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Linking stream flow and groundwater to avian habitat in a desert riparian system

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Abstract. Increasing human populations have resulted in aggressive water development in arid regions. This development typically results in altered stream flow regimes, reduced annual flow volumes, changes in fluvial disturbance regimes, changes in groundwater levels, and subsequent shifts in ecological patterns and processes. Balancing human demands for water with environmental requirements to maintain functioning ecosystems requires quantitative linkages between water in streams and ecosystem attributes. Streams in the Sonoran Desert provide important habitat for vertebrate species, including resident and migratory birds. Habitat structure, food, and nest-building materials, which are concentrated in riparian areas, are provided directly or indirectly by vegetation. We measured riparian vegetation, groundwater and surface water, habitat structure, and bird occurrence along Cherry Creek, a perennial tributary of the Salt River in central Arizona, USA. The purpose of this work was to develop an integrated model of groundwater–vegetation–habitat structure and bird occurrence by: (1) characterizing structural and provisioning attributes of riparian vegetation through developing a bird habitat index (BHI), (2) validating the utility of our BHI through relating it to measured bird community composition, (3) determining the riparian plant species that best explain the variability in BHI, (4) developing predictive models that link important riparian species to fluvial disturbance and groundwater availability along an arid-land stream, and (5) simulating the effects of changes in flow regime and groundwater levels and determining their consequences for riparian bird communities. Riparian forest and shrubland vegetation cover types were correctly classified in 83% of observations as a function of fluvial disturbance and depth to water table. Groundwater decline and decreased magnitude of fluvial disturbance caused significant shifts in riparian cover types from riparian forest to shrublands. Variability in the BHI was best explained by the cover of deciduous riparian tree species, primarily *Populus fremontii*, *Platanus wrightii*, and *Salix gooddingii*. The distributions of these plant species were well explained by the depth to groundwater and magnitude of fluvial disturbance along the stream. Bird species diversity and richness were significantly higher in sites with higher habitat indices. This quantitative linkage between surface and groundwater, plant species composition, habitat complexity, and bird communities has implications for water management and in determining environmental flows.

Key words: avian; bird; environmental flows; groundwater; habitat index; instream flow; Populus fremontii; *riparian; stream; stream flow;* Tamarix ramosissima.

Introduction

Relationships between habitat structure and vertebrate species diversity are well established in the ecological literature (MacArthur and MacArthur 1961). For example, MacArthur (1964) found that the vertical distribution of foliage was important in explaining forest bird (warbler) species richness. More structurally and compositionally diverse habitats often provide greater extent and more varied resources for a larger number of species than do more compositionally and structurally homogeneous habitats (Roth 1976, Powell and Steidl 2000, 2002, Tews et al. 2004, McElhinny et al. 2005, Kissling et al. 2008). We define habitat in terms of vegetation structure and provisions (sensu Canterbury et al. 2000).

The distribution, composition, and abundance of riparian vegetation along streams are determined in large part by fluvial disturbance and moisture availability, both of which are functions of hydrologic regime (Merritt and Poff 2010, Stromberg et al. 2010). Biota are particularly vulnerable to altered flows along arid-land streams. For example, reduced flooding and physical

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disconnection of rivers from floodplains reduces off-channel habitats, such as sidearms, oxbow lakes, wet meadows, and marshes (Gore and Shields 1995, Nilsson and Berggren 2000), causes native riparian tree mortality (Scott et al. 1999, Shafroth et al. 2000, Lite and Stromberg 2005), and can benefit nonnative riparian trees (e.g., *Tamarix*; Cleverly et al. 1997, Pockman and Sperry 2000, Horton et al. 2001*a*, *c*, Merritt and Poff 2010).

Linking stream flow, groundwater, vegetation structure, and riparian bird community composition through the development of a habitat index (bird habitat index, hereafter BHI or index) has not been explicitly described. Our approach builds upon indices of habitat heterogeneity developed by others (Wiens 1974, Freemark and Merriam 1986) and expands recent research linking hydrology to terrestrial wildlife (Bateman et al. 2008, Brand et al. 2010, 2011). Our model relates riparian habitats to hydrology, namely stream flow and groundwater levels. Lastly, we test our model of predicted habitat indices using observed bird abundance, diversity, and richness, thereby linking instream flows to bird habitat.

