

THESIS

DIFFERENTIATING EXISTING HABITAT OF THE INVASIVE TAMARISK
(*TAMARIX* SPP.) FROM POTENTIAL HABITAT OF THE ENDANGERED
SOUTHWESTERN WILLOW FLYCATCHER (*EMPIDONAX TRAILLII EXTIMUS*)
THROUGH MAXIMUM ENTROPY MODELING

Submitted by

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Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of: Master of Science

Colorado State University

Fort Collins, Colorado

Summer 2010

COLORADO STATE UNIVERSITY

June 29, 2010

WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY PATRICIA M. YORK ENTITLED DIFFERENTIATING EXISTING HABITAT OF THE INVASIVE TAMARISK (*TAMARIX* SPP.) FROM POTENTIAL HABITAT OF THE ENDANGERED SOUTHWESTERN WILLOW FLYCATCHER (*EMPIDONAX TRAILLII EXTIMUS*) THROUGH MAXIMUM ENTROPY MODELING BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

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ABSTRACT OF THESIS

DIFFERENTIATING EXISTING HABITAT OF THE INVASIVE TAMARISK (*TAMARIX* SPP.) FROM POTENTIAL HABITAT OF THE ENDANGERED SOUTHWESTERN WILLOW FLYCATCHER (*EMPIDONAX TRAILLII EXTIMUS*) THROUGH MAXIMUM ENTROPY MODELING

Biological control of the exotic plants known collectively as tamarisk (*Tamarix* spp, saltcedar, tamarisk) in southwestern states is controversial regarding the protection of the federally endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus*). The songbird sometimes nests in tamarisk where floodplain-level invasion replaces native habitat. Biological control with the saltcedar leaf beetle (*Diorhabda elongate*) began along the Virgin River, Utah, in 2006, enhancing the need for comprehensive understanding of the tamarisk-Flycatcher relationship. I used maximum entropy (Maxent) modeling to separately quantify the current extent of dense tamarisk habitat (>50% cover) and the potential extent of habitat available for *E. traillii extimus* within the studied watersheds. I used transformations of 2008 Landsat Thematic Mapper images and a digital elevation model as environmental input variables.

Maxent models performed well for the Flycatcher and tamarisk with Area Under the ROC Curve (AUC) values of 0.960 and 0.982, respectively. Classification of thresholds and comparison of the two Maxent outputs indicated little spatial overlap between predicted suitable habitat for *E. traillii extimus* and predicted dense Tamarisk stands. Dense tamarisk habitat comprised 1,000 km² within the study area, of which 8.5% was also modeled as potential habitat for *E. traillii extimus*. Potential habitat modeled for the Flycatcher constituted 230 km², of which 38.1% also contained dense tamarisk habitat. Results showed that both native vegetation and dense tamarisk habitats exist in the study area and that most tamarisk infestations do not contain characteristics that satisfy the habitat requirements of *E. traillii extimus*. Based on this study, effective biological control of *Tamarix* spp. may initially reduce the suitable habitat available to *E. traillii extimus* within the study area, but has the potential to increase suitable habitat if native vegetation replaces tamarisk in biocontrol areas.

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ACKNOWLEDGEMENTS

First and foremost, I would like to thank my advisor, Dr. Thomas Stohlgren, for taking me in as an orphaned graduate student and showing me patience and support, especially through the writing process. I would not have completed this project if it was not for his generosity and compassion. I would also like to thank my committee members for their support and contributions to my professional development. Dr. James Graham kept me on track and aided me through the difficulties associated with remote sensing and modeling, two topics I had only briefly discussed before beginning this project. Dr. Curtis Flather provided me with insight into the world of songbirds and helped me understand the complications associated with modeling their habitats. Dr. Sarah Sloane kept me grounded as a scientist and a researcher in the field of ecology. She reminded me of the importance of remaining unbiased and communicating my research effectively, especially to those outside the discipline. I would also like to thank all of the members of the Stohlgren group. Dr. Paul Evangelista and Dr. Sunil Kumar were extremely helpful when it came to developing my methods and analyzing my results, and Kirstin Holfelder was both an amazing friend and editor through this process. In addition, I would like to thank Dr. Jill Baron, without whom I would not have found my place in this amazing research group.

I could not have completed this thesis without the constant and loving support of my husband, Adam York, and the rest of my family and friends. I thank Adam for

standing by my side through the ups and downs, and for helping me power through when no one else could. I thank my father, Dr. Fred Perrino, for being an outstanding scientist role model, and for helping me understand the politics and pressures of graduate school. I thank my mother and Girl Scout leader, Sue Perrino, for facilitating the experiences that fueled my love of the natural world, and for providing such loving and positive support throughout my life. I also need to acknowledge my revered instructor, Dr. Richard Knight, who provided me with two teaching assistantships in the second year of my research. Never have I met a man so passionate and dedicated to his work and his students. I feel a deep gratitude that I was able to experience Dr. Knight as a mentor and absolute role model in the field of Conservation Biology.

I would also like to thank the U.S. Geological Survey's Invasive Species Science Program in Reston, Virginia, for funding this study, the Natural Resource Ecology Laboratory at Colorado State University for logistical support, and Mark Sogge, Eben Paxton, and the Colorado Plateau Research Station for providing me with Flycatcher breeding site data.

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I. INTRODUCTION

Humans have dramatically altered the global distribution of species over the past few centuries (Chaplin III et al. 2000). This movement of species coupled with the disturbance of native habitats has facilitated the invasion of exotic plants and animals around the world, threatening the survival of many native species (Vitousek et al. 1997). Although exotic and native species coexist in many modern habitats, conservation efforts typically focus on single-species management of either the introduced or the threatened species. Chemical, mechanical, and biological control efforts geared at eradicating exotic species can have negative effects on native populations, especially on sensitive species of endangered, threatened, or endemic status (Innes & Barker 1999; Cory & Myers 2000; Matarczyk et al. 2002). New strategies are needed that combine conservation efforts for both introduced and threatened species existing within the same landscape.

Riparian corridors often represent only 1-3% of the landscape but are vital to biodiversity, especially in arid regions (Naiman et al. 1993; Naiman & Decamps 1997; Patten 1998). Riparian areas are also highly susceptible to invasion by introduced species due to their relatively abundant resources (Stohlgren et al. 1998). In the southwestern United States, disturbance of the natural flow regime through damming and agricultural divergences has dramatically altered riparian habitats. The lowered water table and reduced peak flows hinder successful propagation of native cottonwood (*Populus* spp.) and willow (*Salix* spp.) species, reducing the abundance of mature native riparian forests

(Lite & Stromberg 2005). Members and hybrids of the exotic genus *Tamarix* (*Tamarix* spp, saltcedar, tamarisk) are adapted to the altered flow regime given their ability to extract deep water through an extensive tap root (Everitt 1980). Tamarisk currently occur within most large river systems of the southwestern United States and are estimated to have replaced 470,000 – 650,000 ha of native riparian habitat (Robinson 1965; Zavaleta 2000). Tamarisk's success further suppresses the ability of cottonwood and willows to reproduce (Lytle & Merritt 2004; Stromberg et al. 2007a; Merritt & Poff 2010).

