tree cover reached just 10% and 30% respectively. Percent tree and shrub cover showed less significant, gradual decreases across their full range of values in the Herbaceous Wetland Model. By far the most significant effect on PHS for both models were their respective proximity to freshwater variables (**Figs. 2.4f and 2.5f**). PHS decreased precipitously from 0.90 to 0 within 5 km of moderately recurring freshwater (fresh water pixels with a 50% inter-annual recurrence period or higher). PHS decreased even more steeply from 0.95 to 0 within just 2.5 km of discretely classified herbaceous wetland cover.

**Table 2.3: Performance Metrics** – True Skill Statistic (TSS), Receiver Operating Characteristic (ROC), and accuracy results (ACC) for each model fitted with the Random Forest Algorithm. Results are broken down further by the divisions in data: calibration data (used to train models) and validation data (used to test models). All four models performed similarly across metrics, so variable importance values were used to determine the top models.

| Model | Metric | Sensitivity | Specificity | Calibration | Validation |
|---|---|---|---|---|---|
| Low FW Recurrence | TSS | 97.37 | 98.67 | 0.96 | 0.80 |
| | ROC | 97.41 | 98.67 | 0.997 | 0.93 |
| | ACC | 97.30 | 98.74 | 0.98 | 0.90 |
| Moderate FW Recurrence | TSS | 97.70 | 99.53 | 0.97 | 0.88 |
| | ROC | 97.70 | 99.57 | 0.998 | 0.96 |
| | ACC | 97.44 | 99.75 | 0.99 | 0.94 |
| High FW Recurrence | TSS | 97.59 | 97.66 | 0.95 | 0.86 |
| | ROC | 97.78 | 97.59 | 0.998 | 0.96 |
| | ACC | 96.93 | 98.27 | 0.98 | 0.93 |
| Herbaceous Wetland | TSS | 97.67 | 98.42 | 0.96 | 0.83 |
| | ROC | 97.85 | 98.24 | 0.998 | 0.96 |
| | ACC | 97.11 | 98.92 | 0.98 | 0.91 |

**Table 2.4: Relative Variable Importance –** Variable Importance ranging from 0–1 for each of the four models. The final variable listed in the table is a different distance to freshwater or distance to herbaceous wetland variable for each model. Proportions do not sum to one due to averaging across permutations and model runs.

| **Variable** | **Herbaceous Wetland** | **25% Recurrence** | **50% Recurrence** | **75% Recurrence** |
|---|---|---|---|---|
| Seasonal Water | 4.3 | 3.3 | 3.2 | 4.6 |
| Built-up | 2.4 | 3.9 | 1.8 | 4.1 |
| Herb | 1.2 | 1.6 | 1.9 | 1.1 |
| Tree | 2.1 | 1.7 | 1.5 | 1.0 |
| Shrub | 1.8 | 3.7 | 2.3 | 0.9 |
| Distance to FW/HW | 66.7 | 70.2 | 72.0 | 75.6 |

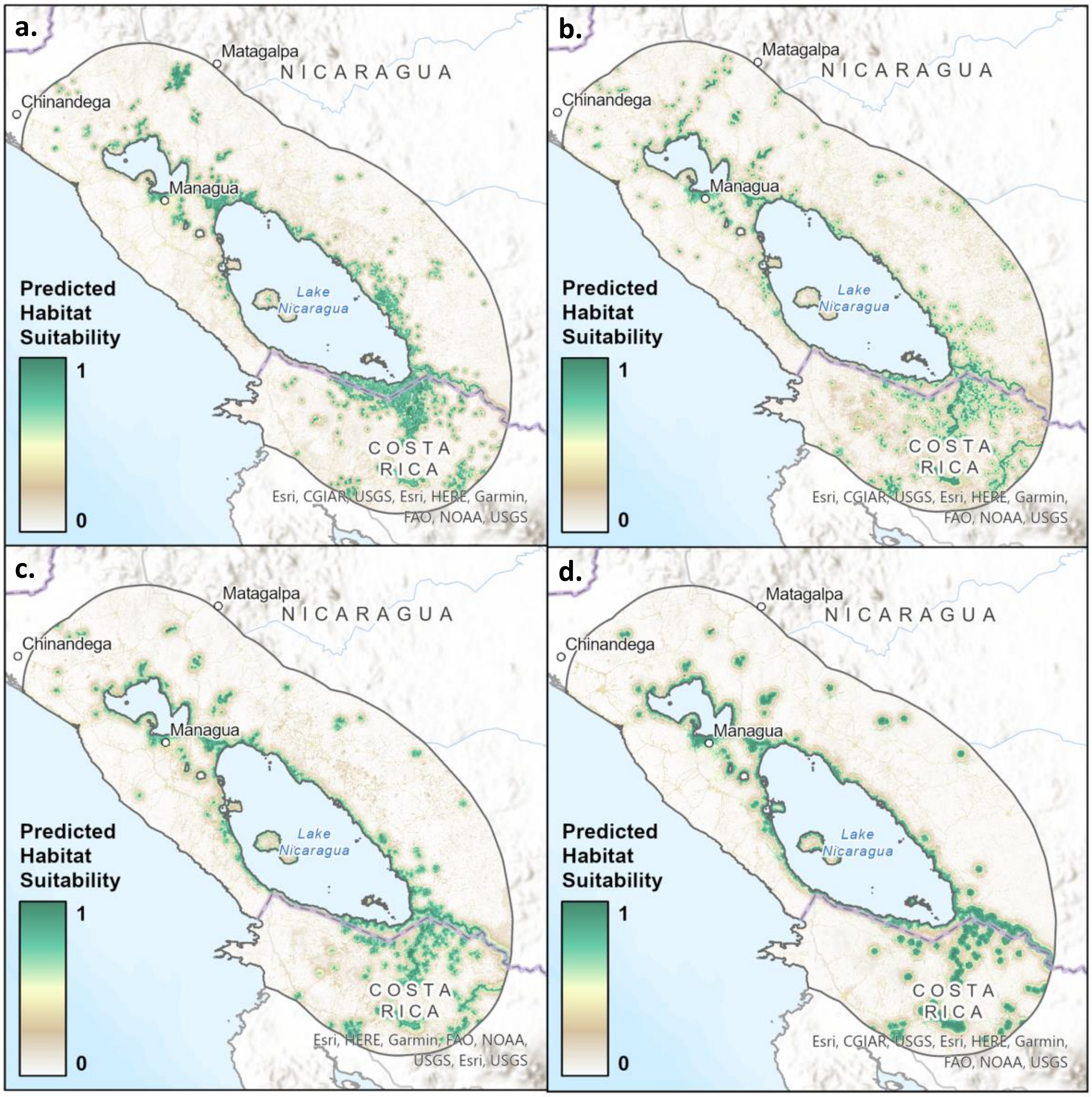

**Figure 2.2: Predicted Habitat Suitability of the Nicaraguan Grackle** – **2.2a: Herbaceous wetland model prediction surface -** This model predicted the greatest area of suitable habitat while also delineating vegetation contributions within highly suitable habitat. **2.2b: 25% Recurrence model prediction surface -** This model predicted the least suitable habitat and did not well delineate vegetation contributions within suitable habitat. **2.2c: 50% Recurrence model prediction surface -** This model predicted a balanced degree of suitable habitat while also delineating vegetation contributions within highly suitable habitat very well. **2.2d: 75% Recurrence model prediction surface -** This model predicted suitable habitat that was overly constrained to highly recurrent fresh water and did not well delineate vegetation contributions within suitable habitat.