The aim of our study was to determine the relationships between surface flows and fluvial disturbance, groundwater levels, characteristics of the riparian vegetation, and measures of the avian community. Our research objectives included: (1) characterizing structural and provisioning attributes of riparian vegetation through developing a bird habitat index (BHI), (2) validating the utility of our BHI through relating it to measured bird community composition, (3) determining the riparian plant species that best explain the variability in BHI, (4) developing predictive models that link important riparian species to fluvial disturbance and groundwater availability along an arid-land stream, and (5) simulating the effects of changes in flow regime and groundwater levels to determine the consequences of groundwater decline for bird communities along an arid-land stream in the Sonoran Desert.

Methods

Field study design

Cherry Creek (see Plate 1) is a perennial stream in the Sonoran Desert in central Arizona, United States (Appendices A and B). The stream is located on the Tonto National Forest at 516753E, 3729660N (UTM coordinates). Cherry Creek derives water from local groundwater sources (e.g., springs and seeps) and monsoon-driven precipitation. The watershed area above our study site is 721 km^2. Cherry Creek along our study reach is braided and dynamic during episodic extreme floods.

We measured woody vegetation in 12 m diameter (113 m^2) circular plots oriented along transects established perpendicular to the stream. We placed 14 transects systematically at 50-m intervals along the length of the stream. Four to six plots were established along each transect, with streamside plots placed at a distance of 6 m from the active channel on either side of the stream. Subsequent plots were placed at 20-m intervals along each transect for a total of 95 plots.

Hydrologic conditions

Groundwater measurements.—To determine the relationships between surface and groundwater, a grid of eight groundwater wells was established in 2008 and seven additional wells were established in 2009. Wells were installed along three transects spanning the width of the riparian zone and separated by 100 m along the length of the valley. Along each transect, one well was placed immediately adjacent to the stream to serve as a staff gage to measure water surface level of the stream. All wells and staff gages were instrumented with Hobo U20 (Onset Computer Corporation, Pocasset, Massachusetts, USA) or Solinst Levelogger Gold (model 3001) water level loggers (Solinst Canada Limited, Georgetown, Ontario, Canada). Depth to water (±0.5 cm) and temperature (±0.1°C) were measured at 15-min intervals. One well was instrumented with an unsubmerged pressure transducer to measure atmospheric pressure to correct groundwater measurements for barometric changes.

Stream measurements.—Stream flow was measured over a range of flows (0.057–1.42 m^3/s) when the study site was visited between July 2008 and October 2009. Rating curves were constructed using stage (measured by hand when discharge was measured and continuously using a pressure transducer), and used to relate discharge to surface stage and groundwater levels. The stream flow record from Cherry Creek near Globe (U.S. Geological Survey, USGS stream flow gage 09497980) was obtained and exceedance probabilities (percentage of the time that each daily flow value is equaled or exceeded) calculated and plotted for the period between May 1965 and October 2009. Flood frequency and recurrence interval of flooding was calculated from a time series of instantaneous peak flow for the period 1965 to 2008, following USGS guidelines (USGS 1988).

Each vegetation plot and groundwater well, as well as a detailed topography of the site, was surveyed by a USGS hydraulic modeling team using a Trimble survey grade global positioning system (Trimble Navigation Systems, Sunnyvale, California, USA)(GPS; Waddle and Bovee 2009). The survey equipment consisted of Trimble 5800 and R8 receivers using real-time kinematic positioning (RTK) and multipath reduction. Such survey-grade systems use carrier phase processing that enables centimeter accuracy. A Leica TC800 total station (Leica Camera, Allendale, New Jersey, USA) was used to survey areas where the GPS equipment could not be used. All data were recorded in Universal Transverse Mercator (SI) coordinates, zone 12 N, using the WGS84 horizontal datum, and the NAVD88 vertical datum. Hydraulic models were developed by the USGS modeling team using River 2-D, a two-dimensional, depth-averaged, finite-element hydrodynamic model (University of Alberta, Canada; Waddle and Bovee 2009). These models provided an estimate of depth and velocity for every cell in our study area (converted to a triangulated irregular network) over a range of discharges (0.13–283 m^3/s).

Water table measurements.—To estimate depth to water table in the vegetation sampling plots, we used a spline fit to interpolate a groundwater surface (0.3-m grid size) within our groundwater well grid. We used measurements from a period of stable, low stream flow (0.13 m^3/s; 5 October 2009) to avoid confounding effects of groundwater recharge or discharge related to floods or pulses in stream flow. Surveyed elevations of each plot enabled us to calculate the depth to groundwater at each of the vegetation plots over the modeled range of flows. To calculate average rooting depth of *P. fremontii* along our study reach, we excavated six individuals ranging in age from 10 to 16 years old using a backhoe. In these excavations, we measured rooting depth and depth to water table at the time of excavation.

