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RESEARCH ARTICLE

A habitat overlap analysis derived from Maxent for Tamarisk and the South-western Willow Flycatcher

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Abstract Biologic control of the introduced and invasive, woody plant tamarisk (*Tamarix* spp, saltcedar) in south-western states is controversial because it affects habitat of the federally endangered South-western Willow Flycatcher (*Empidonax traillii extimus*). These songbirds sometimes nest in tamarisk where floodplain-level invasion replaces native habitats. Biologic 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. We 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. We 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 moderate spatial overlap between predicted suitable habitat for *E. traillii extimus* and predicted locations with dense tamarisk stands, where flycatcher habitat will potentially change flycatcher habitats. Dense tamarisk habitat comprised 500 km^2 within the study area, of which 11.4% was also modeled as potential habitat for *E. traillii extimus*. Potential habitat modeled for the flycatcher constituted 190 km^2, of which 30.7% 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 biologic control of *Tamarix* spp. may, in the short term, reduce suitable habitat available to *E. traillii extimus*, but also has the potential in the long term to increase suitable habitat if appropriate mixes of native woody vegetation replace tamarisk in biocontrol areas.

Keywords Niche modeling, species interactions, Tamarisk, South-western Willow Flycatcher, habitat overlap analysis

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1 Introduction

Humans have dramatically altered the global distribution of species over the past few centuries (Chapin 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 biologic control efforts geared at eradicating exotic species can have negative effects on native populations, especially when control efforts alter the critical habitat of sensitive species of endangered, threatened, or endemic status (Innes and Barker, 1999; Cory and Myers, 2000; Matarczyk et al., 2002). New strategies are needed that simultaneously consider conservation efforts for both introduced and threatened species existing within the same landscape.

Here we focused on riparian corridors which often represent only 1%–3% of the landscape in the arid south-western United States, but are vital to biodiversity (Naiman et al., 1993; Naiman and Décamps, 1997; Patten, 1998). Riparian areas are highly susceptible to invasion by introduced species due to their relatively abundant resources (Stohlgren et al., 1998). In the south-western United States, alteration of the natural flow regime through damming and withdrawals for agricultural, industrial, and household consumption has dramatically altered riparian habitats. Lowered water tables and reduced peak flows associated with damming and diversions hinder successful propagation of native cottonwood (*Populus* spp.) and willow (*Salix* spp.) species, reducing the abundance of mature native riparian forests (Lite and Stromberg, 2005). Members and hybrids of the exotic genus *Tamarix* (*Tamarix parviflora, T. ramosissima, T. chinensis*, etc.) are adapted to the altered flow regime given their ability to extract deep water through an extensive tap root (Everitt, 1980). Tamarisk (collectively, and also referred to as saltceder) currently occurs within most large river systems of the south-western United States and is estimated to have replaced 470000–650000 ha of native riparian habitat (Robinson 1965; Di Tomaso, 1998; Zavaleta, 2000). Tamarisk's success further suppresses the ability of cottonwood and willows to reproduce (Lytle and Merritt, 2004; Stromberg et al., 2007; Merritt and 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 and Rinne, 1988). Millions of dollars have been spent by United States government agencies at the local, state, and federal level in efforts to remove tamarisk and restore native habitats (Shafroth and Briggs, 2008). Control techniques have included burning, herbicide treatments, mechanical removal and most recently, biologic control by the saltcedar leaf beetle (*Diorhabda elongata*) (Taylor and McDaniel, 1998; Deloach et al., 2004; Bateman et al., 2010). The saltcedar leaf beetle defoliates tamarisk plants with repeated defoliation events leading to gradual die back. Controversies surrounding biocontrol methods arose due to the possible repercussions for suitable habitat of the endangered South-western Willow Flycatcher (*Empidonax traillii extimus*) (Dudley and Deloach, 2004; Sogge et al., 2008).

The South-western Willow Flycatcher (hereafter, flycatcher) is one of four recognized subspecies of willow flycatchers existing throughout the United States and southern Canada. 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 south-western subspecies occupies breeding sites in Arizona, western New Mexico, and southern portions of California, Nevada, Utah, and Colorado (Paxton et al., 2007). Extensive surveys conducted since 1993 have produced a current estimate of just over 1200 flycatcher territories located at 284 breeding sites throughout the bird's range (Durst et al., 2007). A territory is defined as the specific nesting location of one breeding pair, and a breeding site is defined as a collective area containing one or more flycatcher territories. Most breeding sites contain five or less territories, and only a few sites contain more than 50 territories (Durst et al., 2007).