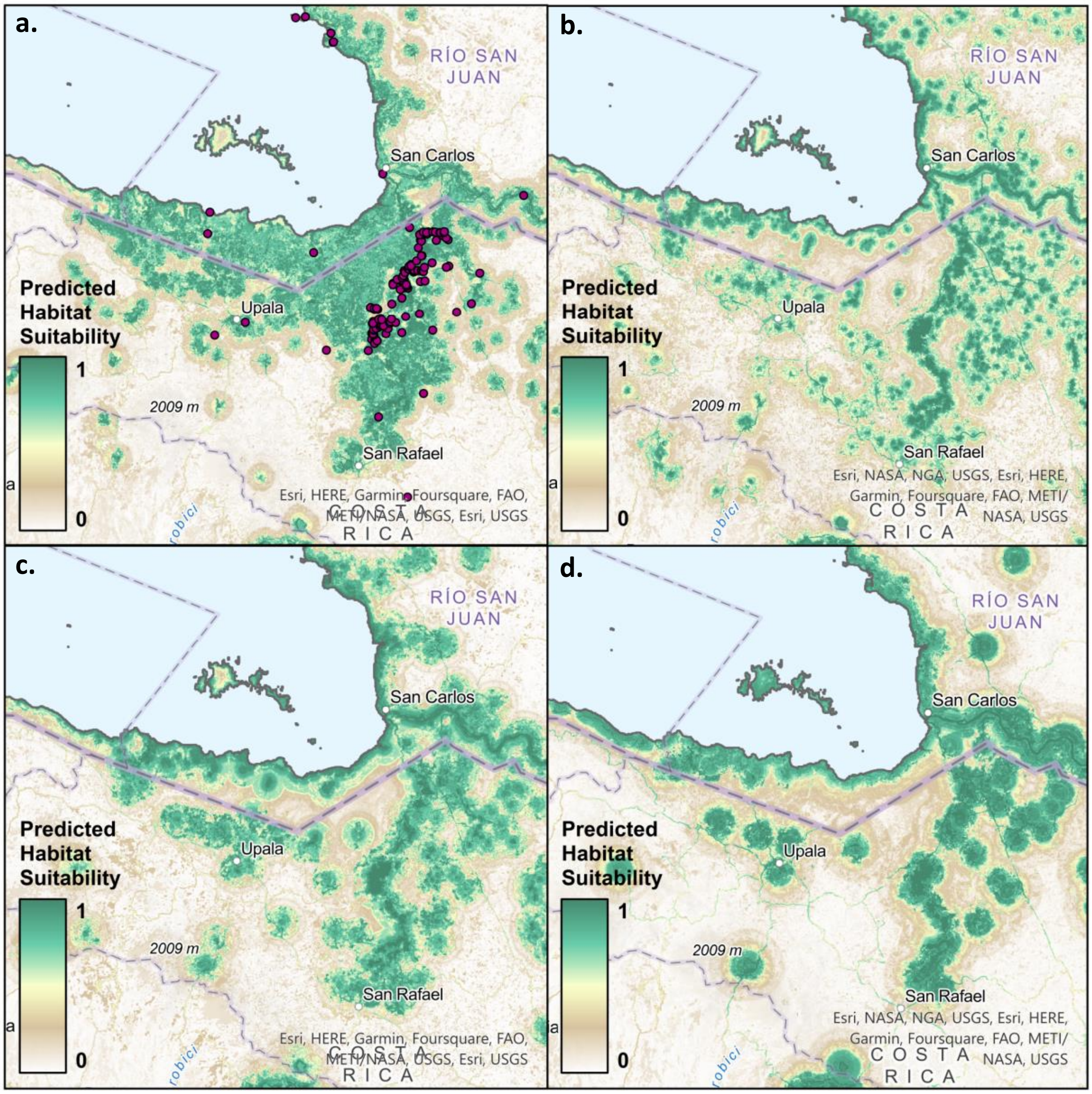

**Figure 2.3: Predicted Habitat Suitability of NICGRA in Focal Areas** – **2.3a: Herbaceous wetland model prediction surface -** Habitat suitability is highest in close proximity to wetlands with moderate herbaceous cover, and sparse tree and shrub cover. **2.3b: 25% Recurrence model prediction surface -** Habitat suitability is lower overall, but highest in close proximity to low recurrent fresh water, moderate herbaceous cover, and sparse tree and shrub cover. **2.3c: 50% Recurrence model prediction surface -** Habitat suitability is highest in close proximity to moderately recurrent fresh water, high herbaceous cover, and very sparse tree and shrub cover. **2.3d: 75% Recurrence model prediction surface -** Habitat suitability is highest in close proximity to highly recurrent fresh water, very high herbaceous cover, and very sparse tree and shrub cover. Probability of occurrence is highest when distance to freshwater is within 250 m.

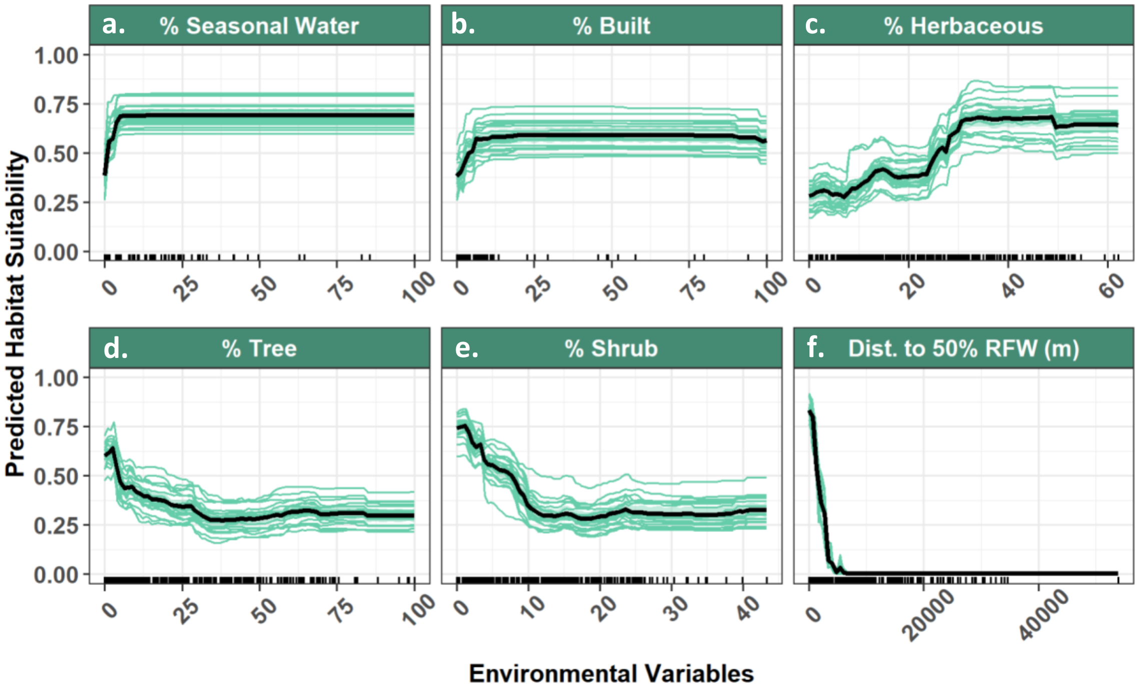

**Figure 2.4: Response Plots for Moderate Recurrence Model** – Response plots were generated with the *biomod2* package in R. Tick marks along the x axis represent the frequency of pixels with that value within the study area. **2.4a. % Seasonal Water -** PHS rises rapidly from 0.35 to 0.70 as the percent seasonal water per pixel increases from 0 to 5%. **2.4b. % Built-up -** PHS rises rapidly from 0.35 to 0.60 as the percent built-up per pixel increases from 0 to 10%. **2.4c. % Herbaceous -** PHS rises gradually from 0.30 to 0.65 as the percent herbaceous per pixel increases from 0 to 35%, dropping slightly after 50%. **2.4d. % Tree -** PHS decreases gradually from 0.65 to 0.30 as the percent tree per pixel increases from 0 to 30%. **2.4e. % Shrub -** PHS decreases gradually from 0.70 to 0.35 as the percent shrub per pixel increases from 0 to 10%. **2.4f. Distance from 50% recurrent freshwater -** PHS decreases rapidly from 0.90 to 0.0 as Distance from 50% recurrent freshwater increases from 0 to 5-km.

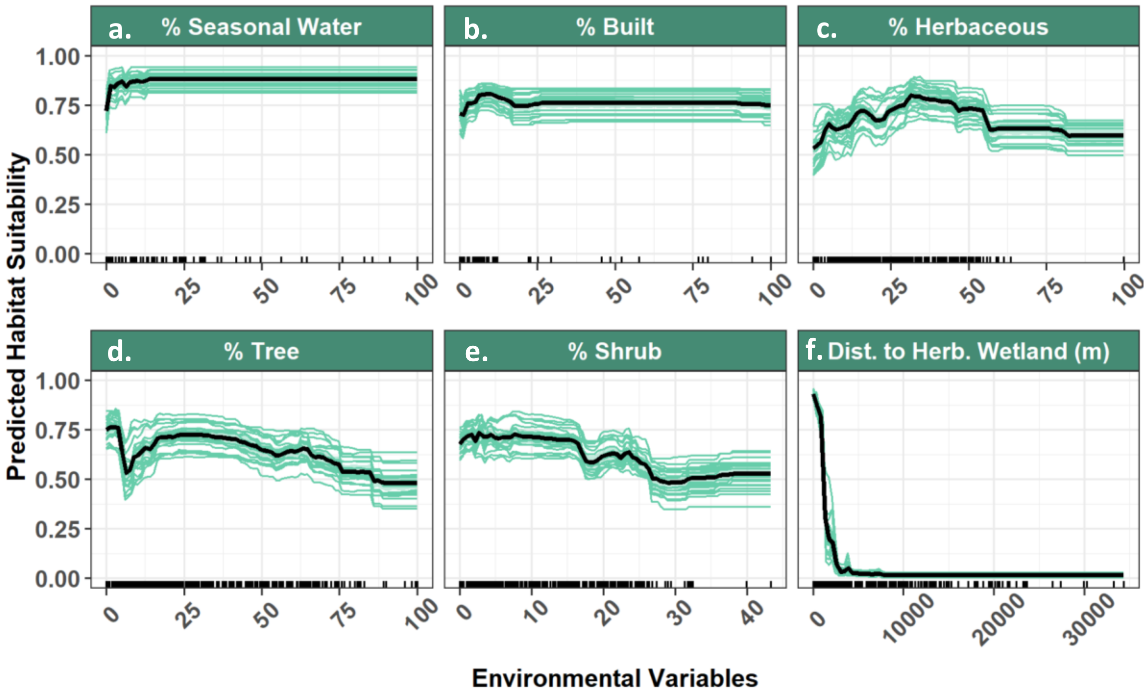

**Figure 2.5: Response Plots for Herbaceous Wetland Model** – Response plots were generated with the *biomod2* package in R. Tick marks along the x axis represent the frequency of pixels with that value within the study area. **2.5a. % Seasonal Water -** PHS rises from 0.75 to 0.88 as the % seasonal water per pixel increases from 0 to 10%. **2.5b. % Built-up -** PHS rises slightly from 0.70 to 0.75 as the percent built-up per pixel increases from 0 to 10%. **2.5c. % Herbaceous -** PHS rises gradually from 0.60 to 0.75 as the percent herbaceous per pixel increases from 0 to 35%, dropping gradually back to 0.65 as herbaceous cover reaches 63%. **2.5d. % Tree -** PHS decreases gradually from 0.75 to 0.50 as the percent tree per pixel increases from 0 to 90%. **2.5e. % Shrub -** PHS decreases gradually from 0.70 to 0.50 as the percent shrub per pixel increases from 0 to 30%. **2.5f. Distance from herbaceous wetland -** PHS decreases rapidly from 0.95 to 0.0 as distance from herbaceous wetland increases from 0 to 2.5 km.