The altered ecosystems represent degraded habitat for many native species, and restoration has become a high-priority goal for many natural resource managers (Szaro & Rinne 1988). Millions of United States dollars have been spent by government agencies at the local, state, and federal level in efforts to remove tamarisk and restore native habitats (Shafroth & Briggs 2008). Control techniques have included burning, herbicide treatments, mechanical removal and most recently, biological control by the saltcedar leaf beetle (*Diorhabda elongata*) (Taylor & McDaniel 1998; Deloach et al. 2004). Controversies surrounding biocontrol methods arose due to the possible repercussions for the endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (Dudley & Deloach 2004; Sogge et al. 2008).

The Southwestern Willow Flycatcher (hereafter, Flycatcher) is one of four recognized subspecies of Willow Flycatchers existing throughout the United States and southern Canada. Neotropical migrants, these birds winter in Central and South America, and occupy breeding territories in riparian areas of North America for four to five months of the year. The Flycatcher subspecies occupies breeding sites in Arizona, western New Mexico, and the southern portions of California, Nevada, Utah, and Colorado (Paxton et

al. 2007). Extensive Flycatcher surveys conducted since 1993 have produced a current estimate of over 1,200 territories located at 284 breeding sites throughout the bird's range (Durst et al. 2007). A site is defined as a location where at least one Flycatcher pair has established a breeding territory, and a territory is generally referred to as the specific location of one nesting pair. Most breeding sites contain five or less territories, and only a few sites contain more than 50 territories (Durst et al. 2007). The United States Fish and Wildlife Service listed the Flycatcher as endangered in 1995 (United States Fish and Wildlife Service 1995). The alteration of riparian habitat has been linked as the major factor in the subspecies' decline (Unitt 1987). In fact, Durst et al. (2007) estimated that throughout its range, approximately 27% of Flycatcher breeding sites were located in areas dominated (>50% cover) by tamarisk.

Quantitative models are valuable tools when assessing habitat suitability for species at landscape scales. Ground surveys can be labor-intensive and expensive, and models enable researchers to focus these efforts by determining areas of investigative importance (Morissette et al. 2006). Maxent (maximum entropy modeling; Phillips et al. 2006) uses presence-only data to assess the distribution of a species by estimating the probability of its ability to survive and reproduce in a certain area (Phillips et al. 2006). Maxent performs better than other models in many ecosystems including both terrestrial (Elith et al. 2006) and aquatic environments (Kumar et al. 2008), and appears to fit general relationships even under situations where sample sizes are small (Kumar & Stohlgren 2009).

Both tamarisk (Evangelista et al. 2009) and the Flycatcher (Hatten & Paradzick 2003; Paxton et al. 2007; Hatten et al. 2010) have been modeled individually at the

landscape level. However, they have not been comparatively modeled for the same landscape. In this study I demonstrate how single-species predictive modeling techniques can be combined to provide information for multi-species management purposes. My goals were to quantify the amount of habitat dominated by tamarisk and available to the Flycatcher within the study area, and to further the understanding of the relationship between this endangered bird and invasive plant.

II. METHODS

Study Area

I conducted this study within the Great Basin Region. The area includes the five United States Geological Survey watershed cataloguing units flowing into the Overton (northern) arm of Lake Mead (Fig. 1). I downloaded Shapefiles of these watersheds from the United States Geological Survey National Hydrology Dataset Geodatabase website (<http://nhdgeo.usgs.gov/>). The total area studied equates to 34,180 square kilometers (km²). The landscape is characterized by a mix of Mojave Desert to the south and Great Basin Desert to the north and represents the northern limits of the Flycatcher's range. Tamarisk is present in many riparian corridors of these watersheds, and dense tamarisk habitat (>50% cover) is common along eastern drainages. Biological control of tamarisk with the saltcedar leaf beetle (*Diorhabda elongata*) began along the Virgin River near St. George, Utah, in 2006. The area impacted by the beetles and intensity of defoliation events have increased in each subsequent year (Hultine et al. 2009).

Datasets

I used six Landsat Thematic Mapper scenes from eight months of the growing season for the analyses (Path 40, Row 33; Path 39, Rows 33, 34, and 35; and Path 38, Rows 34 and 35; March through November, excluding July). I downloaded the images at 30-meter resolution from the United States Geological Survey Earth Explorer website

<http://edcsns17.cr.usgs.gov/EarthExplorer/>). I collected images for each month dated within ten days of each other when possible, although April, June, and November data acquisition dates were further apart in order to acquire cloud-free images. I created mosaics of individual bands 1-5 and 7 and clipped each to the project extent with ERDAS Imagine 2009 software. I used the mosaics to create environmental model input variables for both the tamarisk and Flycatcher individual models.

I downloaded 175 tamarisk presence points from the National Institute for Invasive Species Science website collected between 2000 and 2004 (www.niiss.org). I used the points to run an initial tamarisk model. In November, 2009, I traveled to the study area for initial model field verification. I randomly selected points within three prediction categories (high, medium, and low), and I evaluated model accuracy for 81 points. Of the 81 points, 48 contained tamarisk with a cover value greater than 50%. I used these 48 points as input for all remaining tamarisk models. I used the remaining 33 points, along with 44 additional collected points, as absence points. This designation of cover value is important because it represents areas dominated by tamarisk as opposed to the location of only a single or a few plants. This designation is also consistent with previous models predicting dense tamarisk habitat, along with surveys regarding Flycatcher habitat. A conceptual framework is included (Appendix 1).

I received Flycatcher breeding site presence points from United States Geological Survey staff based out of the Colorado Plateau Research Station. Eleven Flycatcher sites were located within the study area. Surveys conducted at sites over the course of eleven years quantified total number of territories per site per survey year. Due to the dynamic nature of Flycatcher breeding sites, not every site was surveyed each year, and surveyed

sites did not necessarily contain Flycatcher territories each year (Appendix 2). On average, surveys documented 61 territories in the study area each year. More detailed survey results were not provided due to the sensitivity of data associated with endangered species. Of the 11 breeding sites, seven existed in sites dominated by native vegetation and four existed in sites dominated by tamarisk. Absence points were not determined for the Flycatcher. Unlike tamarisk “absence,” Flycatcher absence is more speculative. Flycatchers move around and utilize different areas for different purposes during a single breeding season. The absence of a Flycatcher nest does not necessarily indicate that the area is unsuitable as habitat. Flycatchers have high fidelity to sites where they successfully fledged a chick, and higher fidelity with more chicks fledged (Paxton et al. 2007). This fidelity makes them likely to return to one particular site even if others are available.