Highly suitable flycatcher breeding habitat tends toward heterogeneous mixes of riparian vegetation, both in terms of plant age and species composition. Nesting sites specifically tend toward riparian edge habitat (Paxton 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). Durst et al. (2007) estimated that throughout its range, approximately 27% of flycatcher breeding sites were located in areas dominated ($>50\%$ cover) by tamarisk. Tamarisk often forms dense homogenous thickets and may not provide the optimal heterogeneous mix necessary for flycatcher breeding.

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 (Morisette et al., 2006). Maxent (maximum entropy modeling; Phillips et al., 2006) uses presence-only data to predict the distribution of a species over the modeled landscape by correlating occurrences (presence) with patterns in the included environmental variables (Phillips et al., 2006). Comparison of Maxent results for terrestrial and aquatic environments indicted that Maxent performs as well with presence-only data as other spatial distribution models, which often require both presence and absence data (Elith et al., 2006; Kumar et al., 2009; Elith and Graham, 2009). Maxent also appears to fit general relationships even under situations where sample sizes are small (Kumar and Stohlgren, 2009).

Both tamarisk (Evangelista et al., 2009) and the flycatcher (Hatten and Paradzick, 2003; Paxton et al., 2007; Hatten et al., 2010) have been modeled individually at the landscape level. However, we could not find examples of where they were comparatively modeled for the same landscape. In this study we demonstrate how single-species predictive modeling techniques can be combined to provide information for multi-species management purposes. Our 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 factors contributing to the co-occurrence of this endangered bird and invasive plant species in the study area.

2 Methods

2.1 Study area

We 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). We downloaded Shapefiles of these watersheds from the United States Geological Survey National Hydrology Data set Geodatabase website[1)]. The total area studied equates to 34180 km^2. 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. (Unitt 1987). Tamarisk is present in many riparian corridors of these watersheds, and dense tamarisk habitat ($>50\%$ cover) is common along eastern drainages. Biologic control of tamarisk with the saltcedar leaf beetle (*D. 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; Bateman et al., 2010).

The study area encompasses 34180 km^2 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 dominant tamarisk invasion ($>50\%$ cover).

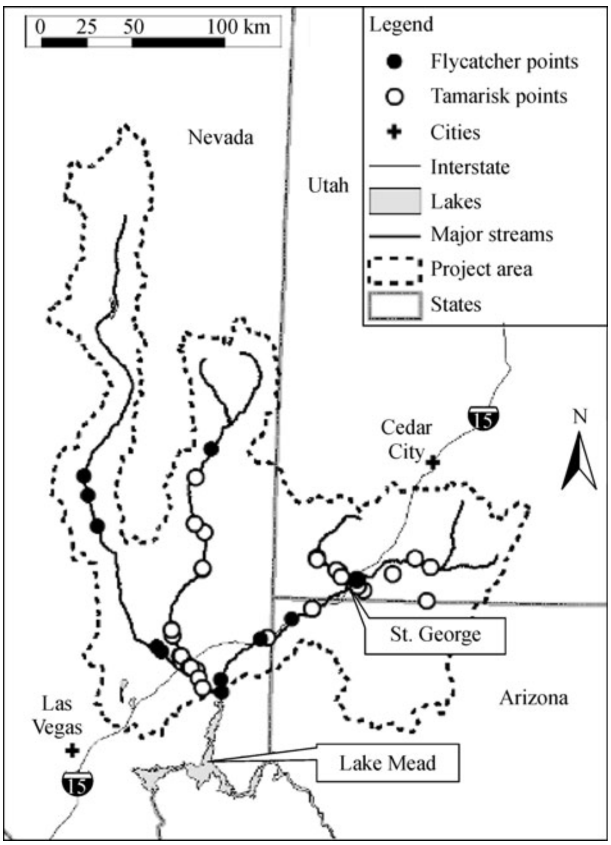

Fig. 1 Study area map

2.2 Data sets

We used six Landsat Thematic Mapper (TM) scenes to represent an eight month growing season (Path 40, Row 33; Path 39, Rows 33–35; and Path 38, Rows 34 and 35; March through November, excluding July, 2008). We downloaded the images at 30-m resolution from the United States Geological Survey Earth Explorer website[2)]. We 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. We created mosaics of individual bands 1–5 and 7 and clipped each to the project extent (Leica ERDAS Imagine 9.1, 2009). We used the mosaics to create environmental model input variables for both the tamarisk and flycatcher individual models.