The averaged prediction surfaces indicated a restricted, fragmented distribution within the larger range delimited by the IUCN and BirdLife International. To determine the realistic range area of the NICGRA I calculated the area of the prediction surfaces from the top two models by thresholding habitat suitability at the optimized cutoff value for each model (**Fig. 2.6**). This cutoff value reflects the threshold that minimizes the absolute difference between sensitivity (percentage of presence correctly predicted) and specificity percentage of absence correctly predicted) within each model. I used the model with the greatest area covered by potential suitable habitat (Herbaceous Wetland Model) and the best model based on freshwater recurrence (Moderate Recurrence Model) to estimate the total distributional area within the BLI-IUCN Range. Based on this cutoff criterion, habitat suitability was thresholded at 0.55 for the Herbaceous Wetland Model and 0.59 for the Moderate Recurrence Model. Before estimating the area, I extended the BLI-IUCN range polygon to areas with multiple sightings of NICGRA that were not previously included in the range map (see dashed “Extended Range” in **Fig. 2.6**). The Herbaceous Wetland Model estimated the total area of suitable habitat at 38% of the BLI-IUCN range (3,237.89 km$^2$ vs. 8,466.27 km$^2$). The Moderate Recurrence Model estimated the total area of suitable habitat at 29% of the BLI-IUCN range (2,484.64 km$^2$ vs. 8,466.27 km$^2$). The minimum bounding polygon, an estimate of “extent of occurrence”, was approximately 14,900 km$^2$ for both models.

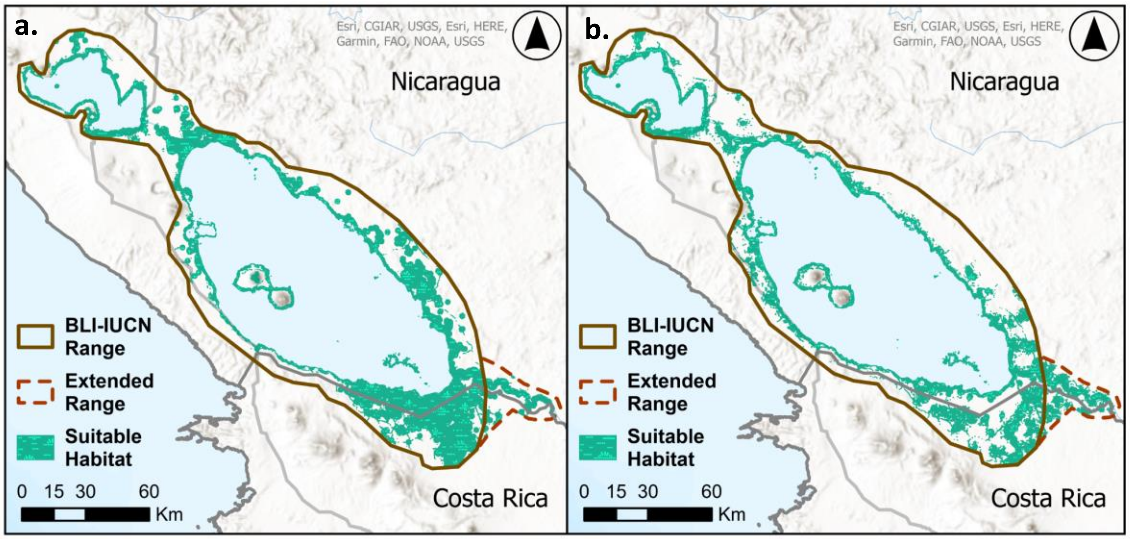

**Figure 2.6: Predicted vs. BLI-IUCN Range Area Comparison – 2.6a: Herbaceous wetland model -** Suitable habitat was thresholded at 0.55 and above with a total area of 3,237.89 km$^2$. **2.6b: 50% Recurrence model -** Suitable habitat was thresholded at 0.59 and above with a total area of 2,484.64 km$^2$.

## DISCUSSION

Our observations and the results of the analyses suggest an urgent need to reassess the conservation status of the Nicaraguan Grackle. Our proposal for reclassification is based on strong evidence that the NICGRA seldom occur further than 250 m from the shores of Lakes Managua and Nicaragua and their adjacent rivers and wetlands (e.g. Tisma, El Guayabo, and Los Guatuzos, Mateare, Momotombo, Caño Negro). This confirms their strict dependency on a single, specific habitat type—one that is significantly restricted and fragmented within the BLI-IUCN range boundary. It is important to note that while distance to recurring fresh water appears to be a powerful predictor of NICGRA habitat suitability, it is a proxy for the more complex combination of environmental variables associated with fresh water (such as specific types or species of vegetation) that are selected for by NICGRA.

The IUCN criteria for listing a species include five main categories that focus on various aspects of reduction or limitations in population size and geographic range, and 3) probability of extinction in the wild. These five criteria are further broken down into sub-criteria requirements that are unique to each listing status (i.e. “Vulnerable”, “Endangered”). A species need only meet one of the five main criteria to qualify for listing (see IUCN 2012 for complete listing criteria). I suggest that NICGRA meets Category B1 under the “Vulnerable” listing criteria on geographic range. I estimated an “extent of occurrence” of 14,900 km$^2$, which is less than the 20,000 km$^2$, set for the Vulnerable category. Category B1 also requires indication of at least two of subcategories a-c, which NICGRA meets by exhibiting: a) Severely fragmented distribution (**Fig. 2.1**) and b) Continuing decline, observed in the number of locations or subpopulations.

The IUCN states that the area of occupancy of NICGRA is 19,300 km$^2$, but our area estimates of their range polygon (with uninhabitable open water removed) was under 8,500 km$^2$. This is a significant discrepancy that warrants immediate re-evaluation of the range area criterion. Furthermore, using an ‘inhabited polygon” to determine the range of a habitat specialist with limited, fragmented habitat may not be appropriate for risk assessment. The use of a habitat suitability map can better delineate areas where fragmentation occurs, while also establishing an understanding of baseline associations between the species and features of their environment.

It is also noteworthy that the Nicaraguan population of the NICGRA does not appear to be stable, since the species is no longer found in historical areas. My coauthors have documented declines and disappearances at multiple sites within NICGRA range. Since 2007, authors MT and WA have conducted long term research in and around Rivas. In areas where the bird was historically present, not a single report has been recorded in almost 10 years. The recovery of water levels in wetlands such as Tisma Lagoon in abundant water years has not coincided with the recovery of NICGRA sightings. MT and WA revisited the site after wetland recovery following years of drought and, unfortunately, few NICGRA were detected. A plausible cause-effect mechanism behind the disappearance of the NICGRA at historical sites is linked to anthropization (crops, fires, cattle), and extreme climatic oscillations resulting in severe weather events that severely affect surface water levels and incumbent vegetation. Loss of NICGRA at these major wetland sites with repeated observations suggest that declines and extirpations may be occurring (though not yet detected) throughout their known distribution.

Approximately half of NICGRA observations used in this study were located in and around Caño Negro reserve in Costa Rica. While this is likely due to higher sampling effort associated with birding tourism, it will be important for any population-focused study in the future to investigate this location as a potential reservoir for the species.

There are a number of anthropogenic activities that impact NICGRA or its habitat directly and indirectly. Perhaps one of the biggest potential threats to NICGRA habitat is the proposed interoceanic canal that would potentially alter the salinity of Lake Nicaragua and the surrounding wetlands. Some of the coauthors of this article have participated in previous surveys (November 2013, April 2014) along the proposed route of the Nicaraguan transmarine canal. The proposed route goes through the NICGRA's distribution in San Miguelito wetlands and cuts through Lake Nicaragua.

The increasing occurrence of droughts is associated with decreases in precipitation that have occurred in the last 30 years. The precipitation in Granada, where wetlands such as El Guayabo, and a portion of Lake Nicaragua are located, has decreased 6% the last 30 years from historical records (Milán, 2012). Continued trends of declining or erratic precipitation and lengthening dry periods are expected under climate change (Kent et al. 2015, Chadwick et al. 2016). Climate change will create precipitation fluctuations (ECLAC, 2010; MARENA, 2012), which may cause both droughts and floods that would threaten NICGRA populations. Even without further reductions in precipitation on the Pacific dry coast, the current levels of precipitation may be insufficient to sustain current water levels if temperatures continue to increase and if rain occurs more in high intensity events separated by dry spells (Naumann et al. 2018).

The modeled importance of herbaceous vegetation in wetlands supports the observed affinity of NICGRA with tall grasses and grass-like plants such as cattails. However, coauthors have observed three main threats to cattail and emergent vegetation distribution and abundance in Nicaragua. The first threats are frequent droughts that desiccate emergent herbaceous vegetation, making them susceptible to fires, and diminishing suitable habitat. The second threat is the expansion of cultivated areas. It is common during dry and first part of the rainy season (April to June), to use of both lakes and wetlands shores to cultivate rice, melons, and squash. These activities are typically preceded by the habitat destruction using fire. The third threat to emergent vegetation like cattails is cattle ranching. Ranchers move cattle to lakes and wetlands shores for grazing, and the ruminants usually venture into the cattail clusters, fragmenting the natural association of this plant.

The results do not support the statement that cattle grazing provides additional habitat that benefits the species' distribution (Jaramillo & Burke, 1999; Martínez-Sánchez & Will, 2010). Although NICGRA does forage in the grassy areas of cattle ranches, the species only forages close to recurrent or permanent fresh water (as mentioned by Miller and Griscom, 1922). Cattle grazing is a major driver behind deforestation in Central America (Wassenaar et al. 2007), and it is prominent in Nicaragua's Dry Pacific ecoregion (Tobar-López et al. 2019). In the municipalities of Tisma, El Guayabo, Mateare, and San Miguelito, cattle ranching is one of the main economic activities, and ranches are generally close to wetlands and lakes. Ranchers from afar also move their cattle seasonally to water sources within the wetlands, which may coincide with times the birds are nesting and raising young. Cattle ranching represents a threat to NICGRA habitat, not a boon for new foraging opportunities.