Tamarisk Model Variables

I based the Maxent model predicting tamarisk occurrence at densities greater than 50% on Evangelista et al. 2009. The variables found as most suitable to predict tamarisk dominance within the landscape included tasseled cap transformation, normalized difference vegetation index (NDVI), and band 3 from October. Tasseled cap transformations, originally developed to understand changes in agricultural lands, generate three orthogonal bands from the six-band Landsat composite. The three generated bands represent measurements of soil brightness (band 1), vegetation greenness (band 2), and soil/vegetation wetness (band 3) (Kauth & Thomas 1976). NDVI is commonly used to detect characteristics of vegetation such as canopy density. In a study

of the Colorado River delta, an arid landscape with similar riparian vegetation characteristics to this study, NDVI performed best among indices in identifying vegetation percent cover (Nagler et al. 2001). NDVI is calculated with the third (red visible) and fourth (near-infrared) Landsat Thematic Mapper bands and the non-linear equation:

$$\text{NDVI} = (\text{band 4} - \text{band 3}) / (\text{band 4} + \text{band 3})$$

October band 3 (red visible) is used to detect tamarisk during senescence when the plant turns a distinguishable bright yellow-orange color (Everitt & Deloach 1990). Due to the lower elevation in this study area compared to that used in Evangelista et al. 2009, and the presence of the saltcedar leaf beetle which has been shown to extend the growing season of tamarisk by three to four weeks (Dudley & Deloach 2004), I used both October and November band 3 in my analyses.

I did not include variables such as distance to water, elevation, or slope in the tamarisk models. These three variables describe topographic features of the landscape, not the unique spectral signatures that distinguish dense tamarisk infestation from other vegetation (see Evangelista et al. 2009). The goal of the tamarisk modeling effort was to detect areas already dominated by tamarisk, and not simply suitable for tamarisk. Variables derived from remote sensing images enabled me to use the unique spectral signatures of tamarisk to detect actual areas of tamarisk dominance.

Flycatcher Model Variables

I based the model predicting suitable habitat for the Flycatcher on Paxton et al. (2007). The protocol for surveying Flycatcher breeding sites requires surveyors to rank

the relative amount of native vs. exotic vegetation into one of four categories (1: >90% native, 2: mixed with >50% native, 3: mixed with >50% exotic, or 4: >90% exotic) and to determine the dominant woody vegetation at each site (Sogge et al. 1997) (Appendix 2). Results from surveys and previous models indicated that environmental variables thought to be important to Flycatchers include vegetation density, amount of edge habitat, and size of patch (Sogge et al. 1997; Sogge & Marshall 2000; Paxton et al. 2007). Flycatcher habitat tends toward heterogeneous mixes of both vegetation age and species composition, and nesting sites specifically tend toward riparian edge habitat (Paxton et al. 2007).

Flycatchers typically arrive at nesting areas from late April through May and return to wintering grounds in September, and occasionally as late as October (Finch & Stoleson 2000). Where previous models used variables from the months of June or July exclusively, I added variables from five additional months throughout the breeding season to incorporate the timing of migration. I thought that environmental variables from the months in which nesting sites were determined may be important in predicting suitable habitat for the Flycatcher. In addition, knowing that Flycatchers sometimes produce more than one brood per year (Paxton et al. 2007), I thought environmental variables depicting habitat quality toward the end of the breeding season may be important as well. I created variables by transforming Landsat Thematic Mapper mosaics from April, May, June, August, September and October. I used NDVI to quantify vegetation density, and circular neighborhood statistics at four spatial levels to quantify patch size, heterogeneity, and edge proximity. I created a variable depicting topographic slope from a digital elevation model and used neighborhood statistics to analyze

floodplain characteristics. Since Flycatchers are obligate riparian species, I included a Euclidean “distance to water” variable, also derived from the digital elevation model, to exclude densely-vegetated upland areas that may otherwise appear suitable.

Data Analyses

I separately modeled dense tamarisk habitat and suitable habitat for the Flycatcher with Maxent software v.3.2 (www.cs.princeton.edu/~schapire/maxent/). For each initial model, I used all environmental variables as inputs (all variables listed in Appendices 3 & 4). After the initial run, I excluded all variables with contributions less than 1.0% and ran the model again. This step reduced the variables included in the second model for tamarisk from twenty-three to fourteen and for the Flycatcher from sixty-nine to nine. From the second model outputs, I tested the contributing variables for cross-correlations with Predictive Analytics Software Statistics (SPSS for Windows, Rel. 18.0.0. 2009. Chicago: SPSS Inc.). For highly correlated variables (Pearson correlation coefficient >0.80), I removed the variable with a lower contribution in the second model. After removing all correlations, I ran each model a final time, the tamarisk model with ten environmental variables, and the Flycatcher model with five.

To measure the predictive performance of the tamarisk model, I used features available through Schroder’s ROC/AUC software (<http://brandenburg.geoecology.uni-potsdam.de/users/schroeder/download.html>). This software requires presence and absence points to test threshold-dependent measures including correct classification rate, sensitivity (true positives), specificity (true negatives), and Cohen’s maximized Kappa, along with threshold-independent measures such as Area Under the Receiver Operating

Characteristic (ROC) Curve (AUC). I randomly generated ten 34-point subsets (approximately 70%) of the 48 training points. I used each subset to run a separate Maxent model. I restricted the variables in each subset model as I did for the full tamarisk model. I used each final subset model output to determine the prediction values for the respective 14 excluded presence points and a random selection of 14 of the 77 collected absence points. I pooled the subset prediction values to run Schroder's analysis with a total of 140 presence and 140 absence points, and I reported the results of this analysis. I used Raster Calculator, an ESRI ArcGIS 9.2 Spatial Analyst tool, to average the prediction values of the ten final subset raster outputs. I used this average of the subset models for the habitat comparison.

As with the tamarisk data, I randomly generated ten eight-point (approximately 70%) subsets of the 11 Flycatcher training points. I used each subset to run separate Maxent models. I removed variables in each subsequent run of the separate subset models as before, and I averaged the prediction values of the ten subset final model outputs. I used this average model in the habitat comparison. I was unable to use Schroder's ROC/AUC software to test the predictive performance of the Flycatcher model due to the lack of absence points.

Habitat Overlap Analysis

To compare the resulting continuous model outputs, I defined threshold values which I used to categorize the continuous predictive values. I chose thresholds consistent with well-performing criteria (Liu et al. 2005; Jimenez-Valverde & Lobo 2007). For the tamarisk model, I used the "sensitivity-specificity difference minimizer" criteria (0.255),

generated from Schroder's ROC/AUC analysis of prediction values from the 48 training points used in the full model and a random subset of 48 out of the 77 absence points. I reclassified all prediction values less than 0.255 in the continuous model output to the value of one, representing the absence of dense tamarisk stands (defined as >50% cover), and all prediction values greater than 0.255 to the value of two, representing presence of dense tamarisk stands.

Since the southwestern willow Flycatcher currently occupies less territory than historically, I determined three threshold levels to represent potential past, current, and future habitat suitability. A relatively robust approach to threshold selection that tends toward high values of sensitivity and specificity is to average the prediction values for the model-building presence points (Liu et al. 2005). This approach is considered good especially when the prevalence of model-building data changes, as is the case with the dynamic Flycatcher habitat. The approach resulted in a threshold value of 0.624 for the Flycatcher model. I added two additional thresholds, one above and one below this value. I sorted the 11 prediction values resulting from the Flycatcher model and averaged the top, middle, and bottom thirds of the ordered prediction values. I used the mean between the bottom and middle third as the lower threshold, and the mean between the middle and top third as the higher threshold value. This method resulted in lower and higher threshold values of 0.515 and 0.851, respectively. I reclassified all prediction values in the continuous model output below each respective threshold to the value of three, representing habitat not suitable for the Flycatcher, and all values above each respective threshold to the value of four, representing suitable habitat for the Flycatcher.