Vegetation and index development

Vegetation measurements.—Multiple structural attributes (e.g., plant size variation, cover, and vertical distribution of foliage) and the relative abundance of each of these attributes determine structural complexity of avian habitat (McElhinny et al. 2005). To quantify habitat complexity, we measured 18 vegetation characteristics at each plot (Table 1).

Variables measured to quantify avian habitat included plant species abundance (percent cover and basal area) and size of woody species. Stem size and stem size diversity were determined by calculating the quadratic mean and standard deviation of selected woody species occurring within each circular plot. Quadratic mean diameter corresponds to basal area, stand volume, and other ecologically important stand characteristics, and therefore is preferred to arithmetic mean for characterizing size classes of woody vegetation (Curtis and Marshall 2000).

Woody vegetation cover was measured as the percent canopy cover of all woody vascular plant species 1 m aboveground. Stem diameter of every stem present was measured using calipers for several woody species of particular interest: *Platanus wrightii* (Arizona sycamore), *Alnus oblongifolia* (Arizona alder), *Populus fremontii* (Fremont cottonwood), *Salix gooddingii* (Goodding willow), *Tamarix ramosissima* (saltcedar), *S. exigua* (sandbar willow), *Fraxinus velutina* (velvet ash), and *Juglans major* (Arizona walnut). Though herbaceous riparian species may be more vulnerable than woody species to minor groundwater declines (Stromberg et al. 1996, Stromberg in Haney et al. 2008), we focused upon woody species here due to the central role of woody vegetation in governing avian habitat structure. However, due to the role of herbaceous vegetation in providing other resources (nest-building material, food, and other provisions), cover of herbaceous vegetation was also measured.

Table 1. Variables included in the bird habitat index (boldface type) used to describe habitat structural complexity along Cherry Creek, Arizona, USA ($n = 54$).

Bird habitat variables	Values across all plots (mean ± SE)
Canopy cover (%)	54.5 ± 35.4
Basal area (cm²/plot)	**449.3 ± 737**
Quadratic mean woody diameter	**4.12 ± 4.8**
Quadratic standard deviation woody diameter	4.1 ± 5.4
Riparian tree overstory cover (%)	23.0 ± 32.3
Abundance of seedlings	72.4 ± 199.9
Foliage height diversity (H')	**1.1 ± 0.5**
Foliage hits	**7.3 ± 4.7**
Foliage height diversity (H') 0–1.5 m	0.74 ± 0.33
Mean vegetation cover height class 1 (%)	**2.2 ± 1.0**
Mean vegetation cover height class 2 (%)	1.2 ± 0.2
Mean vegetation cover height class 3 (%)	0.6 ± 1.3
Mean vegetation cover height class 4 (%)	**0.3 ± 1.0**
Standard deviation vegetation cover height class 1 (%)	1.2 ± 0.5
Standard deviation vegetation cover height class 2 (%)	**1.1 ± 0.7**
Standard deviation vegetation cover height class 3 (%)	0.5 ± 0.9
Standard deviation vegetation cover height class 4 (%)	0.3 ± 0.8
Sandy substrate (%)	0.57 ± 0.31

We measured foliage height diversity and percent vegetation cover using the pole method described by Carothers (1974) at five points within each circular plot. Measurements were taken from the center point of each plot and at four additional points, sampled 3 m away from the center point in each of the cardinal directions. Foliage height diversity was estimated by tallying the number of times living vegetation intersected a 10 cm disk surrounding the pole at each height class (e.g., 0–0.013 m, 0.013–0.6 m, 0.6–1.5 m, 1.5–3.0 m, 3.0–4.5 m, 4.5–6.0 m, 6.0–9.0 m, and >9.0 m). Diversity was calculated with the Shannon diversity index (H). Percent vegetation cover was determined by estimating cover in each of four height classes (0–1.5, 1.6–4.0, 4.1–9.0 and >9 m), using modified Braun-Blanquet cover classes (>1%, 1–5%, 6–25%, 26–50%, 51–75%, and 76–100%; Braun-Blanquet 1965). Height classes corresponded to distinct vegetation community types found at the site (i.e., herbaceous plants, shrubs, and trees).

BHI development.—We related avian habitat to instream flows by first developing a bird habitat index by using a subset of ecologically important variables measured at each plot. To construct the BHI, we included only those variables with high factor weightings in principal components analysis (PCA; Appendix C). Variables were identified based upon the number of significant factors determined by scree plots, factors with eigenvalues ≥ 1, and significance ($P \leq 0.05$) as determined by the broken-stick model (Legendre and Legendre 1998). Therefore, BHI included variables that contributed to significant factors in the PCA, reduced redundancy and collinearity, and did not significantly differ from the index produced using the full model. We standardized (mean = 0 and standard deviation = 1) each of the selected variables and calculated their sum, which gave us a habitat index for each vegetation plot. This index was set to values between 0 and 1.