## CONCLUSIONS

It is time to reconsider the current “extent of occurrence” listed for the “range area criterion” for this species. This criterion listed by Birdlife International (2023), which is based on globally established criteria by the International Union on the Conservation of Nature (IUCN 2012), has been used in part to justify the current conservation status of “Least Concern”. Based on the results, I produced a new “extent of occurrence” of 14,900 km$^2$, which is under the threshold of 20,000 km$^2$ to be listed as “Vulnerable”. I also propose a new “area of occupancy” for the Nicaraguan Grackle of 2,500-3,300 km$^2$ instead of the 19,300 km$^2$ area of occupancy listed by the BirdLife International (BLI and Handbook of the Birds of the World, 2023). This updated area estimate is less than 1/5th the original area. Combined with the fragmented distribution of the grackle, the number of sites where they are no longer found, and an extent of occurrence under 15,000 km$^2$, this suggests an IUCN Red List classification of “Vulnerable” rather than one of “Least Concern.”

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# **Chapter 3:** Characterizing vegetation structure to support habitat selection modeling for desert riparian songbirds: comparing and combining UAS and satellite image products.

## ABSTRACT

Vertical and horizontal vegetation structure are key variables for ecological patterns and processes. Limited spatial resolution and vertical structure information from publicly available satellite systems may hinder vegetation mapping. Unmanned aerial systems can produce fine-resolution (< 10-cm) 3D vegetation height models, which may complement remotely sensed vegetation texture. I aimed to 1) create 3D digital vegetation models using standard cameras on commercially available UAS, 2) compare the contributions of satellite image texture analysis and vegetation height models created with UAS in resource selection functions, and 3) characterize relationships between vegetation structure and nest site selection of the endangered Least Bell's Vireo and several other desert riparian songbirds. The highest ranking model included both satellite-derived image texture products and UAS-derived vegetation height. Predictors of the relative probability of nest site selection in the top model included: *vegetation height* ($P$ = 0.018), *distance to river* ($P$ < 0.0001), *entropy* ($P$ < 0.001), and *biomass of perennial grasses and forbs* ($P$ = 0.15). *Distance to river* and *vegetation height* had a positive influence on the relative probability of selection, while *entropy* had negative influence on the relative probability of selection. The relationships between the modeled covariates and relative probability of nest site selection must be interpreted and applied with caution, as all models require further revision. Nonetheless, satellite and UAS-derived imagery products complemented one another in resource selection functions, adding

information on both the vertical and horizontal dimensions of vegetation structure that may be useful in future investigations.

## INTRODUCTION

Remote sensing products are a cornerstone of ecological modeling and biodiversity conservation (Kasische *et al.* 1997; Wang *et al.* 2010). Satellites allow for image capture over a large, contiguous extent, which is useful for predictive mapping applications, including habitat selection modeling. Many of the image products used by ecologists are proxies for a variable of interest that cannot be directly measured at the desired scale of inference or that requires summarization over broad spatial extents. Image texture metrics are one group of remotely sensed measurements used to characterize variation in surface and vegetation structure from satellite imagery. However, publicly available remote sensing products are often offered at resolutions that are too coarse for corresponding image texture to align well with the species' behavior or the goals of the study (Guisan and Thuiller, 2005; Austin 2007; Franklin 2012). Recent advances in unmanned aerial systems (UAS) or "drone" technology have opened up ways to characterize habitat at significantly finer (< 1 m), biologically relevant scales. UAS methods that use frequent image capture with high degrees of overlap can also produce three dimensional models of landscapes (Singh and Frazier, 2018). Detailed image products are important for species that occupy small (< 15–30 m), but critical habitat patches throughout their larger breeding range. Additionally, some biomes are naturally spatially constrained, like desert riparian ecosystems.

The Amargosa River, flowing through the Mojave Desert of southern Nevada and California, supports a fantastic diversity of both migratory and residential desert songbirds. However, limited availability of fresh water in this region makes the few riparian areas highly desirable for residential development, agriculture, cattle grazing, and feral ungulate foraging (Krueper 1996). Competition between desert riparian songbirds and human land use over riparian areas has increased in recent years as droughts have made the availability of above-ground fresh water even more scarce (Sogge 2010). These challenges are further compounded by the spread of invasive riparian vegetation like Tamarisk in the desert southwest (Di Tomaso 1998), which may limit suitable nesting structure for native desert riparian songbirds (DRS; Dudley and DeLoach 2004; York et al. 2011). Trends in land conversion and development in dry areas with depleted groundwater sources suggest an urgent need to identify key habitat selection features and restore degraded habitat for DRS. Efficient conservation management for DRS will require an investigation of habitat features that are highly associated with nest site selection for multiple species. Vegetation height and arrangement (structure) across a breeding patch could have a significant influence on habitat selection for DRS (Fish and Wildlife Service 1998). While some bird species specialize in nesting in one or few species of plants, the focal birds of this investigation have been documented as nesting in several plant species that provide suitable structure (Allen *et al.* 2018). Information about nest site section preferences can be used to inform restoration practices along reaches of the Amargosa that have undergone Tamarisk removal and require re-vegetation.

Five desert songbird species are at the heart of this study. The endangered Least Bell’s Vireo (*Vireo bellii pusillus;* LBVI) is one of the most notable species that breeds along the Amargosa. The LBVI currently breeds in the riparian vegetation that buffers select streams in southern California and extreme western Arizona (Fish and Wildlife Service 1998). The LBVI is a foliage-gleaning insectivore that relies on dense vegetation within 2 m of the ground for nesting and foraging (Fish and Wildlife Service 1998). LBVI tend to nest in dense riparian shrub, growing on moist sandy soils, and under sheltering tree species such as cottonwood (*Populus fremontii*). Although LBVI breed in several types of riparian habitat, the amount of riparian forest across the southwest is highly constrained by the desert climate. The Black-tailed Gnatcatcher (*Polioptila melanura*; BTGC) is a small desert resident songbird found throughout the Sonoran, Mojave, and Chihuahuan deserts. Unlike the LBVI, the BTGC is not an obligate riparian species. The BTGC can be found in desert riparian willow-scrub, desert thorn scrub, and other arid habitats where it energetically gleans for insects (Farquhar *et al.* 2002). In the same genus, the Blue-gray Gnatcatcher (*Polioptila caerulea*; BGGC) is the most widespread bird included in the study. BGGC have a complex seasonal distribution. Many populations breed throughout the eastern and the southwestern United States, and winter along a narrow strip from the Amargosa basin along the entire Pacific Coast of Mexico. BGGC can also be found year-round in central Mexico and along the coastal USA from central California to Virginia. In the Southwest, Blue-grey Gnatcatchers breed and forage in willow-cottonwood woodlands near fresh water (Kershner *et al.* 2012). The Crissal Thrasher (*Toxostoma crissale*; CRTH) is a desert resident occupying a similar, but more constrained distribution than the Black-tailed Gnatcatcher. The CRTH forages for insects on the ground in dense, low vegetation by using its long, curved bill to explore leaf litter (Cody 1999). This species breeds and resides in desert scrub and riparian thickets (Cody 1999). The Verdin (*Auriparus flaviceps*; VERD) is the 5th and final desert songbird included in this study. This small desert resident can usually be found gleaning insects from the distal branches of thorny riparian trees, desert scrub, and chaparral (Webster 1999). These five species of desert songbirds share the desert riparian habitat of Amargosa Canyon but have a wide variety of within-habitat vegetation structure preferences. The inclusion of species with potentially diverse nest site selection preferences was deliberate, with the goal of informing vegetation restoration at degraded sites upstream that applies to as many species as possible.

Vegetation height and heterogeneity (key elements of vertical and horizontal structure, respectively), are often important variables for habitat mapping (Wood *et al.* 2012). While LIDAR surveys can provide direct measures of vertical and horizontal structure, availability and cost of data at biologically relevant scales limit its application. Many of the publicly available LIDAR data products also have a minimum vegetation height of 2 m (Farwell *et al.* 2021), which can further limit its application in studies focused on understory or ground-nesting birds. In recent years, affordable drones have been used to create digital surface models (DSM) and digital terrain models (DTM) using photogrammetry and structure-from-motion technology (Rosnell *et al.* 2013; Change *et al.* 2017). Digital surface models are a three-dimensional map of all features in a study area, including rocks, vegetation, and terrain. Digital terrain models are a subset of DSMs that only contain the base elevation or “ground layer” under all other surface features. Recently, researchers have begun experimenting with the idea that a digital vegetation model (DVM) may be produced by subtracting the DTM from the DSM, leaving only above-ground features on the landscape. Furthermore, corrections for slope can be applied to the initial DVM to allow for height measurement of individual vegetation features, providing a precise representation of vegetation height structure that mirrors canopy height models produced LIDAR. These products do not require a 2-m minimum vegetation height, and can accurately estimate ground vegetation when the canopy is not closed. In additional to height, the horizontal dimension of vegetation structure is also an important predictor of bird species richness and habitat preferences (Culbert *et al.* 2012; Farwel *et al.* 2020). Remotely sensed image texture is a direct measurement of horizontal structure and heterogeneity. It has also been used as a proxy for estimating vegetation density and vertical structure (Hoppus *et al.* 2002). This is often based on moderate-resolution satellite imagery, like Landsat (15-m to 30-m pixels). However, fine resolution (< 1 m) vegetation structure may be a more powerful predictor of habitat selection preferences in our study system because riparian forest is highly constrained in the southwest and multiple vegetation features fit within a single 15-m pixel of the Landsat 8 panchromatic band.

## Objectives and Research Questions:

The main objectives of this research are to 1) identify ways to improve variables used in habitat-selection modeling by using free or low-cost UAS and remote sensing technologies to characterize horizontal and vertical vegetation structure, and 2) to pinpoint nest site resource selection for five species of desert riparian songbirds. Supporting this, I will pursue the following research questions:

1) How do UAS-derived vegetation height (vertical structure) and Landsat-derived image texture (horizontal vegetation structure) variables compare and complement each other in resource selection functions?
2) What are the key associations between horizontal and vertical vegetation structure variables and desert songbird nest site selection?