I chose reclassification values so that when multiplied, each product resulted in a unique value. I multiplied the reclassified tamarisk output with each of the reclassified Flycatcher outputs. Each raster calculation resulted in a habitat overlap analysis raster containing four classes: habitat not dominated by tamarisk and not suitable for Flycatcher (overlap analysis value 3), habitat not dominated by tamarisk and suitable for Flycatcher (overlap analysis value 4), habitat dominated by tamarisk and not suitable for Flycatcher (overlap analysis value 6), and habitat both dominated by tamarisk and suitable for Flycatcher (overlap analysis value 8). I translated the number of 30-m resolution pixels occurring in each class to square kilometers of habitat and calculated percentages of overlapping habitat.

III. RESULTS

Tamarisk Prediction Models

The Maxent model predicting the occurrence of tamarisk and using all training points performed quite well with an Area Under the (ROC) Curve (AUC) score of 0.982. Ten variables contributed to the final tamarisk model (Table 1). The top two contributing variables (June tasselled cap wetness and band 3 from October) were also ranked in the top three contributing variables in the study by Evangelista et al. 2009.

The tamarisk model also performed well according to Schroder's external model performance analysis of pooled subset data. The AUC score was calculated as 0.874 with a 95% confidence interval of [0.827, 0.914]. This AUC score significantly exceeds the AUC critical value (set at 0.70, $p < 0.0001$). Schroder's external model analysis of the "P-Optimal" criteria calculated the correct classification rate at 82.6%, sensitivity at 91.5%, specificity at 73.8%, and the Cohen's kappa statistic as 0.65. Fielding and Bell (1997) suggested that a kappa score between 0.40 and 0.75 signifies good model performance.

The average AUC value for the ten tamarisk subset models was 0.972 and ranged from 0.944 to 0.985. The subset models included five to eight variables in their respective final runs. June tasselled cap wetness ranked as the top predictor variable in seven of the ten subset models with an average contribution of 42.5%, and October band 3 ranked in the top three predictor variables in six of the ten subset models (Table 2).

Flycatcher Prediction Models

The Maxent model predicting suitable habitat for Flycatcher and using all 11 training points also performed well with an AUC score of 0.960. Five variables contributed more than 1.0% to the final Flycatcher model (Table 3). The top predicting variable (May NDVI standard deviation neighborhood statistic, radius 120 m) contributed 44.3% to model prediction. Higher standard deviation of NDVI within this 4.5-ha neighborhood signified greater prediction of suitable habitat for the Flycatcher (Fig. 2).

The average AUC score for the ten eight-point subset models was 0.955 and ranged from 0.901 to 0.971. The subset models used three to six variables in their respective final runs. Habitat heterogeneity within a 120-m radius neighborhood (represented as standard deviation of NDVI) also ranked as the top contributing variable in seven of the ten subset models, four models with this variable representing May and three models with this variable representing September (average contribution 58.4%). Distance to water ranked as the second or third most contributing variable in nine of the ten subset models and had an average contribution of 22.8%. Other highly ranking variables in the ten subset models represented floodplain characteristics.

Habitat Overlap Analysis

The habitat overlap analysis compared the individual habitat model outputs to examine the relationship between tamarisk and the Flycatcher. Habitat overlap occurred in four categories: 1) not dominated by tamarisk and not suitable for Flycatcher; 2) not dominated by tamarisk and suitable for Flycatcher; 3) dominated by tamarisk and not suitable for Flycatcher; and 4) dominated by tamarisk and suitable for Flycatcher (Fig. 3).

For all analyses, the first category included approximately 33,000 km², representing 97% of the modeled landscape.

I used one tamarisk threshold (0.255) and three Flycatcher thresholds (0.515, 0.624, and 0.851) to compute the habitat overlap analysis. I performed one-tail t-tests of the means to assess differences in habitat predicted by the three Flycatcher thresholds. I used one-tail tests of significance since lower thresholds would logically predict greater amounts of suitable habitat. I averaged the area calculated for categories of suitable habitat (excluding area determined as not dominated by tamarisk and not suitable for Flycatcher) within each threshold, and tested these averages for significant differences. Tests revealed that threshold values were not significantly different: p-values equal 0.247, 0.287, and 0.267 for tests between the low and middle, middle and high, and low and high thresholds, respectively. Since the thresholds were not significantly different in the prediction of habitat area, I will discuss further results as averages within each overlap analysis category (Fig. 4). This analysis calculated approximately 1,000 km² of dense tamarisk habitat (>50% cover) and approximately 230 km² of suitable habitat for the Flycatcher within the study area. Of the area modeled as suitable for the Flycatcher, 38.1% was also modeled as densely invaded by tamarisk. Of the area modeled as densely invaded by tamarisk, only 8.5% was also modeled as suitable habitat for the Flycatcher.

IV. DISCUSSION

Data Quality

I downloaded much of the data for the purposes of this study from varying sources. I needed six separate Landsat Thematic Mapper scenes to represent all parts of the study area, meaning that I combined scenes from different days to form one environmental variable. This can be problematic when identifying specific pieces of the landscape and especially when differentiating between varying spectral signatures. Atmospheric “noise” can vary considerably, even within a few hours, and differences in noise can produce differences in adjoining Landsat Thematic Mapper images (Song et al. 2001; Song & Woodcock 2003). This issue did not appear to affect the outcome of the models, but it is difficult to discern small differences that may not have occurred with data from the exact same date and time.

I used the 175 tamarisk points downloaded from www.niiss.org to create the initial tamarisk model. Field verification produced false-positive results under three circumstances. A desert shrub known commonly as creosote bush (*Larrea tridentata*), agricultural fields, and irrigated lawns appeared as highly predicted areas of tamarisk habitat seven, four, and four times out of 81, respectively. Without knowing any attributes of the downloaded points, I had no indication if the points had been taken in stands of tamarisk with greater than 50% cover, or if there were flaws associated with

data acquisition. With the collection of both presence and absence points during the verification trip, I was able to re-run Maxent with data of known origin. The use of this collected data greatly reduced the occurrence of false-positives in the final tamarisk model (down from 46.3% to 26.2%).

Individual Model Performance

The final model predicting dense tamarisk habitat performed quite well according to the various criteria examined. The top contributing variables (June tasseled cap wetness and band 3 from October) were consistent with previous models that also used transformations of remotely sensed images to detect tamarisk habitat (Everitt & Deloach 1990; Evangelista et al. 2009). As in these previous modeling studies, we can speculate that the spectral signatures unique to tamarisk phenology provide us with the ability to distinguish heavy infestations from other vegetation. These results provided additional evidence that modeling dense tamarisk habitat with remote sensing is viable at the landscape scale.