We downloaded 175 tamarisk presence points from the National Institute for Invasive Species Science website collected between 2000 and 2004[3)]. We used these points to estimate an initial tamarisk model. In November, 2009, we traveled to the study area for initial model field verification. We randomly selected 81 points within three prediction categories (high, medium, and low) derived from the initial tamarisk model. Of the 81 points, 48 contained tamarisk with a cover value greater than 50%. We used these 48 points as input for all remaining tamarisk models. We used the remaining 33 points, along with 44 additional randomly collected points, as absence points. Our focus on points with tamarisk cover exceeding 50% 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.

We 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 between 1997 and 2008 quantified total number of territories per site per survey year, although not every site was surveyed each year. Due to the dynamic nature of flycatcher breeding, surveyed breeding sites did not necessarily contain flycatcher territories each year. On average, surveys documented 61 occupied 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 because birds can be present but go undetected. Therefore, the failure to

1) http://nhdgeo.usgs.gov/
2) http://edcsns17.cr.usgs.gov/EarthExplorer/
3) http:// www.niiss.org

detect a flycatcher nest does not necessarily indicate that the area is unsuitable as habitat. Moreover, flycatchers have high fidelity to sites where they successfully fledged young (Paxton et al., 2007) – behavior that can result in occupancy in subsequent breeding years even if the territory has become marginal or unsuitable. Because of detectability issues and site fidelity behavior, and a relatively small number of observations, we expect the estimation of a flycatcher model to be characterized by higher uncertainty than the tamarisk model.

2.3 Tamarisk model variables

We based the Maxent model predicting tamarisk occurrence at densities greater than 50% on the published results of Evangelista et al. (2009). The variables found in the published results as most suitable to predict tamarisk dominance within the landscape included tasselled cap transformation, normalized difference vegetation index (NDVI), and Landsat band 3 from October. Tasselled cap transformations, originally developed to understand changes in agricultural lands, generate three orthogonal bands from the six-band Landsat composite (Huang et al., 2002). The three generated bands represent measurements of brightness (band 1, dominated by surface soils), greenness (band 2, dominated by vegetation), and wetness (band 3, includes interactions of soil, vegetation and moisture patterns) (Kauth and 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 TM bands and the nonlinear equation:

$$\mathrm{NDVI} = (\mathrm{band}\ 4 - \mathrm{band}\ 3)/(\mathrm{band}\ 4 + \mathrm{band}\ 3). \qquad (1)$$

Visible red-light reflectance in October (Landsat band 3) has previously been used to detect tamarisk during senescence when the plant turns a distinguishable bright yellow-orange color (Everitt and 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 and Deloach, 2004), we based our Landsat TM band 3 assessments on both October and November imagery.

The goal of the tamarisk modeling effort was to detect areas already dominated by tamarisk, and not simply suitable for tamarisk. Therefore, we 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). Variables derived from remote sensing images enabled us to use the unique spectral signatures of tamarisk to detect actual areas of tamarisk dominance.

2.4 Flycatcher model variables

We based the model predicting habitat suitability for the flycatcher on Paxton et al. (2007). 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 and Marshall, 2000; 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 and Stoleson, 2000). Where previous models used variables from the months of June or July exclusively, we added variables from five additional months (April, May, August, September, and October) to span the entire breeding season. We thought that environmental variables from the months in which nesting sites were selected 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), we thought environmental variables depicting habitat quality toward the end of the breeding season may be important as well.

We used the NDVI data sets to represent vegetation density for each month of the growing season, and we created a variable from a digital elevation model to depict topographic slope. We reclassified each NDVI data set and the slope data set using the ArcMap Spatial Analyst Iso Cluster Unsupervised Classification tool and used the created data sets to calculate circular neighborhood statistics at four spatial extents (0.28, 1.13, 2.54, and 4.52 ha) (Paxton et al., 2007). We used FOCALSUM of the reclassified NDVI and slope data sets to represent patch size and floodplain size, respectively. We used FOCALSTD of the reclassified NDVI and slope data sets to represent habitat heterogeneity and edge proximity. We used FOCALVARIETY of the reclassified NDVI data sets to alternatively represent habitat heterogeneity. Since flycatchers are obligate riparian species, we 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.