## METHODS

### Study Area and Overview:

In this study I used Landsat 8-derived image texture and UAS-derived digital surface models to characterize vegetation and potential nesting habitat of five desert riparian songbirds. This study took place along the Amargosa River, which flows for 297 km from its headwaters north of Beatty, NV, through Shoshone and Tecopa, CA, to Death Valley where it drains into a belowground aquifer (Bureau of Land Management, 2019; **Fig. 3.1**). Often referred to as the "jewel of the desert", the Amargosa provides critical riparian habitat to desert fauna. The Amargosa River flows underground for all but ≈ 35 miles of its length (Bureau of Land Management, 2019) and I selected one of its largest riparian areas as my study site. I conducted vegetation mapping and nest site selection modeling at Amargosa Canyon, which is relatively small at less than 1-km$^2$ (**Fig. 3.1**). The nest site data for all five study species were collected by expert field naturalist Len Warren with Point Blue Conservation Sciences from 2005 to 2019. Nest survey effort was exhaustive, covering the full study area for the entirety of the nesting season. All nests within the study site were recorded and monitored throughout the breeding season from April through August.

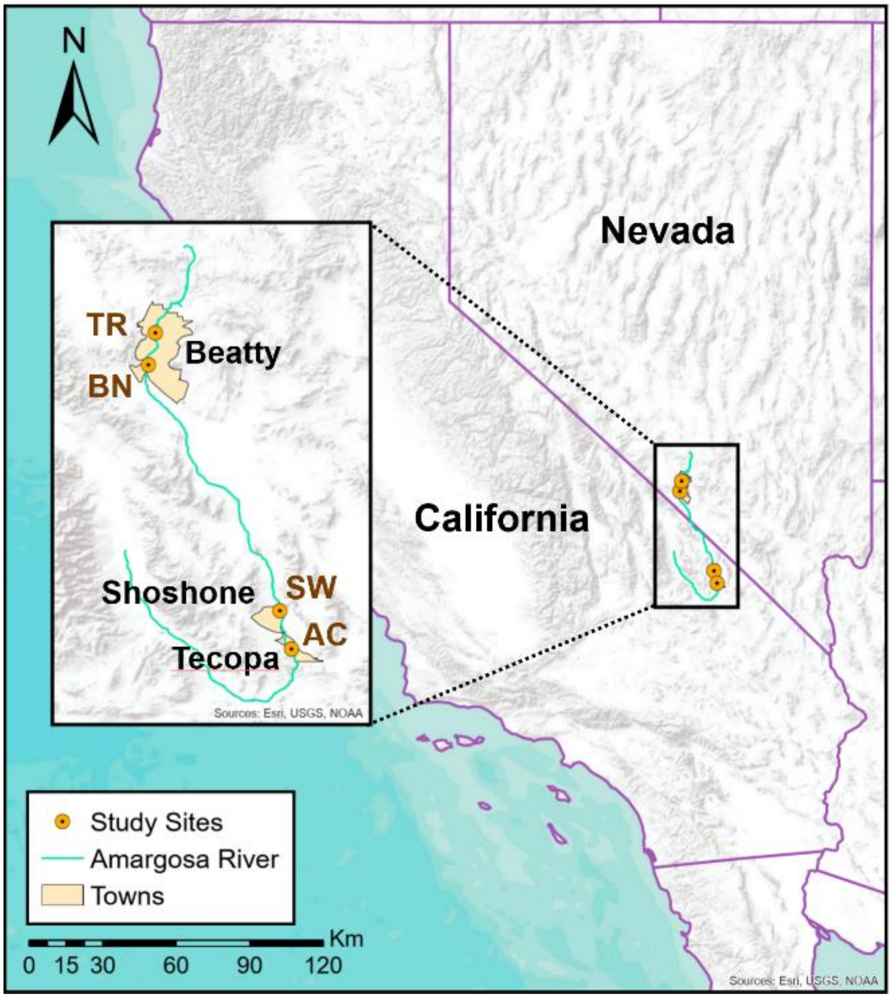


**Figure 3.1: Map of Study Area and Restoration Target Sites -** I selected the largest riparian site along the Amargosa River where it flows aboveground to conduct the habitat selection analyses (AC = Amargosa Canyon). Results from nest site selection modeling at AC will be used to inform restoration practices at two sites in Nevada owned by The Nature Conservancy (TR = Torrance Ranch, BN = Beatty Narrows) and one site in Shoshone, CA (SW = Shoshone Wetlands).

### Vegetation Texture Analysis:

I acquired imagery from the Landsat 8 15-m panchromatic band to generate texture products. Landsat scenes were captured within two weeks of the UAS flights for compatible vegetation phenology and cropped to the extent of the study area. Once imagery was acquired, I calculated the grey level co-occurrence matrix (GLCM) and derived a suite of 1st and 2nd order texture measures (Marceau *et al.* 1990). Using the *glcm* package in the R programming environment (Zvoleff 2016; v. 4.3.0 R Core Tea, 2023), I calculated two 1st order and six 2nd order texture measures: *mean, variance, dissimilarity, entropy, angular second moment, homogeneity, correlation,* and *contrast*. I used a 3x3 moving window approach to calculate the 2nd order textures measures. All eight texture measures were then evaluated for collinearity using pair-wise Pearson's correlation tests. Based on previous findings relating bird richness to texture measures (Farwell et al 2020; 2021) and elimination of texture variables correlated at 0.7 or above, I selected the *homogeneity, dissimilarity, entropy*, and *correlation* texture products for modeling (**Fig. 3.2**). *Homogeneity* measures the similarity of values between neighboring pixels, with higher values indicating greater smoothness or uniformity in an image. *Dissimilarity* measures the difference in values between neighboring pixels, with higher values indicating greater differences between pixels in an image. *Correlation* measures the linear dependency of neighboring pixel values. *Entropy* captures how disorderly pixels are relative to their neighbors, with higher values indicating greater differences between them. See Table one in Farwell et al. (2021) for excellent definitions of the remaining, unused texture measures.

### UAS image capture and Ground control points:

I acquired high-resolution (< 5 cm) imagery with a DJI Phantom 4 Pro quad-copter drone equipped with the stock RGB camera. This drone model cost less than $2,000, which is affordable relative to the cost of UAS LIDAR sensors or aerial LIDAR services that often start around $8,000. Thus, this model is an attainable option for most small research grants. I used the Pix4D Capture mobile software on a Samsung Galaxy S9 plus mobile phone to plan and operate flights. I flew a double-gridded flight plan to capture images with a high degree (>80%) of overlap at 45˚ and 90˚ viewing angles to facilitate creating three-dimensional maps. All flights were flown at 300 feet (91 m) to minimize flight time and potential disturbance to wildlife at the study site. Before flights began, I placed 10 high-contrast ground targets for ground control points throughout the study area. All ground control points were georeferenced using a Trimble Geo7X GPS unit connected to a Zephyr 2 Antenna. Ground control points were processed with the GPS Pathfinder software (v.5.90) for differential correction to a NOAA Continuously Operating Reference Station in Baker, CA.

### UAS Data Processing:

All imagery acquired by the drones was processed in the Pix4D Mapper computer software (Pix4D S.A., Prilly, Switzerland). Once a basic true-color image overlay was produced, I manually corrected ground control points by matching the digital waypoints to the ground targets captured in the imagery. The digital surface model, orthomosaic, and digital terrain model resulting from the point cloud densification were scaled up from 5 cm per pixel to 10 cm per pixel to reduce processing time during the modeling phase (**Fig. 3.3**). I calculated the digital vegetation model by subtracting the digital terrain model from the digital surface model in R. The resulting digital vegetation model then had the base elevation values zeroed to allow for accurate vegetation height measurements. As all features on the landscape were captured by the surface model, non-vegetation features such as rocks needed to be eliminated from the digital vegetation model. This was achieved through supervised random forest image classification, described below.

### Nest Site Selection Analysis and Image Classification:

I used the R programming environment to build resource selection functions \to determine what habitat characteristics are associated with nest site selection (R Core Team 2023, version 4.2.3). I included the following publicly available environmental variables in addition to vegetation texture and height variables to round-out the nest site selection models: above ground annual biomass, above ground perennial biomass, and distance to the Amargosa river (Robinson *et al.* 2019, Allred *et al.* 2021, Jones *et al.* 2021). Variables were arranged into competing models that were ranked with AIC (Akaike 1973). Any two variables with a high correlation coefficient (e.g. $r \geq 0.7$) were not used in the same model. I used logistic regressions (generalized linear models) to fit the nest site selection model with nest site data pooled across species and years. The definition of available habitat is a critical component of resource selection functions (McClean *et al.* 1998, Cooper and Millspaugh 2001).

Habitat or “resource” availability for the nest site selection model was defined by using image classification to determine the presence or absence of vegetation across the whole study area. Supervised image classification was performed on the true-color orthomosaic produced with the drone (**Fig. 3.4**). I created training polygons with nine classes of vegetation, rock, and bare ground using ArcGIS Pro (v 3.1). Training polygons were sampled with 1000 random points that were stratified by polygon size. Sampled points were used to train the random forest classification, which generated nine unique feature classes. Feature classes were manually grouped by category (vegetation or non-vegetation), with the combined vegetation class representing available habitat.

The random forest image classification was used to produce a binary raster of vegetation and non-vegetation for the study area (**Fig. 3.4**). Background points for the resource selection function were randomly generated within the vegetation boundaries of the raster as it was used to define available habitat. The binary habitat availability layer was also used to mask the initial vegetation model to remove all non-vegetation features (**Fig. 3.3**). I used band 8 of a scene captured by Landsat 8 on 10-19-2019 (the 15-m panchromatic band) to produce the texture metrics. Based on the high degree of correlation between texture variables, four of the eight texture metrics were selected for modeling: *homogeneity*, *dissimilarity*, *entropy*, and *correlation* (**Fig. 3.2**).