The final model predicting suitable habitat for the Flycatcher also performed well according to model criteria. An environmental variable from the month of May contributed to almost half of the Maxent model's prediction. This variable represented the heterogeneous character of a large (4.5-ha) habitat at the time of season when Flycatchers were establishing breeding territories. Heterogeneity within and beyond the breeding territory is thought to be important to Flycatcher breeding success (Durst et al. 2007), and its importance as a predictor of suitable habitat for the Flycatcher was consistent with previous models (Hatten & Paradzick 2003; Paxton et al. 2007; Hatten et

al. 2010). However, these previous models investigated this habitat characteristic in the months of June and July. The results of this study suggest that environmental variables from May describing habitat heterogeneity at larger neighborhood spatial scales are important in predicting suitable breeding habitat for the Flycatcher.

Habitat Overlap Analysis

The main reason for the Flycatcher's decline to endangered status is thought to be the destruction of high quality, native habitat, mostly due to the regulation of rivers in the southwestern United States and confounded by the widespread invasion of tamarisk (Durst et al. 2007). This analysis allowed me to examine the relationship between tamarisk and the Flycatcher within the study area. The models showed that 38.1% of suitable habitat for the Flycatcher is densely invaded by tamarisk, and only 8.5% of area densely invaded by tamarisk is also considered suitable as breeding grounds for the Flycatcher within the study area. This study contributed further evidence to the thought that dense tamarisk stands are not considered high quality habitat by the Flycatcher. The Flycatcher currently nests in dense tamarisk stands approximately 27% of the time, and the results of this study suggest that the birds may be nesting in areas of dense tamarisk only because native vegetation options are currently unavailable.

Important to consider is the sensitive nature of this endangered bird and the limitations regarding habitat available for breeding. The suggestion of introducing biocontrol agents as a way to rid western rivers of tamarisk produced much controversy because of these issues. Even if the Flycatcher only deems dense tamarisk stands as suitable 8.5% of the time, the fact remains that they do nest in tamarisk more regularly

than this amount suggests. In addition, 38% of habitat available to the Flycatcher within the study area is dominated by tamarisk, suggesting that whether the bird prefers it or not, tamarisk makes up a considerable fraction of available breeding habitat. Considering the Flycatcher is listed as endangered, any habitat that facilitates successful breeding attempts is important in terms of the species' survival. Therefore, it is important to recognize the limitations of this modeling approach when assessing management for the Flycatcher. Although this modeling method provides insight into the tamarisk-Flycatcher relationship, field knowledge of species behavior should always be assessed before determining management plans. While this study showed that effective biocontrol coupled with the reintroduction of native vegetation has the opportunity to increase the suitable habitat available to the Flycatcher by 38%, it is also apparent that biocontrol will initially reduce the habitat available to the Flycatcher within the study area by the same percentage. Precautions must be taken to ensure new native habitat is available for individuals moving out of biocontrolled areas.

Over all, the habitat overlap analysis demonstrated how comparison of single-species habitat models can help determine implications for multi-species management. The methods presented in this study offer a promising opportunity for concurrent management of invasive and endangered species existing within the same landscape. When attempting to manage separately for two or more interacting species, this type of research is invaluable (Zavaleta et al. 2001). Efforts to control exotic species can have negative effects on native populations, especially those of endangered, threatened, or endemic status (Matarczyk et al. 2002). One interpretation of this study is that some areas of native vegetation that once consisted of high-quality suitable habitat for the

Southwestern Willow Flycatcher may now be dominated by tamarisk. Therefore, restoration efforts, completed with concern for the Flycatcher, may have the potential to reestablish high quality territory for this endangered songbird.

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Table 1. The contributions of variables for the Maxent model predicting dense tamarisk habitat and using all 48 training points

<i>Environmental Variable</i>	<i>Contribution (%)</i>
June Tasseled Cap Wetness	28.3
October Band 3	15.7
October Tasseled Cap Wetness	13.2
September Tasseled Cap Brightness	12
September NDVI*	11.8
August NDVI*	8.4
November Band 3	5.6
October NDVI *	2
August Tasseled Cap Greenness	1.9
March NDVI*	1.1

* NDVI refers to the normalized difference vegetation index

Table 2. The five most common variables with predictive contributions to the ten thirty-four-point tamarisk subset models

<i>Environmental Variable</i>	<i>Subset Models (#)</i>	<i>Average Contribution (%)</i>
November Band 3	10	8.4
August Tasseled Cap Greenness	9	4.7
September NDVI*	8	15.1
June Tasseled Cap Wetness	7	42.5
October Band 3	7	20.8

* NDVI refers to the normalized difference vegetation index

Table 3. The contributions of variables for the Maxent model predicting suitable habitat for the Flycatcher and using all 11 training points

<i>Environmental Variable</i>	<i>Contribution (%)</i>
May NDVI ^a Standard Deviation (r = 120 m) ^b	44.3
Distance to Water	19.7
October NDVI ^a Cell Variety (r = 30 m) ^b	15.8
Slope Standard Deviation (r = 30 m) ^b	10.8
Slope Sum (r = 60 m) ^b	9.4

^aNDVI refers to the normalized difference vegetation index

^bRadius of the circular neighborhood statistic calculated for the variable.