2.5 Data analyses

We separately modeled dense tamarisk habitat and habitat suitability for the flycatcher with Maxent software v.3.2[1]. For each initial model, we used all candidate

1) http://www.cs.princeton.edu/~schapire/maxent/

environmental variables as inputs. After estimating the initial model, we excluded all variables that contributed less than 1.0% to tamarisk or flycatcher models (Evangelista et al., 2009). This step reduced the variables included in the second model for tamarisk from 23 to 14 and for the flycatcher from 69 to nine. From the second model outputs, we 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), we removed the variable with the lower predictive power. After eliminating candidate predictors due to cross-correlations, we estimated a final model. This model specification process resulted in a tamarisk model with ten environmental variables, and a flycatcher model with five.

To measure the predictive performance of the tamarisk model, we used features available through Schroder's ROC/AUC software[1]. 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 (the proportion of correctly classified points), along with threshold-independent measures such as Area Under the Receiver Operating Characteristic (ROC) Curve (AUC). A ROC curve is created by plotting sensitivity against '1-specificity' for all possible thresholds. The AUC is then calculated by measuring the probability that a random presence point falls within the predicted range of occurrences, and that a random absence point falls out of the range. The AUC statistic ranges between 0.5 (indicating that the analysis is no better than random), and 1.0 (indicating perfect discrimination) (Fielding and Bell, 1997; Pearce and Ferrier, 2000). We report the "P Fair" criteria statistics where the difference between sensitivity and specificity is minimized. We were unable to use Schroder's ROC/AUC software to test the predictive performance of the flycatcher model due to the lack of "true" absence points. For this analysis, we relied on Maxent-generated AUC values alone.

2.6 Habitat overlap analysis

To compare the resulting continuous Tamarisk and Flycatcher model outputs, we defined cut-off threshold values and converted the continuous predictive values to binary data sets. For the Tamarisk model, we used the "sensitivity-specificity difference minimizer" criteria (0.255) (Jiménez-Valverde and Lobo, 2007), 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. We 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.

Because we lacked absence data for the flycatcher we used a relatively robust approach to cut-off threshold selection that tends toward high values of sensitivity and specificity by averaging the prediction values for the model-building presence points (Liu et al., 2005). This approach is considered appropriate when the prevalence of model-building data changes, as is the case with the dynamic occupancy of flycatcher habitat (Liu et al., 2005). We used this approach to determine a threshold value of 0.624 for the flycatcher model. We reclassified all prediction values in the continuous model output below 0.624 to the value of three, representing habitat of low suitability for the flycatcher, and all values above 0.624 to the value of four, representing highly suitable habitat for the flycatcher.

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

3 Results

3.1 Tamarisk model

The Maxent model predicting the occurrence of dense tamarisk stands performed quite well with a Maxent-generated 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 0.952, which significantly exceeds the AUC critical value (set at 0.70, $p < 0.0001$). Schroder's external model analysis of the "P-Fair" criteria calculated the correct classification

1) http://brandenburg.geoecology.uni-potsdam.de/users/schroeder/download.html

Table 1 Contributions of variables for the Maxent model predicting habitat dominated by tamarisk

Environmental variable	Contribution/%
June tasselled cap wetness	28.3
October band 3	15.7
October tasselled cap wetness	13.2
September tasselled cap brightness	12
September NDVI	11.8
August NDVI	8.4
November band 3	5.6
October NDVI	2
August tasselled cap greenness	1.9
March NDVI	1.1

rate at 88.5%, sensitivity at 87.5%, specificity at 89.6%, and the Cohen's kappa statistic as 0.77. Since the correct classification rate, sensitivity, and specificity statistics are proportional indices, values closer to 100% indicate better model performance (Pearce and Ferrier 2000). Fielding and Bell (1997) suggested that a kappa score greater than 0.75 signifies excellent model performance.

3.2 Flycatcher model

The Maxent model predicting habitat suitability for the flycatcher also performed well with a Maxent-generated AUC score of 0.960. Five variables contributed to the final Flycatcher model (Table 2). The top predicting variable (May NDVI standard deviation neighborhood statistic, radius 120 m) contributed 44.3% to model prediction. Prediction of suitable habitat for the flycatcher increased with greater standard deviation of NDVI, measured at the 4.5-ha-neighborhood scale (Fig. 2).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.