## RESULTS

I compared 44 competing resource selection functions with Akaike's Information Criterion (AIC) (**Table 3.1**). Competing models were created with all combinations of predictor variables, except where correlation between two variables met or exceeded 0.70. The highest ranking model was a "combination" model which included both satellite-derived image texture products and UAS-derived vegetation height. Significant covariates (predictors) of the relative probability of nest site selection in the top model included: *vegetation height* ($P = 0.018$), *distance to river* ($P < 0.0001$), and *entropy* ($P < 0.001$). The *biomass of perennial grasses and forbs* covariate was not significant at ($P = 0.15$). *Distance to river* and *vegetation height* had a positive influence on the relative probability of selection, while *entropy* had negative influence on the relative probability of selection (**Table 3.2**). I scaled all covariate data when fitting each model to improve the interpretation of the coefficient estimates ($\beta$). The "effect size" of scaled coefficient estimates should be interpreted as every increase or decrease in one standard deviation of the covariate resulting in an increase or decrease of $\beta$ in the relative probability of selection. Positive coefficient estimates indicate a higher relative probability of use and negative values indicate a lower relative probability of use. It is important to note that resource selection functions using a logit link for a binomial response (e.g. selected, not selected) do not result in an absolute probability of use or selection. Instead, the result is a relative probability of use or selection based on the log of the odds ratio.

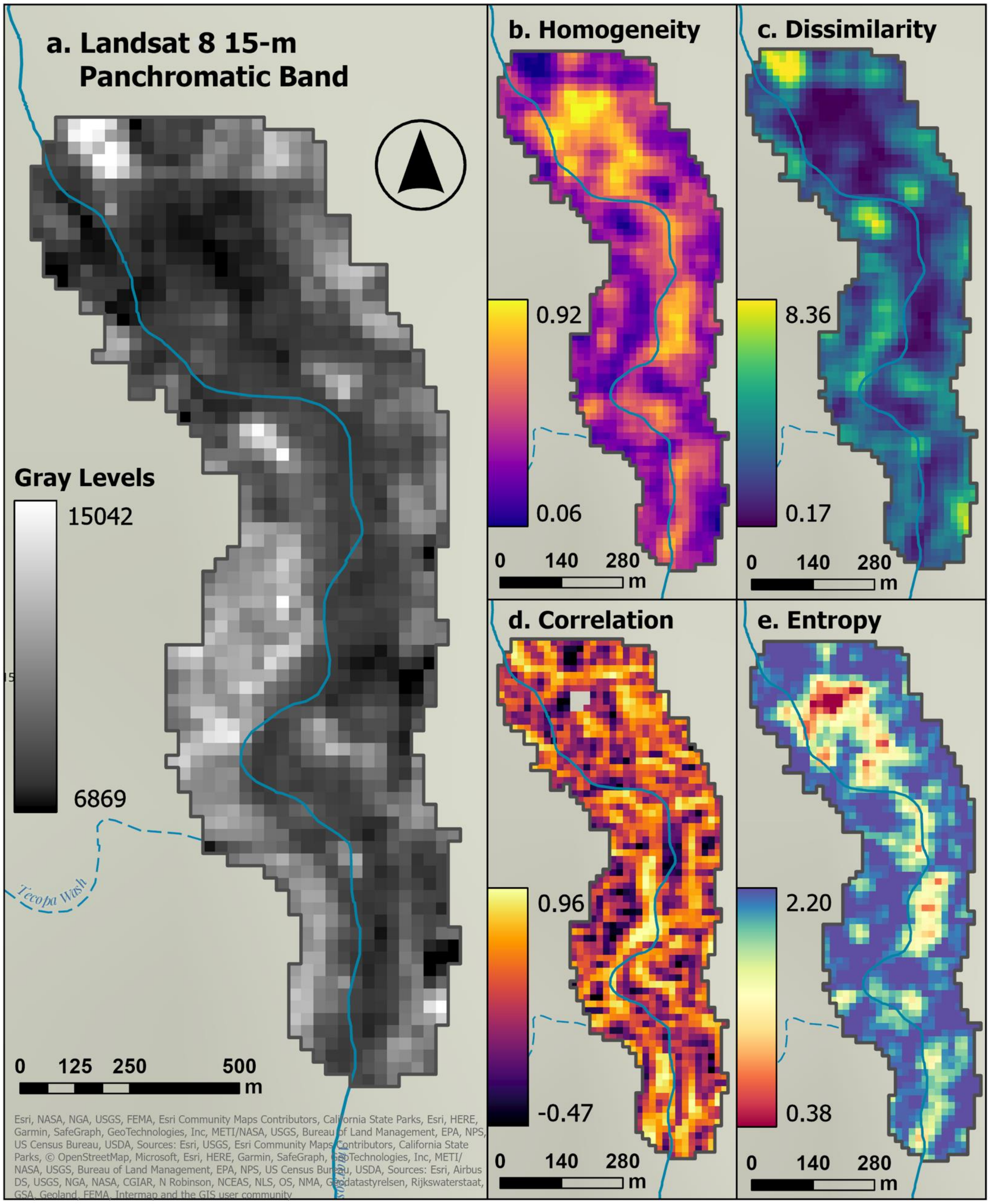
I used the highest ranking model to produce two prediction surfaces representing the relative probability of nest site selection at our study site (**Fig. 3.5**). For each prediction surface, rasters were either scaled up to the common 15 m grain of the satellite image texture variables (**Fig. 3.5c**) or scaled down to the 10 cm grain of the UAS vegetation height variable (**Fig. 3.5b**) to allow for the comparison of results at the native scale of the remote sensing and UAS products. I resampled all rasters in R using a bilinear interpolation method in the *terra* package. The relative probability of nest site selection was highest at the Northern portion of our study site, where most nests have been found over the survey period.

**Table 3.1: Model Section** – The top model with the lowest AIC score included UAS-derived vegetation height, satellite-derived image texture (entropy), biomass of perennial grasses and forbs, and distance to the Amargosa river. To limit the size of the table, only the top 15 models (cumulative AICwt = 0.9) and the null model were included. Covariates with significant coefficient estimates are highlighted in bold.

| Model | Variables | AIC | Δ AIC | AICwt |
|---|---|---|---|---|
| combo5p | **dvm** + biom.Peren + **dist.Riv** + **entropy** | 440.70 | 0 | 0.22 |
| combo5a | **dvm** + biom.Ann + **dist.Riv** + **entropy** | 441.50 | 0.80 | 0.15 |
| combo1a | **dvm** + biom.Ann + **dist.Riv** + **homog** + **correl** | 442.45 | 1.75 | 0.09 |
| combo1p | **dvm** + biom.Peren + **dist.Riv** + **homog** + **correl** | 443.13 | 2.43 | 0.06 |
| sat13 | **dist.Riv** + **entropy** | 443.38 | 2.68 | 0.06 |
| sat7p | biom.Peren + **dist.Riv** + **entropy** | 443.68 | 2.98 | 0.05 |
| sat5p | biom.Peren + **dist.Riv** + **entropy** + correl | 443.78 | 3.08 | 0.05 |
| sat5a | biom.Ann + **dist.Riv** + **entropy** + correl | 443.79 | 3.09 | 0.05 |
| sat7a | biom.Ann + **dist.Riv** + **entropy** | 444.02 | 3.32 | 0.04 |
| combo3p | **dvm** + biom.Peren + **dist.Riv** + **homog** | 444.79 | 4.09 | 0.03 |
| sat4a | biom.Ann + **dist.Riv** + **homog** + **correl** | 444.95 | 4.25 | 0.03 |
| sat2a | biom.Ann + **dist.Riv** + dissim + **entropy** + correl | 444.99 | 4.29 | 0.03 |
| sat1a | biom.Ann + **dist.Riv** + homog + entropy + correl | 445.08 | 4.38 | 0.02 |
| combo3a | **dvm** + biom.Ann + **dist.Riv** + **homog** | 445.13 | 4.43 | 0.02 |
| sat1p | biom.Peren + **dist.Riv** + homog + entropy + correl | 445.75 | 5.05 | 0.02 |
| null | ~1 | 481.11 | 40.42 | 0.00 |

**Table 3.2: Coefficient Estimates** – Coefficient estimates (*β*) of the scaled covariates for the highest ranked model according to AIC. The "effect size" of scaled coefficient estimates should be interpreted as follows: with every increase or decrease in one standard deviation of the covariate, there is an increase or decrease of *β* in the relative probability of selection. Positive coefficient estimates indicate a higher relative probability of use and negative values indicate a lower relative probability of use.

| Variable | Code | $\beta$ | Std. Error | P value |
|---|---|---|---|---|
| Vegetation height (m) | dvm | 0.26 | 0.12 | 0.018 |
| Biomass of perennial grasses and forbs (lbs/acre) | biom.Peren | 0.23 | 0.16 | 0.15 |
| Distance to Amargosa river (m) | dist.Riv | 0.50 | 0.12 | < 0.0001 |
| Entropy (image texture) | entropy | -0.46 | 0.14 | 0.001 |
| Intercept | intercept | -2.72 | 0.16 | < 0.0001 |



Esri, NASA, NGA, USGS, FEMA, Esri Community Maps Contributors, California State Parks, Esri, HERE, Garmin, SafeGraph, GeoTechnologies, Inc, METI/NASA, USGS, Bureau of Land Management, EPA, NPS, US Census Bureau, USDA, Sources: Esri, USGS, Esri Community Maps Contributors, California State Parks, © OpenStreetMap, Microsoft, Esri, HERE, Garmin, SafeGraph, GeoTechnologies, Inc, METI/NASA, USGS, Bureau of Land Management, EPA, NPS, US Census Bureau, USDA, Sources: Esri, Airbus DS, USGS, NGA, NASA, CGIAR, N Robinson, NCEAS, NLS, OS, NMA, Geodatastyrelsen, Rijkswaterstaat, GSA, Geoland, FEMA, Intermap and the GIS user community

**Figure 3.2: Satellite-derived Image Texture Metrics** – **3.2a.** The **Landsat 8 15-m panchromatic band** used to generate all texture metrics with a gray level co-occurrence matrix. **3.2b: Homogeneity –** The similarity of values between neighboring pixels. Higher values indicate greater smoothness or uniformity in an image. **3.2c: Dissimilarity -** The difference of values between neighboring pixels. Higher values indicate greater differences between pixels in an image. **3.2d: Correlation –** the linear dependency of neighboring pixel values. **3.2e: Entropy** –captures how disorderly pixels are relative to their neighbors, with higher values indicating greater differences between them.