Avian community measurements

Point count sampling.—We sampled the bird community at 25 point count stations three to four times during the avian breeding and migratory seasons in May 2010. Stations were selected by stratifying across plots with low, medium, and high BHI scores. We used a 20-m fixed-radius point centered on vegetation plots. Standard procedures call for a 25 m radius (Hutto et al. 1986); however, a smaller radius was used to increase the chances of detecting all birds in a smaller area. Similar to Bibby et al. (1985), our point count stations were spaced $\geq$60 m apart. Two trained observers visited each station, and we reversed the order in which stations were surveyed between visits. Counts began 1 hour after dawn and lasted $\leq$4 hours. Observers counted birds seen and heard for 10 minutes at each station. Surveys began immediately upon arrival at the station and included birds flushed by the observer.

We calculated per-point bird abundance, diversity (Simpson diversity index), and richness. Abundance was calculated as the greatest number of individuals of each species seen or heard per point during any given survey. This method conservatively estimated abundance and ensured that we did not count individuals twice. Diversity and richness measurements used counts from points visited during all four surveys.

Data analysis

To relate avian habitat to instream flows, we compared BHI scores across the riparian floodplain including hydro- and mesoriparian areas (sensu Stromberg et al. 2008). Woody vegetation was classified into distinct cover types using two-way indicator species analysis (TWINSPAN), a hierarchical, divisive cluster analysis technique (Hill and Šmilauer 2005). BHI scores were compared among vegetation cover types using analysis of variance (ANOVA), and in cases of significant differences we conducted pairwise comparisons (Tukey's adjustment) to determine which plant communities significantly differed in habitat quality. If the diversity of habitat significantly differed among vegetation cover types, we related habitat indices to specific woody species abundances that were dominant components of those cover types. To validate our habitat model, we related BHI to bird community abundance, diversity, and richness using linear regression. We determined relationships between dominant tree and shrub species and the habitat index using linear regression.

We used logistic regression to classify measured vegetation plots into vegetation cover types based upon depth to groundwater and fluvial disturbance. Flow velocity at a discharge of 283 m^3/s (exceeded 0.01% of the time; 80-year recurrence interval) was used as a surrogate for intensity of fluvial disturbance. Twenty-seven of the vegetation plots were located outside of the area covered by hydraulic modeling. The remaining 68 plots were used for habitat modeling. Mean velocity in each vegetation quadrat was calculated. We chose groundwater at low flow to model cover types (groundwater levels corresponding to a stable period of stream flow of 0.13 m^3/s; exceedance probability 88%). We combined *Populus*-dominated cover types into a single "riparian forest" cover type, shrub-dominated cover types into a single "shrubland" cover type. We also used logistic regression to model presence–absence of two important species in each of the cover types as a function of depth to water table and intensity of fluvial disturbance; *P. fremontii* was modeled to represent the forest cover type and *Baccharis sarothroides* to represent the shrub cover types. We used these models to predict change in the presence of forest, shrubland, *P. fremontii*, and *B. sarothroides* in response to altered groundwater levels and reduction in the intensity of disturbance. This was accomplished through modeling vegetation response to an imposed lowering of groundwater levels in ArcGIS, and examining vegetation change while holding disturbance intensity constant. We then modeled vegetation change in response to lowered disturbance intensity while holding depth to groundwater constant. Disturbance intensity was represented by velocity in each of the 17 000 5.3-m^2 grid cells in the study area at 283, 142, 108, 71, 57, 28, 21, and 14 m^3/s. Probability of occurrence of each cover type was calculated for each grid cell using spatial analysis in ArcGIS 9.3.1 (ESRI, Redlands, California, USA). The number of grid cells in which probability of occurrence was >0.50 was counted and the area of cells with predicted presence calculated. We evaluated the predictive ability of models (logistic and logistic discriminant analysis) in classifying: (1) vegetation cover types, (2) consolidated cover types (shrubs and riparian forest), and (3) individual species representing each cover type by comparing cross-validation error rates and likelihood ratio.

SAS Stat 9.3 (SAS 2011) was used for all statistical analyses. We evaluated logistic regression model (and logistic discriminant analysis) fit using likelihood ratio and Hosmer-Lemeshow goodness-of-fit tests. Linear regression, power functions, and Spearman rank correlation were used as appropriate. For other statistical tests, when data complied with assumptions of normality and equal variance we used t tests and ANOVA; when data did not comply with assumptions we used nonparametric tests (e.g., Mann-Whitney U test or Kruskal-Wallis test; Zar 1996).