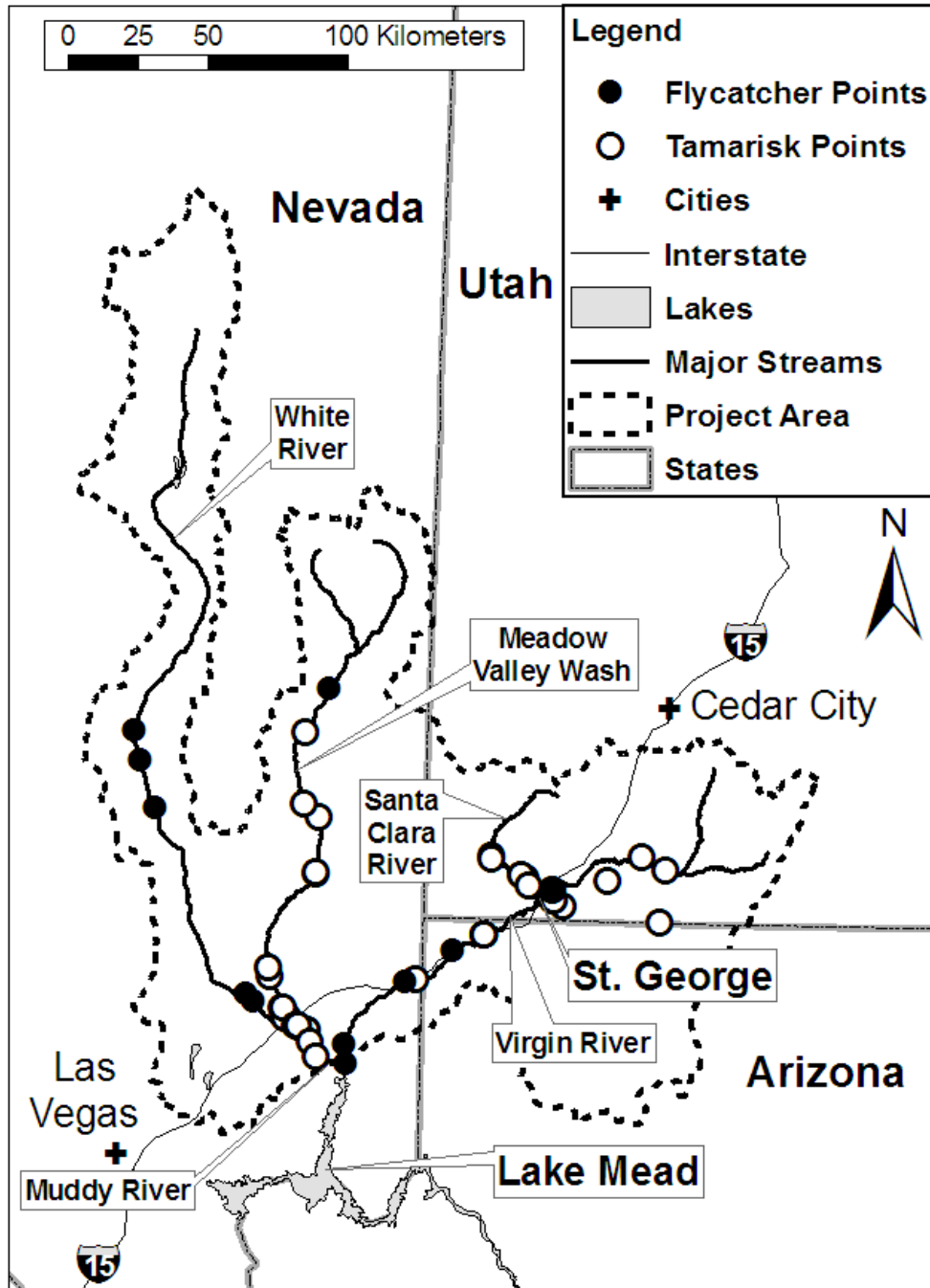


Figure 1. Study area map. The study area encompasses 34,180 km² of landscape. The 11 Flycatcher presence points represent nesting sites and may contain more than one breeding pair. The 48 tamarisk points designate areas with dense tamarisk habitat (>50% cover).

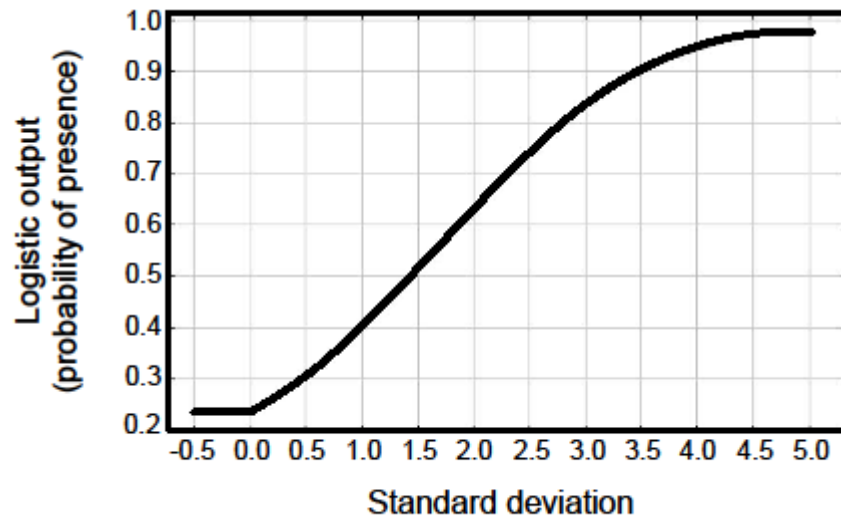


Figure 2. Maxent prediction response curve. The standard deviation of the May NDVI within a 4.5 hectare circular neighborhood (120 meter radius) is the highest contributor to the final Flycatcher Maxent model (44.3%, Table 3). The curve shows how the logistic prediction changes as the standard deviation of this variable increases and all other variables are kept at their average sample value.

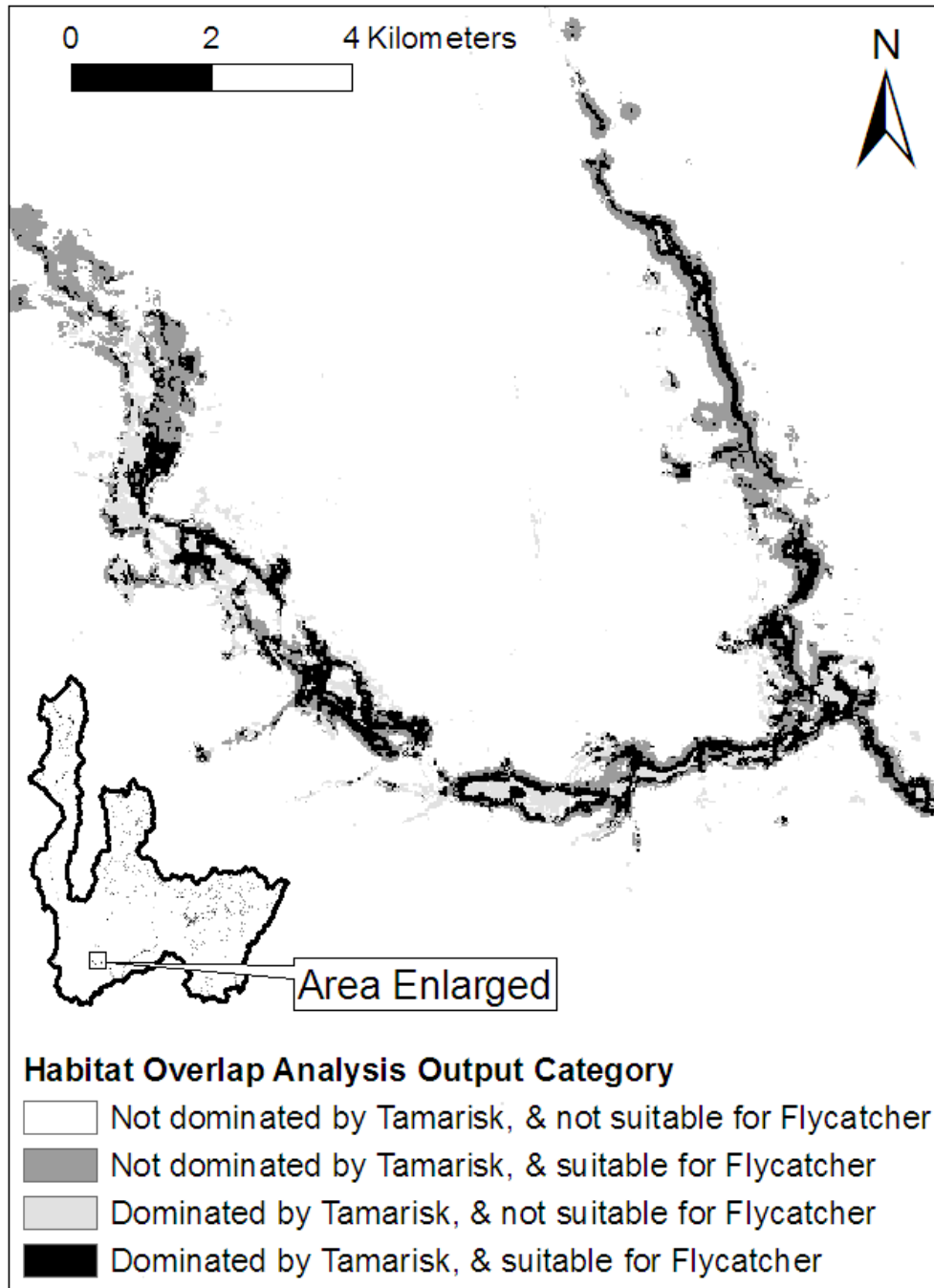
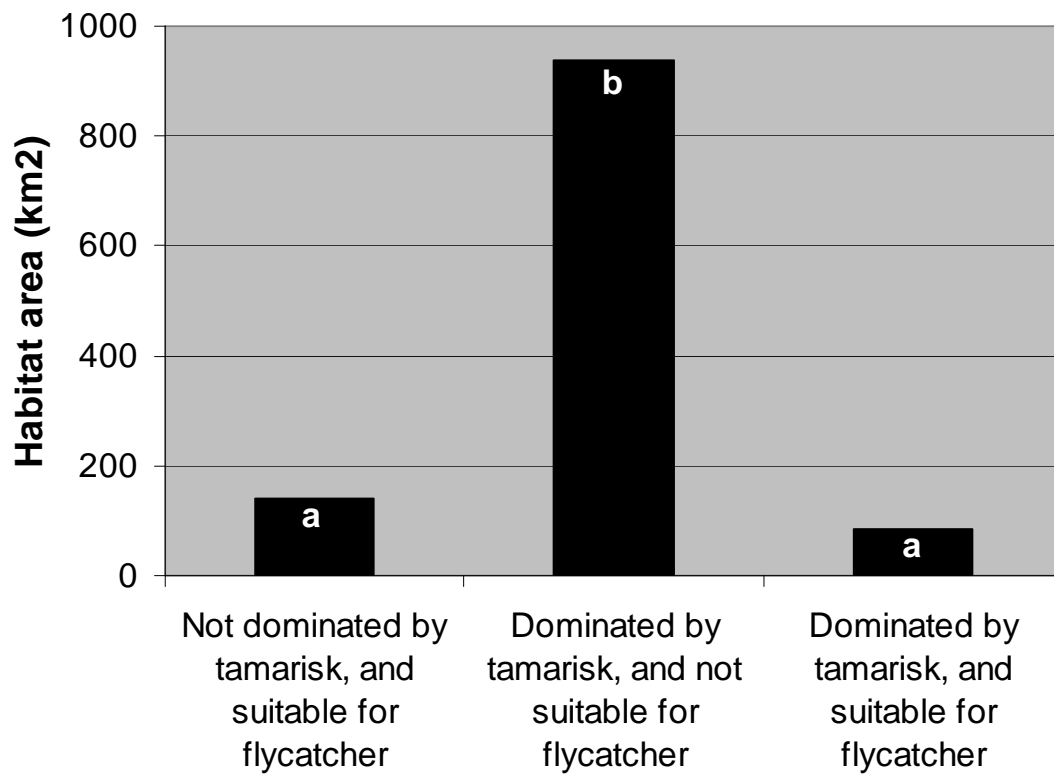