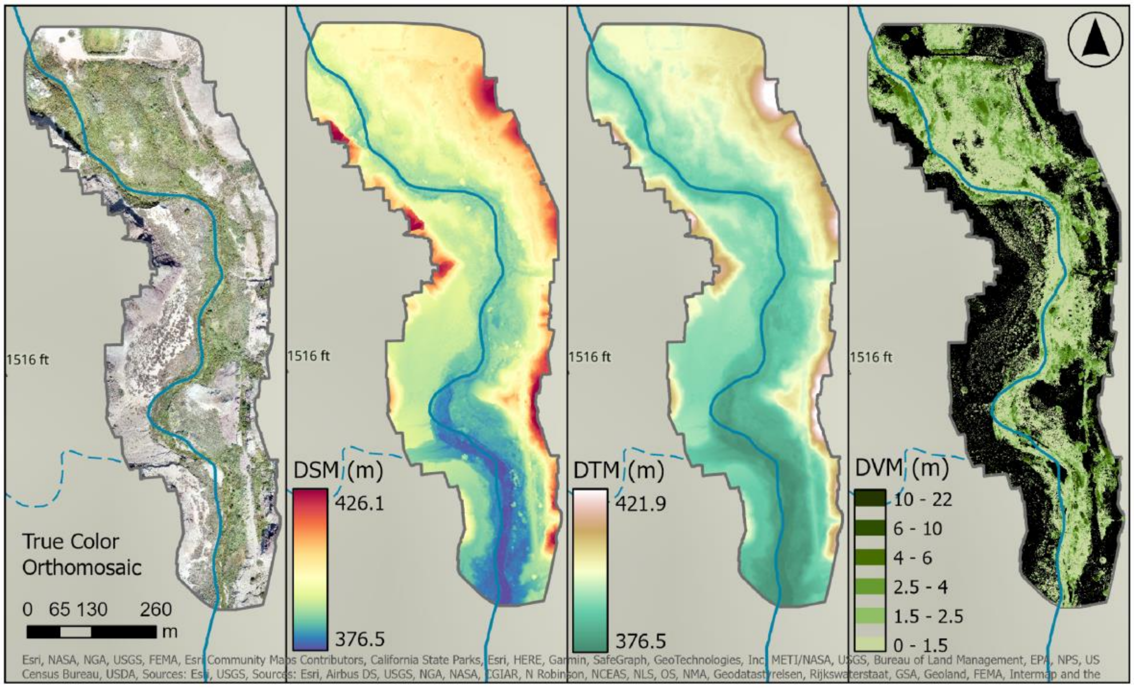


**Figure 3.3: UAS-derived Digital Vegetation Model** – **3.3a:** The true-color orthomosaic produced by Pix4D. **3.3b:** The digital surface model (DSM) created from the image point cloud in Pix4D. **3.3c**: The underlying digital terrain model (DTM) created from the DSM by Pix4D. **3.3d:** The digital vegetation model masked with the binary vegetation cover raster (see **Fig. 3.4d**).

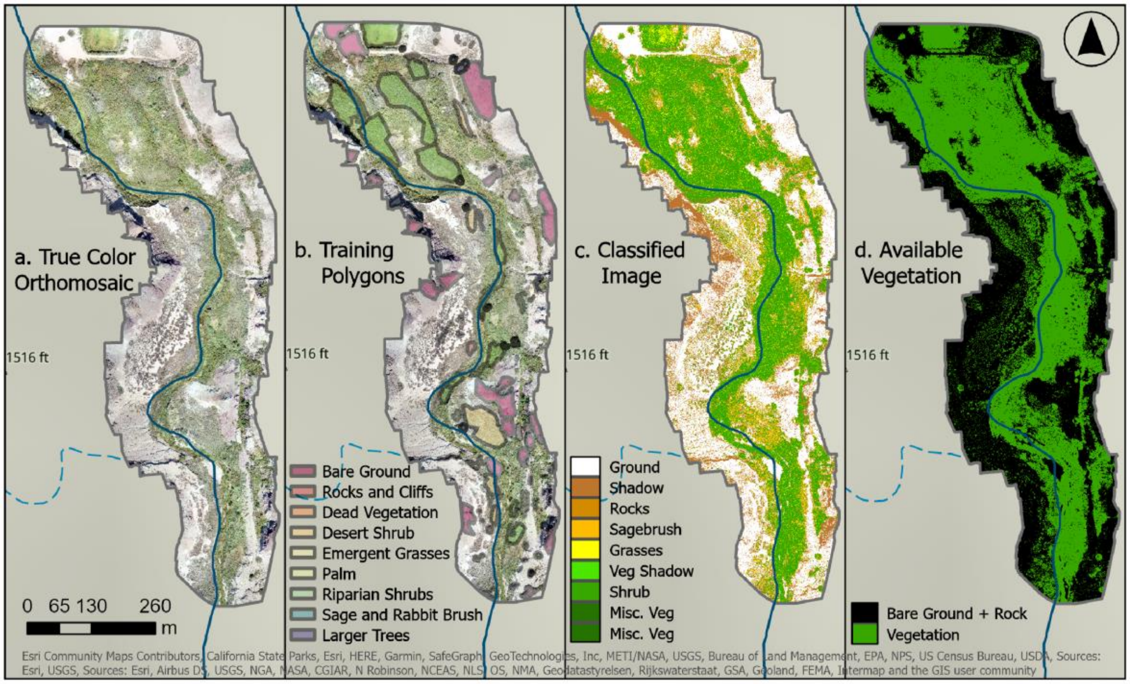
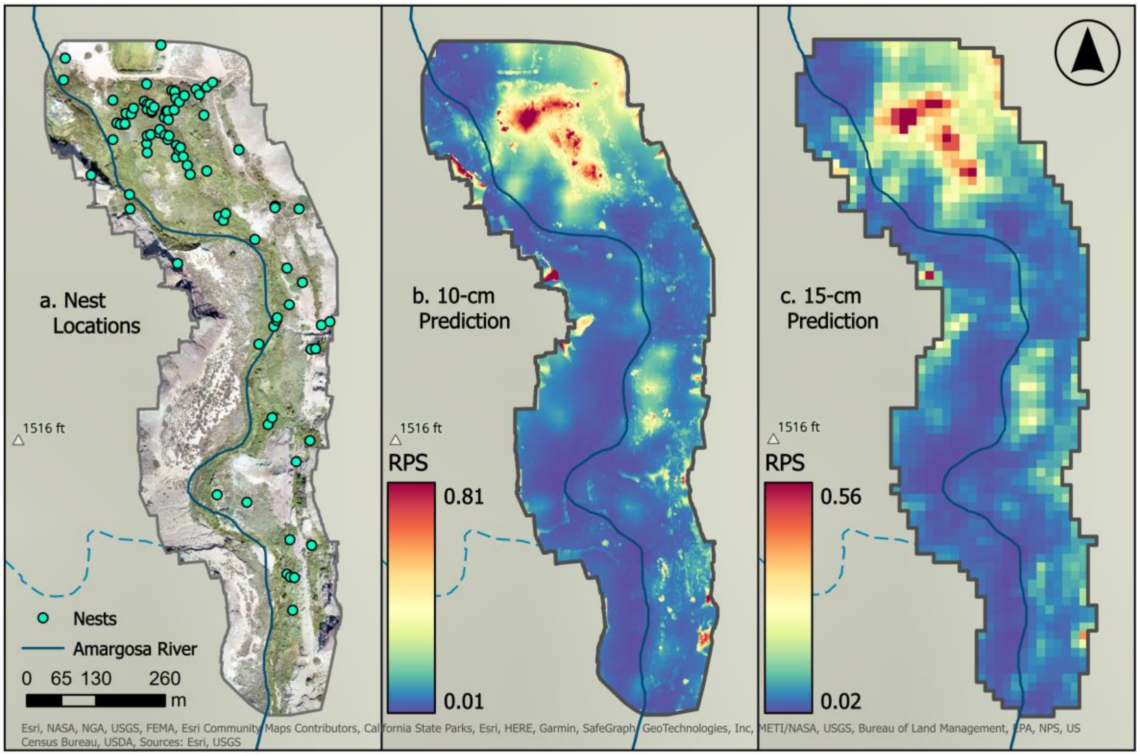


**Figure 3.4: Image Classification** – **3.4a:** Image classification was carried out using the 10-cm orthomosaic created from the drone imagery in Pix4D. **3.4b**: Training polygons of nine feature classes used for the supervised image classification. **3.4c:** The classified image generated by the random forest classification. **3.4d:** The binary raster of vegetation and non-vegetation used to define available habitat in the RSFs.



Esri, NASA, NGA, USGS, FEMA, Esri Community Maps Contributors, California State Parks, Esri, HERE, Garmin, SafeGraph, GeoTechnologies, Inc, METI/NASA, USGS, Bureau of Land Management, EPA, NPS, US Census Bureau, USDA, Sources: Esri, USGS

**Figure 3.5: Nest Locations and Model Predictions** – **3.5a: Nest locations** in Amargosa Canyon (AC) for comparison with prediction surface. 10-cm (**3.5b**) and 15-m (**3.5c**) predictions for the relative probability of selection at AC are based on the highest ranking model according to AIC (**see Table 3.1**). Note that the relative probability of use is predicted at different ranges, with higher maximum values in the 10-cm prediction.