Results

Groundwater and surface water interactions

Stream flow.—Discharge measurements taken along the reach were associated with those measured at the USGS stream flow gage 15 km upstream ($Q_{USGS} = 1.47Q_{study}^{0.84}$; $r^2 = 0.91$, $P < 0.0001$). Modeled velocity at a flow of 283 m^3/s ranged from 0 to 4.88 m/s in the vegetation plots.

Groundwater.—From November 2008 through October 2009, the study area experienced one frontal rainstorm resulting in three major peaks in stream flow. Over the course of the storm, discharge measured at the USGS stream flow gage ranged from a low of 0.17 m^3/s to a high of 106 m^3/s. Three flood pulses during the measurement period provided an opportunity to examine groundwater recharge, stage, and discharge associated with high-flow events, and to develop a better understanding of the linkages and lag times between stream flow, stage, and groundwater levels.

Average daily depth to groundwater was significantly related to daily average discharge measured at the USGS gage several kilometers upstream ($r^2 = 0.67$; $P < 0.0001$). Groundwater profiles indicated that the main channel is losing water to floodplain alluvium across a range of flows (0.28 to 13.6 m^3/s). Surface and groundwater measurements indicate that flow in Cherry Creek is the principal source of water supporting groundwater levels across the floodplain.

Average rooting depth of excavated *P. fremontii* was 1.74 ± 0.22 m (mean ± SE; range 1.25 to 2.51 m) and all roots terminated at or within a decimeter below the low-flow water table (Merritt et al. 2010).

Hydrological and vegetation relations

Vegetation cover types.—We identified 30 species of woody plants in 95 vegetation plots sampled along Cherry Creek. Species richness ranged from 0 (bare plots) to 11 species, and cover ranged from 0% to 250% (multilayered canopies exceed 100% cover).

The most frequently occurring vegetation cover types in the 95 plots sampled were *Populus–Salix gooddingii–Platanus–Tamarix* (20% of plots) followed by *Populus–Salix gooddingii–Baccharis salicifolia–Hymenoclea* and *Hymenoclea–Baccharis sarothroides* which both occurred in 18% of plots. The least frequent cover types were *Salix gooddingii–Baccharis salicifolia* (3%) and *Prosopis–Baccharis sarothroides–Hymenoclea–Acacia greggii* (4%). Intermediate frequency cover types included *Hymenoclea*, *Hymenoclea–Tamarix*, and *Tamarix–Populus–Salix*. There were significant differences in BHI between vegetation types ($F_{8,84} = 2.6$, $P = 0.01$). A linear contrast between shrub-dominated cover types and tree-dominated cover types indicated that BHI was significantly higher in tree-dominated vegetation compared to shrublands ($P = 0.0007$). BHI in the *Populus–Salix–Platanus* cover type was significantly higher than in both *Hymenoclea* and *Hymenoclea–Baccharis sarothroides* cover types ($P < 0.05$; Fig. 4).

Logistic discriminant analysis did a poor job of discriminating between the nine classified vegetation cover types. Neither physical disturbance ($P = 0.07$) or depth to groundwater ($P = 0.2$) were significant discriminators. Likelihood ratio (LR) for this model was significant ($P = 0.01$); however only 6.2% of the plots were correctly classified.

The discriminant function correctly classified 83.2% of the consolidated cover types: riparian forest or shrubland. The model was significant (LR, $P < 0.0001$; Hosmer-Lemeshow (HL) goodness-of-fit $P = 0.55$). Depth to groundwater ($P = 0.03$) and magnitude of fluvial disturbance ($P = 0.05$) were both significant in discriminating between forest and shrub cover types. At the stable modeled flow, depth to groundwater in the riparian forest cover types averaged 1.1 ± 0.10 m (mean ± standard error) and 1.7 ± 0.06 m in shrublands. Average velocity was 2.6 ± 0.20 m/s in riparian forest and 1.3 ± 0.15 m/s in the shrubland cover type.

The logistic regression model predicting *P. fremontii* presence was significant (LR, $P < 0.0001$; HL, $P = 0.67$). On average, 81.9 plots were correctly classified, and depth to groundwater was significant ($P = 0.04$). Physical disturbance did not significantly contribute to the model ($P = 0.08$). The logistic regression model of *Baccharis sarothroides* was also significant (LR, $P = 0.0005$; HL, $P = 0.27$), and 76.0% of classifications were correct. Disturbance magnitude was a significant predictor of *B. sarothroides* presence–absence ($P = 0.006$), and depth to groundwater was not ($P = 0.6$). Disturbance magnitude had a negative effect on *B. sarthroides* presence.