Table 2 Contributions of variables for Maxent model predicting highly suitable habitat for the flycatcher

Environmental variable	Contribution/%
May NDVI standard deviation (r = 120 m)[a)]	44.3
Distance to water	19.7
October NDVI cell variety (r = 30 m)[a)]	15.8
Slope standard deviation (r = 30 m)[a)]	10.8
Slope sum (r = 60 m)[a)]	9.4

Note: a) Radius of the circular neighborhood statistic calculated for the variable

3.3 Habitat overlap analysis

The habitat overlap analysis compared the individual model outputs to examine the relationship between tamarisk and the flycatcher. Habitat overlap occurred in four categories, according to raster calculations (Fig. 3). The first category (habitat not dominated by tamarisk and low flycatcher habitat suitability) included approximately 33000 km², representing 97% of the modeled landscape. The overlap analysis resulted in a calculation of approximately 500 km² of habitat dominated by tamarisk (> 50% cover) and approximately 190 km² of highly suitable habitat for the flycatcher within the study area (Fig. 4). Of the area modeled as suitable for the flycatcher, 30.7% was also modeled as densely invaded by tamarisk. Of the area

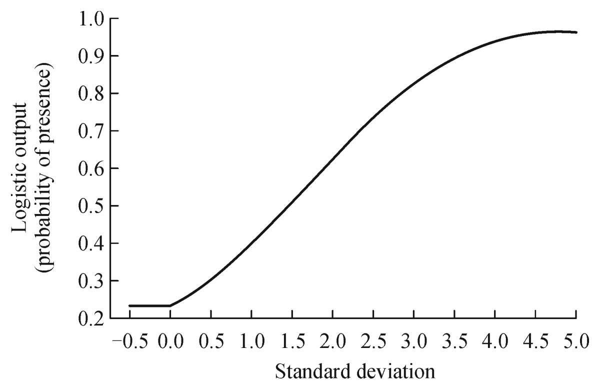

Fig. 2 Maxent prediction response curve

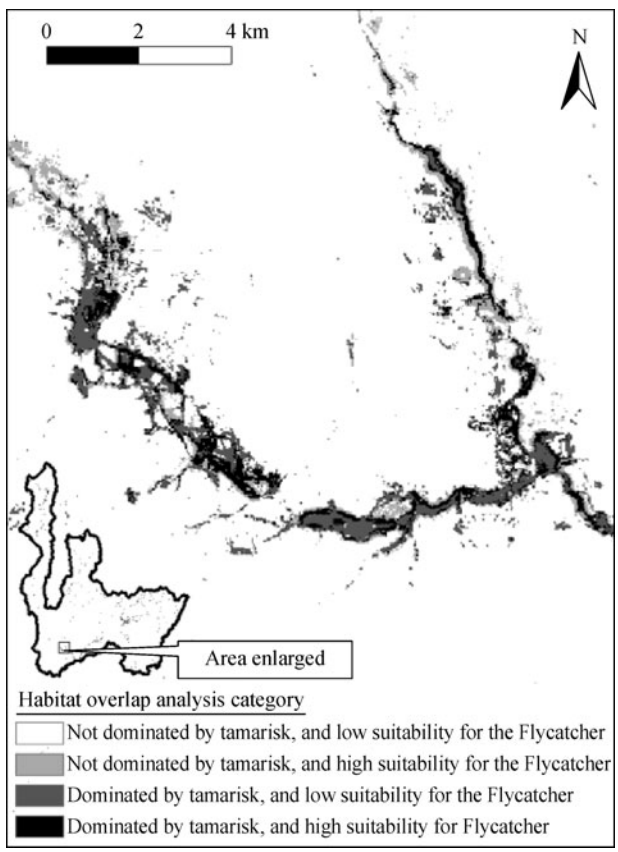

Fig. 3 Habitat overlap analysis map

modeled as densely invaded by tamarisk, only 11.4% was also modeled as highly suitable habitat for the flycatcher.