## DISCUSSION

Through this investigation, I created digital vegetation models from low-cost drone imagery data and built predictive models of relative nest site selection for a community of desert songbirds. In doing so, I used open-source image classification to create an ultra-fine definition of available habitat for the resource selection function. The top-ranked nest site selection model included both satellite-derived image texture variables and the UAS-derived vegetation height variable, suggesting that they offer complementary information for relative probability of nest site selection. Therefore, I expected that nest site selection models including both the UAS-derived vegetation height covariate and vegetation texture covariates to have higher explanatory power. While the top-ranked model contained both satellite and UAS-derived variables, AIC did not improve markedly across our competing models (**Table 3.1**).

Greater vegetation height increased the relative probability of nest site selection, but not as strongly as expected. This may be due to limitations in the nest site dataset, which did not record a height for each nest location. Thus, the maximum height of vegetation at the nest location was used to fit the selection models. Higher levels of entropy, one of four image texture covariates used in the resource selection functions, had a negative influence on the relative probability of selection. Image texture metrics capture heterogeneity in horizontal vegetation structure (Wood *et al.* 2012). Entropy captures how disorderly pixels are relative to their neighboring pixels, with higher values indicating greater differences between them (Baraldi and Panniggiani 1995). Within Amargosa Canyon, higher levels of entropy are likely associated with areas where patches of vegetation types transition. It is possible that species nesting in this community nest within patches of consistent vegetation types, rather than at the edge of transition areas. Annual aboveground biomass of perennial and annual forbs and grasses were not strong predictors of relative probability of nest site selection in any of the models. This is likely due to the fact that few of the birds in this community are grass-nesters. While grasses and forbs are a staple in their broader riparian habitat, nests are typically located in shrubs or trees. These variables were included in the models because they may be good indicators of soil moisture, which is difficult to accurately measure via remote sensing and relevant to the growth and health of other plants in the riparian zone. Within Amargosa Canyon, grasses make up the majority of vegetation closest to the river and along the southern portion of the study site. This can be seen as the homogenous light-green band along the river in the UAS-derived orthomosaic (**Fig. 3.5a**). This vegetation primarily consists of annual and/or invasive grasses like Reed Canary Grass or Cattails, which may explain the lack of nest sites in this area and the low relative probability of selection predicted by the top model. This could also explain why the relative probability of selection increased as distance from the Amargosa river increased. The relationship between nest site selection and the river is also influenced by the constrained extent of the study site, as a study area covering multiple kilometers would have revealed higher relative probabilities of use with proximity to the river.

## CONCLUSIONS

I explored an innovative, low-cost way to use recent advances in drone technology and remote sensing to improve vegetation height models and definitions of available habitat for resource selection functions. The satellite and UAS-derived imagery products complemented one another in the models, adding information on both the vertical and horizontal dimensions of vegetation structure. One of the aims of this investigation was to create predictive models of nest site selection to inform restoration practices for revegetation at target sites upstream. The preliminary status of our top models suggest that the relationships between the modeled covariates and relative probability of nest site selection must be interpreted and applied with caution. More-so, the resource selection functions presented in this study should serve as a baseline for further investigation.

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# CONCLUSION

Global declines in avifauna and Wallacean shortfall necessitate continued biogeographic research with clear aims to inform monitoring and management practices. In my dissertation, I explored avian-habitat relationships in three unique study systems. I created 100-m habitat suitability maps, innovative 10-cm UAS-derived vegetation height products, and predictive surfaces of nest site selection for threatened and endangered songbirds using open source programming platforms and publicly available imagery data. These maps and methods can be used to continue and bolster research on our target species, and other songbirds that live in similar study systems.

In my first chapter, I wanted to know which habitat characteristics were best suited to support wintering WIFL and where these areas were concentrated across their expansive non-breeding range. I hypothesized that WIFL were highly associated with riparian shrub cover and proximity to freshwater and expected habitat to be similar to that in their breeding range. Using publicly available land cover data, long term WIFL survey data, and filtered eBird records, I characterized the habitat of the three western subspecies of Willow Flycatchers (*Empidonax traillii subspp.*) with a range-wide species distribution model. I found that proximity to riparian areas, arid climate, and complex vegetation structure drove WIFL habitat suitability in their non-breeding range. Areas with higher predicted habitat suitability were more concentrated along the pacific coast of Central America. However, there is a significant gap in protected area coverage where predicted habitat suitability is highest on the west coast. Suitable habitat made up less than 11% of land within conservation areas, suggesting a need to prioritize conservation where suitable habitat is concentrated. An early version of the predicted habitat suitability map has already been used to select new survey sites for WIFL on the ground in El Salvador. The most recent versions of the habitat suitability map are 10x finer, offering an even more detailed view of the landscape for conservation planning. This 100-m SDM will be used by conservation collaborators to refine survey site selection and to prioritize areas for land acquisition and/or conservation partnerships.

In chapter two I took a similar approach to modeling habitat for the declining Nicaraguan Grackle (*Quiscalus nicaraguensis*), but with a different end goal and at a much smaller spatial extent. Publications on this species were limited to field guides and its IUCN status of “Least Concern” did not sit well with local ornithologists and birders who had noticed sharp declines in recent years. I aimed to determine key habitat characteristics to get an accurate extent of occurrence and area of occupancy. The current area estimates were based on a loosely defined range polygon that does not adequately reflect the limited distribution of their required habitat type or take into account the coverage of uninhabitable large bodies of freshwater. Using 100-m fractional land cover data and derived variables for freshwater recurrence, I created baseline maps of habitat suitability and refined area estimates. The maps of predicted habitat suitability will be used as evidence to request a timely reassessment of the protection status for this understudied, habitat specialist. My results suggest that the current area listed under the species’ range by the IUCN and BirdLife International of 19,300 km$^2$ is over-estimated. My area of occupancy estimate is less than 1/5th the original area (2,500–3,500 km$^2$). Combined with the fragmented distribution of the grackles required habitat and the number of sites where they are no longer found, this suggests an IUCN Red List classification of “Vulnerable” rather than one of “Least Concern.”

In my third chapter, I wanted to know how UAS-derived vegetation height models and Landsat-derived image texture variables contributed to- and complemented each other in resource selection functions for a desert riparian songbird community in Amargosa Canyon, CA. I aimed to explore a low-cost way to use off-the-shelf drone technology and remote sensing to create ultra-fine resolution vegetation height models and improved definitions of available habitat for nest site selection models. Imagery products from both satellite and UAS complemented one another in the models, adding information on both the vertical and horizontal dimensions of vegetation structure. Another aim of this investigation was to create predictive models of nest site selection to inform restoration practices for revegetation at target sites upstream. The limited predictive capacity of our top models suggest that the relationships between the modeled covariates and relative probability of nest site selection must be interpreted and applied with caution. The model results presented in this chapter should serve as a reference point for further investigation rather than concrete recommendations for restoration of nesting habitat at the target sites upstream.

Each of the studies were not without their weaknesses. Both the WIFL study in chapter one and Mojave Songbird study in chapter three required data pooling prior to analysis. While the WIFL study did not have a low sample size, the records from the long term surveys were limited in their spatial extent. I included eBird records to enhance the spatial coverage of our dataset. However, visual similarities between WIFL subspecies meant that I could not isolate SWFL records. It’s possible that pooling across the three western subspecies limited the specificity of the habitat suitability estimations, painting a picture of broader habitat tolerance than may be exhibited by SWFL. Directly tracking the migration of SWFL with Motus technology would be an excellent way to ground-truth our habitat suitability maps. Due to a limited sample size, the Mojave nest data in chapter 3 were pooled across species and years. While these surveys were incredible in that they recorded every nest within Amargosa Canyon over the study period, the limited extent of our study area resulted in fewer than 100 nests overall. Pooling nest data over species and year could have had significant impacts on the predictive ability of our resource selection functions. Vegetation growth and health can vary significantly between years, and different species may have a wider range of nest site preferences than anticipated. A lack of satellite-derived vegetation type data at grains below 100 m also limited the predictive ability of these models. For chapter two, a lack of consistent survey effort split our data into either location-poor and abundance-rich (field surveys or location-rich and abundance-poor (eBird data). With my expertise, I chose to develop habitat models with the location data without making use of the abundance data available at some sites. The abundance data, while limited in sample size and scope, may have been useful in determining baseline estimates of population size for this species.

Thus, my first recommendation for future research is for the creation of a historical and contemporary population estimate for the Nicaraguan Grackle. This species occupies a freshwater riparian habitat type that is heavily restricted within their range, and exhaustive surveys of this species could easily be completed within a year. The habitat suitability maps I created can be used to plan a stratified survey effort across the entire range of the species. Without baseline population estimates, this species may remain in the “Least Concern” category of conservation status until it approaches the edge of the extinction vortex. Another area of future research I see stemming from my work would be to investigate and identify areas of overlap between suitable habitat for multiple target species in countries like Nicaragua where conservation partnerships are less common. While it is not conceptually appropriate for all species, species distribution models can be created with readily available occurrence and environmental data. The limited availability of conservation funding, limited ability to acquire land, and limited reach in maintaining long term conservation partnerships makes the prioritization of critical habitat designation of the utmost importance. Lastly, based on the limited predictive power of our resource selection functions, I would like to explore additional UAS-derived vegetation products in species-specific nest site selection models. The pixel-based approach to image classification may not have been appropriate for 10-cm imagery. Vegetation types were broken up into a wider array of spectral profiles than may have been needed for vegetation type classification. With additional supervised training inputs and upscaling to quarter, half, or one-meter grains, it may be possible to create both categorical vegetation type and fractional vegetation type cover products. Furthermore, combining the UAS-imagery with even a small sample of on-the-ground vegetation identification would greatly improve the final image product. In the same vein, the use of a multispectral sensor in place of the RGB camera would allow for sensing in the near-infrared band, which can be used to generate NDVI and EVI imagery products.

This conclusion of these three chapters’ marks a milestone, but not an end, in a tremendous learning experience that I will be privileged to continue for the rest of my life. I sincerely hope you have learned something about the habitat and needs of some truly fantastic birds, and where, with help from conservation-minded people, you may continue to find them.