P. fremontii was predicted to occupy 3.1 ha (35%) of the study area, whereas the dominant shrub species *B. sarothroides* had high probability of occupying 5.4 ha (60%) of the study area. This reflects measured frequencies of *P. fremontii* and *B. sarothroides*, which occurred in 44% and 54% of plots, respectively. The cover of shrub vegetation increased from 5.4 to 6.7 ha as a function of groundwater falling 2 m below base level. In contrast, forest cover (*Populus*-dominated) decreased 88% (to 0.37 ha) as a function of a 2-m groundwater decline (Fig. 1a). The relative frequency of riparian forest to shrubland decreased significantly as a function of increasing depth to groundwater, ranging from 58% at base groundwater level to 5% at 2 m below base level (Figs. 1a and 2). A simulated groundwater decline of 2 m below base level resulted in a nearly complete loss of riparian forest and conversion of the valley bottom to shrubland. Predicted loss of riparian forest averaged 4% per decimeter of groundwater decline (Fig. 1a).

In simulations with peak discharge reduced by half (groundwater kept at base level), the areal extent of *Populus*-dominated riparian forest cover fell by 25% and shrubland increased by nearly 30% (Fig. 1b). Incremen-

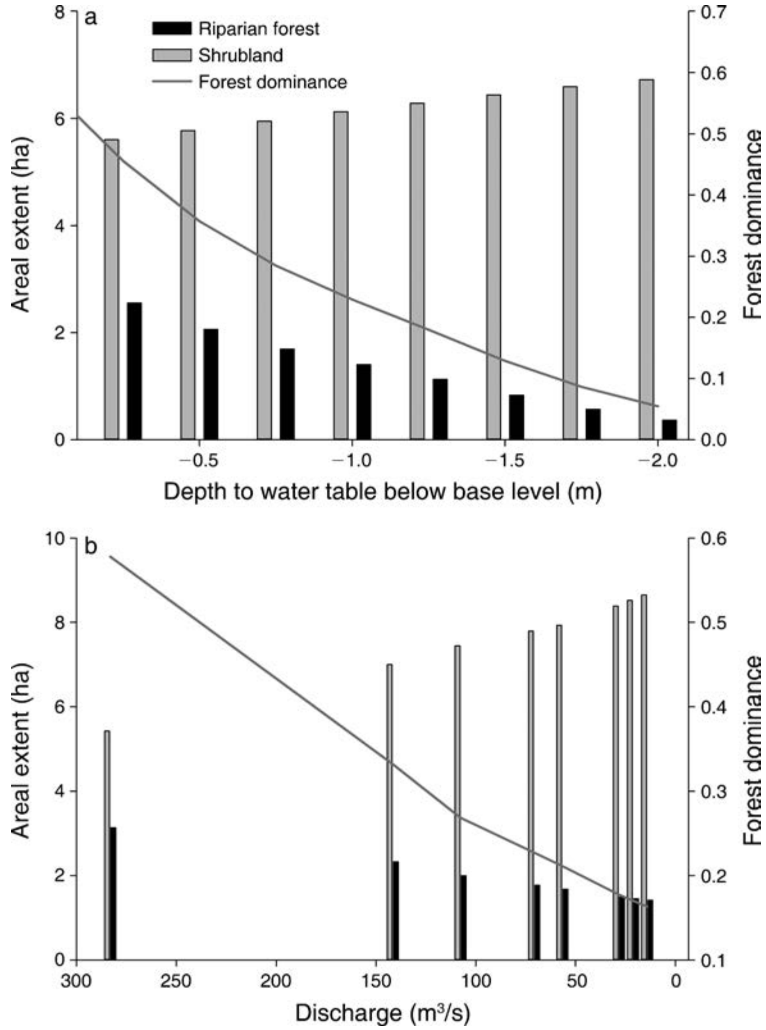

FIG. 1. Areal extent of riparian forest (represented by *Populus fremontii*) and shrubland (represented by *Baccharis sarothroides*) as a function of (a) lowering groundwater levels and (b) intensity of fluvial disturbance along Cherry Creek, Arizona, USA. Logistic regression was used to predict the probability of occurrence of each of these species as a function of (1) groundwater levels, measured when the stream was at baseflow (0.127 m^3/s) and (2) velocity at extreme high flow (283 m^3/s). Velocity at each vegetation plot at this extreme high flow represents the degree of fluvial disturbance to which locations across the floodplain are subjected. Velocities associated with incrementally lower discharges were calculated for all cells in the floodplain using a 2-D hydraulic model. In modeling forest and shrubland response to groundwater decline, fluvial disturbance was held constant [panel (a)]; groundwater levels were held constant as velocity corresponding to incrementally reduced peak flows was modeled [panel (b)]. All cells with a predicted probability of occurrence of forest or shrubland of 0.5 or greater were aggregated, and the areal extent of likely presence of each cover type presented. Forest dominance is the ratio of forest to shrubland. Refer to *Hydrologic conditions*; *Stream measurements* and *Data analysis* in *Methods* for further explanation.

tal reductions in velocity across the floodplain associated with reduced magnitude of peak flow resulted in a 55% reduction in *P. fremontii* cover and an increase in *B. sarothroides* cover by nearly 60% (to Fig. 1b). Reductions in peak discharge by 94% (from 238 to 14 m^3/s) resulted in *P. fremontii* reduction from 35% (3.1 ha) of the valley bottom to 16% (1.4 ha), and an increase in *B. sarothroides* from 60% (5.4 ha) to 96% (8.6 ha).

Modeling vegetation as a function of depth to groundwater and fluvial disturbance.—Depth to groundwater was an important driver of riparian tree species presence (Fig. 3) and abundance (basal area and cover) along Cherry Creek. Riparian tree species were more common in areas with shallow groundwater. For example, *Populus*, *Salix*, and *Tamarix* (Fig. 3) were more likely to occur in areas with shallow groundwater (<1.5 m deep), whereas *B. sarothroides* was common in sites with groundwater depths exceeding 3 m. *Populus* occurred in areas with both high moisture availability and high disturbance, whereas *B. sarothroides*, *H. monogyra*, and other shrubs (with the exception of *Tamarix*) were excluded from areas with high fluvial disturbance, but were not sensitive to depth to groundwater (Fig. 5).