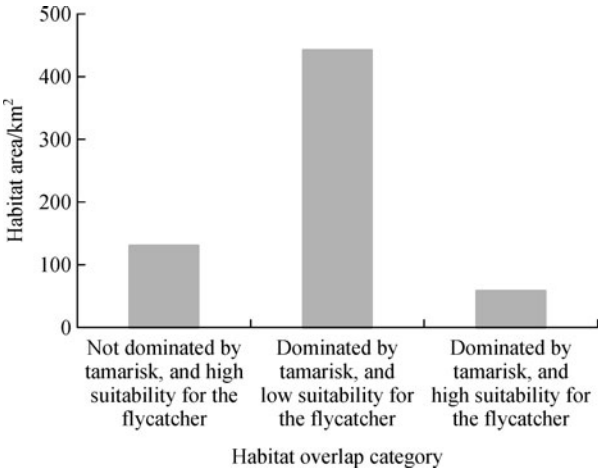

Fig. 4 Habitat overlap analysis

4 Discussion

4.1 Data quality

The data were derived from multiple sources, representing the best available data for modeling. We needed six Landsat TM scenes to represent all parts of the study area, meaning that we combined scenes from different days to form one environmental variable. This can contribute to varying spectral signatures, resulting in weaker models, but this effect seemed minimal in this study. Atmospheric "noise" can vary considerably, even within a few hours, and differences in noise can produce differences in adjoining Landsat TM images (Song et al., 2001; Song and Woodcock, 2003). This issue also 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.

We are confident that the 175 tamarisk points and field verification produced reasonable results with minor exceptions, where false-positive points arose under three circumstances. Creosote bush (*Larrea tridentata*), agricultural fields, and irrigated lawns were predicted as areas of tamarisk habitat seven, four, and four times out of 81, respectively. Without knowing any attributes of the downloaded points, we 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, we were 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%).

4.2 Individual model performance

The final model predicting dense tamarisk habitat performed quite well according to the various criteria examined. The top contributing variables (June tasselled 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 and Deloach, 1990; Evangelista et al., 2009). As in these previous modeling studies, we speculated 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 habitat suitability for the flycatcher also performed well according to model criteria. An environmental variable representing the heterogeneous character of a large (4.5 ha) habitat at the time of season when flycatchers establish breeding territories contributed to almost half of the Maxent model's prediction. 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 and 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 extents are important in predicting suitable breeding habitat for the flycatcher.

4.3 Habitat overlap analysis

This analysis allowed us to examine the relationship between tamarisk and the flycatcher within the study area. 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 south-western United States and confounded by the widespread invasion of tamarisk (Durst et al., 2007). The models showed that 30.7% of highly suitable habitat for the flycatcher is densely invaded by tamarisk, and only 11.4% of area densely invaded by tamarisk is also considered suitable as breeding grounds for the flycatcher within the study area. These results align well with survey data that estimate approximately 27% of flycatcher nests occur in dense tamarisk stands (Durst et al., 2007).

It is important to recognize the limitations of this modeling approach when assessing management for the flycatcher due to 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. Considering the

	Flycatchers: Present	Flycatchers: Absent
Tamarisk: Present	Priority 2 -targeted, and scheduled control of tamarisk -restore native vegetation following control -prevent reinvasion by tamarisk -monitor flycatcher response	Priority 3 -biocontrol of tamarisk -restoration with native vegetation -reintroduce flycatchers(research need) -monitor for natural colonization by flycatchers
Tamarisk: Absent	Priority 1 -manage to prevent tamarisk colonization -monitor flycatcher occupancy	Priority 4 -manage to prevent tamarisk colonization -reintroduce flycatchers(research need)

Fig. 5 Recommended management strategies

flycatcher is listed as endangered, any habitat that facilitates successful breeding attempts is important in terms of the species' persistence. Although this modeling method provides insight into the tamarisk-flycatcher relationship, field knowledge of species behavior should always be assessed before determining management plans. After verification of tamarisk and/or flycatcher presence within the modeled landscape, we recommend that managers utilize different strategies according to the four overlap categories presented in this model (Fig. 5).

Our study indicated that effective biocontrol coupled with the reintroduction of native vegetation may have the opportunity to increase the suitable habitat available to the flycatcher by 30.7%. However, biocontrol efforts may 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.

Overall, the habitat overlap analysis demonstrated how comparison of single-species habitat models can help determine 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). It is possible that areas of native vegetation that once consisted of high-quality suitable habitat for the South-western Willow Flycatcher within the study area 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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