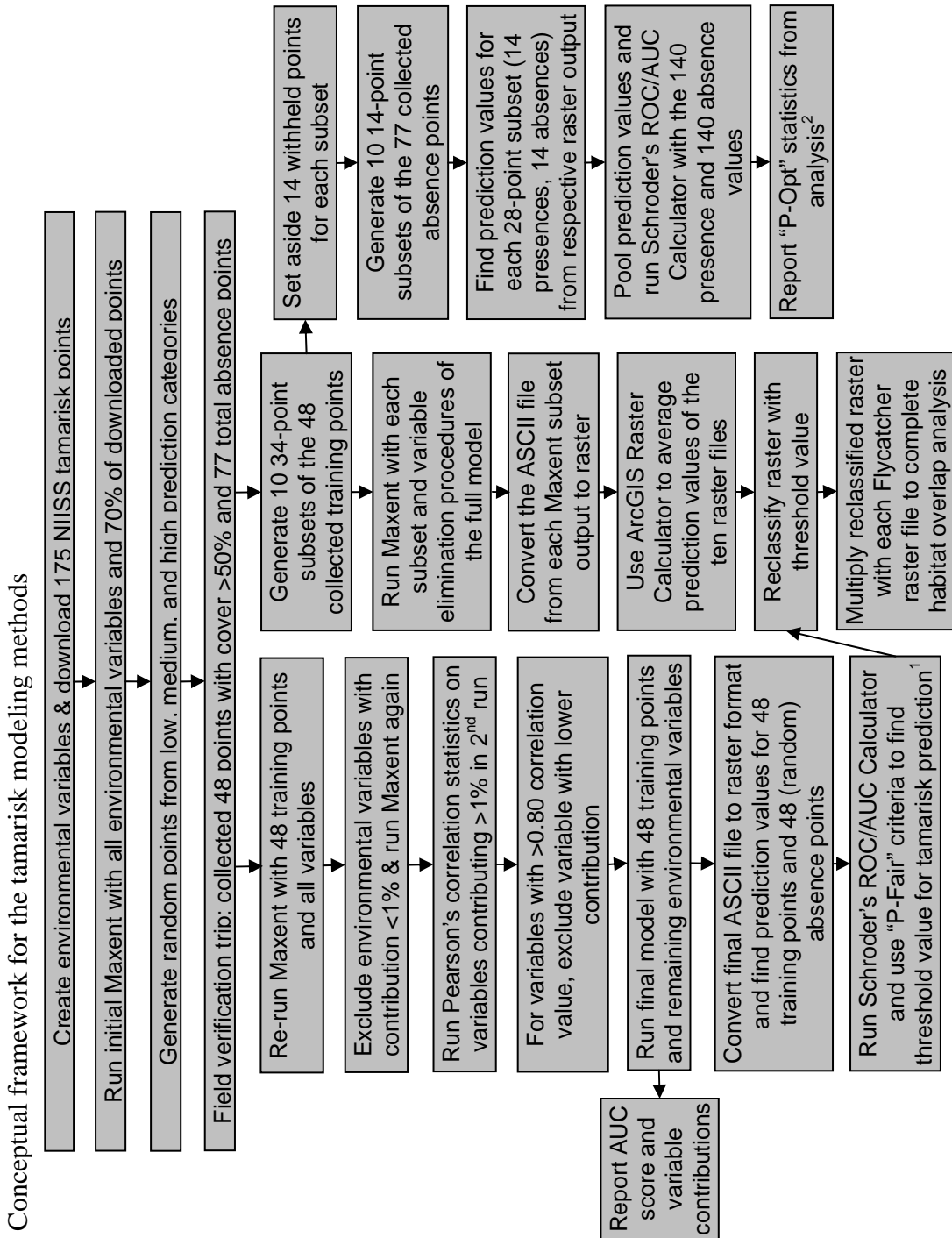
Figure 3. Habitat overlap analysis map. The area displayed is a representative riparian corridor modeled within the study area. Categories represent the four possible outcomes of the habitat overlap analysis.



Habitat overlap category

Figure 4. Habitat overlap analysis data. Three Flycatcher thresholds were initially used in this analysis; these numbers represent the averages across those three thresholds. Letters represent significant differences between categories.