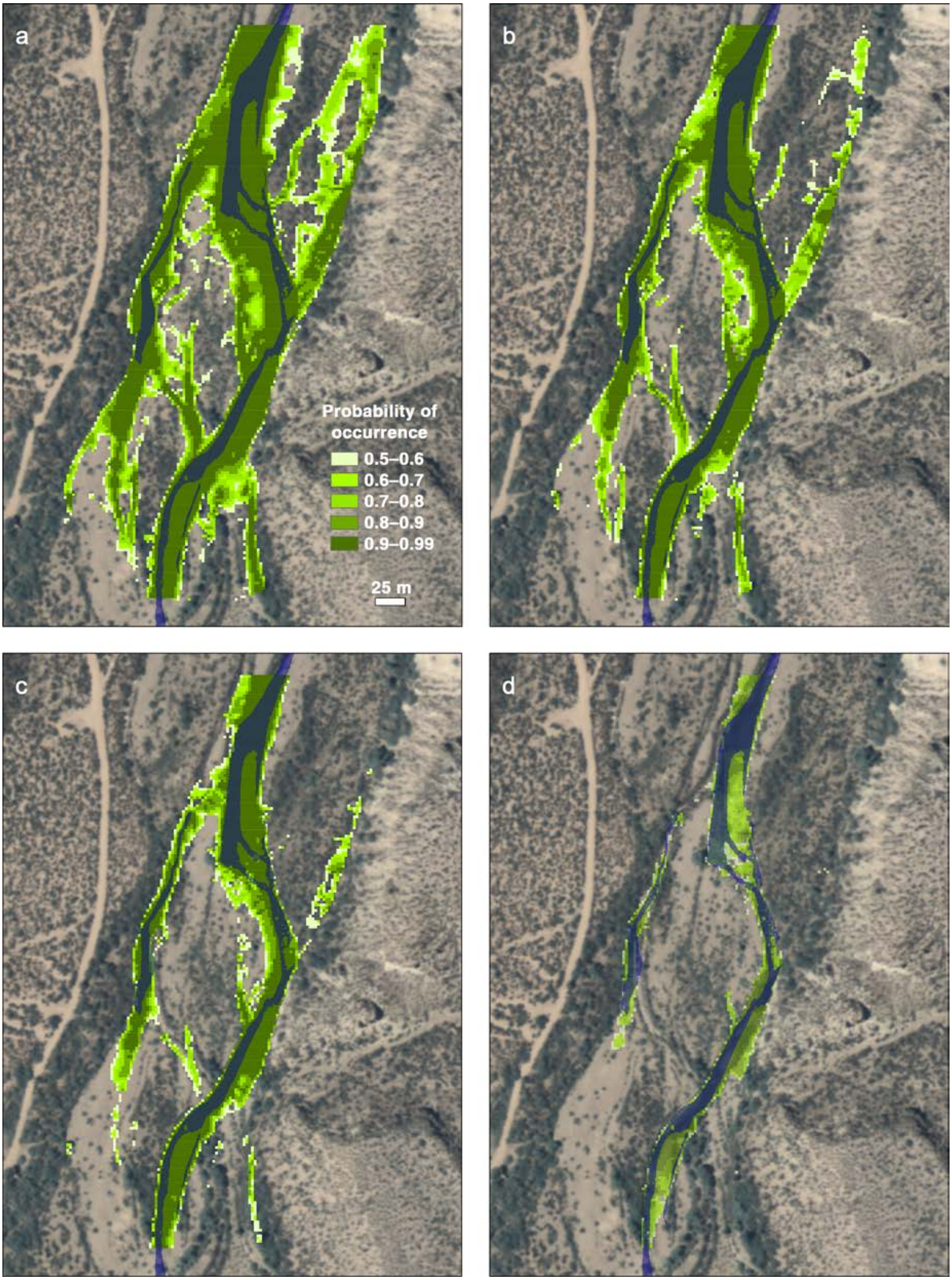

FIG. 2. (a) The probability of occurrence of *Populus fremontii* at base groundwater level (associated with a low stream flow of 0.127 m^3/s) along Cherry Creek, Arizona, USA. Models showing the probability of *P. fremontii* occurrence with groundwater levels lowered (b) 