APPENDIX 1



1. The "P-Fair" criteria were chosen because this criterion calculates the threshold value for which sensitivity equals specificity.

2. The "P-Optimal" criteria were used in the final results reporting because they represent optimal model conditions.

APPENDIX 2

Flycatcher breeding site survey data

Flycatcher breeding site name	Vegetation category (descriptions on page 9)	Dominant vegetation at site	Number of years surveyed (out of 11)	Total territories observed	Average territories per year surveyed
Key Pittman Wildlife Management Area	1	<i>Salix</i> spp.	9	67	7.4
Meadow Valley Wash - Site 1	2	<i>Populus</i> spp.	5	1	0.2
Muddy River - Moapa Valley	3	<i>Tamarix</i> spp.	9	8	0.9
Muddy River Delta - Overton Wildlife Area	2	<i>Salix</i> spp.	8	28	3.5
Pahrnagat Lake NWR	1	<i>Salix</i> spp.	10	135	13.5
Pahrnagat River - North River Ranch	1	<i>Salix</i> spp.	4	22	5.5
Virgin River - Littlefield	3	<i>Tamarix</i> spp.	6	4	0.7
Virgin River - Mesquite	3	<i>Tamarix</i> spp.	11	127	11.5
Virgin River - Morman Mesa	2	<i>Salix</i> spp.	10	96	9.6
Virgin River - Seegmiller	3	<i>Tamarix</i> spp.	10	52	5.2
Virgin River Delta - Lake Mead	2	<i>Salix</i> spp.	6	20	3.3

APPENDIX 3

Environmental predictor variables considered in the initial tamarisk predictive Maxent model including their spatial resolution and data source

Variable Short Name	Variable Long Name	Spatial Resolution	Data Source
apr_ndvi	April NDVI	30 m	Landsat Thematic Mapper
aug_ndvi	August NDVI	30 m	Landsat Thematic Mapper
aug_tc_bright	August tasseled cap brightness	30 m	Landsat Thematic Mapper
aug_tc_green	August tasseled cap greenness	30 m	Landsat Thematic Mapper
aug_tc_wet	August tasseled cap wetness	30 m	Landsat Thematic Mapper
jun_ndvi	June NDVI	30 m	Landsat Thematic Mapper
jun_tc_bright	June tasseled cap brightness	30 m	Landsat Thematic Mapper
jun_tc_green	June tasseled cap greenness	30 m	Landsat Thematic Mapper
jun_tc_wet	June tasseled cap wetness	30 m	Landsat Thematic Mapper
mar_ndvi	March NDVI	30 m	Landsat Thematic Mapper
may_tc_bright	May tasseled cap brightness	30 m	Landsat Thematic Mapper
may_tc_green	May tasseled cap greenness	30 m	Landsat Thematic Mapper
may_tc_wet	May tasseled cap wetness	30 m	Landsat Thematic Mapper
nov_b3	November band 3	30 m	Landsat Thematic Mapper
oct_b3	October band 3	30 m	Landsat Thematic Mapper
oct_ndvi	October NDVI	30 m	Landsat Thematic Mapper
oct_tc_bright	October tasseled cap brightness	30 m	Landsat Thematic Mapper
oct_tc_green	October tasseled cap greenness	30 m	Landsat Thematic Mapper
oct_tc_wet	October tasseled cap wetness	30 m	Landsat Thematic Mapper
sep_ndvi	September NDVI	30 m	Landsat Thematic Mapper
sep_tc_bright	September tasseled cap brightness	30 m	Landsat Thematic Mapper
sep_tc_green	September tasseled cap greenness	30 m	Landsat Thematic Mapper
sep_tc_wet	September tasseled cap wetness	30 m	Landsat Thematic Mapper

APPENDIX 4

Environmental predictor variables considered in the initial flycatcher predictive Maxent model including their spatial resolution and data source

Variable Short Name	Variable Long Name	Spatial Resolution	Source
apr_ndvi	April NDVI	30 m	Landsat Thematic Mapper
aug_ndvi	August NDVI	30 m	Landsat Thematic Mapper
distwater	Distance to water	30 m	Digital Elevation Model
jun_std1, 2, 3, 4	June NDVI standard deviation neighborhood statistic (numbers indicate radius in “pixels”)*	30 m	Landsat Thematic Mapper
jun_sum1, 2, 3, 4	June NDVI sum neighborhood statistic (numbers indicate radius in “pixels”)*	30 m	Landsat Thematic Mapper
jun_var1, 2, 3, 4	June NDVI variety neighborhood statistic (numbers indicate radius in “pixels”)*	30 m	Landsat Thematic Mapper
june_ndvi	June NDVI	30 m	Landsat Thematic Mapper
mar_ndvi	March NDVI	30 m	Landsat Thematic Mapper
may_ndvi	May NDVI	30 m	Landsat Thematic Mapper
may_std1, 2, 3, 4	May NDVI standard deviation neighborhood statistic (numbers indicate radius in “pixels”)*	30 m	Landsat Thematic Mapper
may_sum1, 2, 3, 4	May NDVI sum neighborhood statistic (numbers indicate radius in “pixels”)*	30 m	Landsat Thematic Mapper
may_var1, 2, 3, 4	May NDVI variety neighborhood statistic (numbers indicate radius in “pixels”)*	30 m	Landsat Thematic Mapper
oct_ndvi	October NDVI	30 m	Landsat Thematic Mapper
octndvi_std1, 2, 3, 4	October NDVI standard deviation neighborhood statistic (numbers indicate radius in “pixels”)*	30 m	Landsat Thematic Mapper
octndvi_sum1, 2, 3, 4	October NDVI sum neighborhood statistic (numbers indicate radius in “pixels”)*	30 m	Landsat Thematic Mapper
octndvi_var1, 2, 3, 4	October NDVI variety neighborhood statistic (numbers indicate radius in “pixels”)*	30 m	Landsat Thematic Mapper
sepndvi_std1, 2, 3, 4	September NDVI standard deviation neighborhood statistic (numbers indicate radius in “pixels”)*	30 m	Landsat Thematic Mapper
sepndvi_sum1, 2, 3, 4	September NDVI sum neighborhood statistic (numbers indicate radius in “pixels”)*	30 m	Landsat Thematic Mapper
sepndvi_var1, 2, 3, 4	September NDVI variety neighborhood statistic (numbers indicate radius in “pixels”)*	30 m	Landsat Thematic Mapper
sept_ndvi	September NDVI	30 m	Landsat Thematic Mapper
slope	Slope	30 m	Digital Elevation Model
slope_std1, 2, 3, 4	Slope standard deviation neighborhood statistic (numbers indicate radius in “pixels”)*	30 m	Digital Elevation Model
slope_sum1, 2, 3, 4	Slope sum neighborhood statistic (numbers indicate radius in “pixels”)*	30 m	Digital Elevation Model
slope_var1, 2, 3, 4	Slope variety neighborhood statistic (numbers indicate radius in “pixels”)*	30 m	Digital Elevation Model

*Pixels are 30 m resolution. Radius values are 30 m, 60 m, 90 m, and 120 m for values 1, 2, 3, and 4, respectively.