0.5 m, (c) 1.5 m, and (d) 2.0 m below base level are shown. The area of likely *Populus fremontii* occurrence declines 88% (from 3.1 ha to 0.37 ha) as a function of a 2-m decline in groundwater below base level. Refer to *Methods* for modeling details.

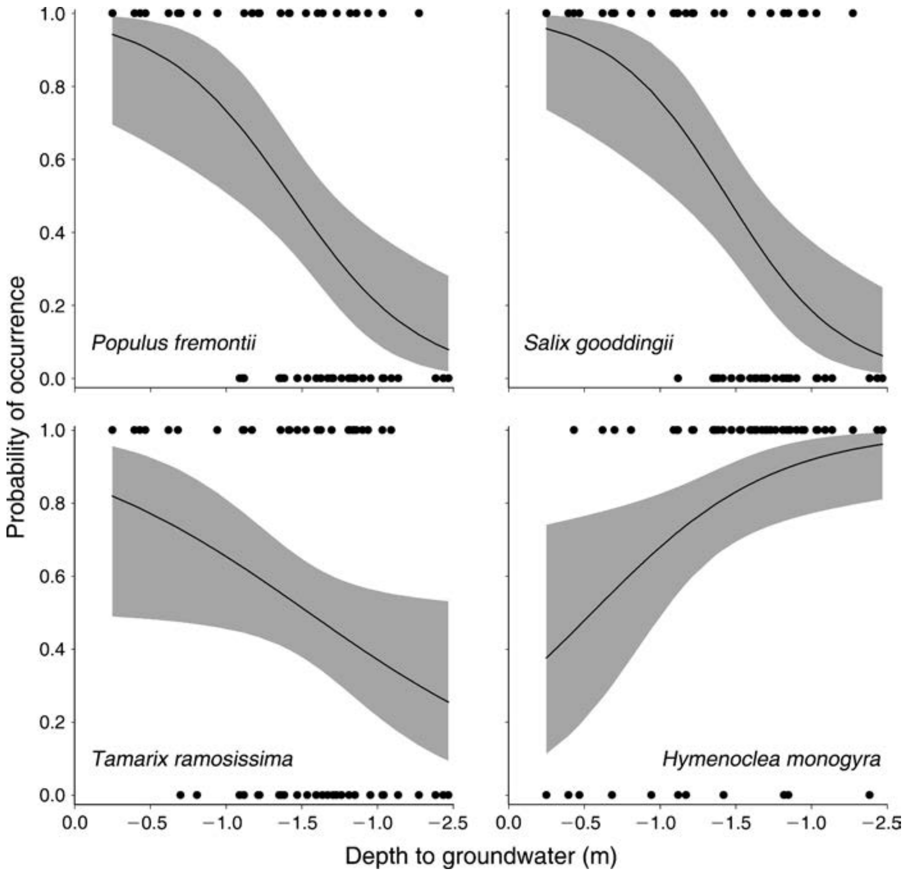

FIG. 3. Probability of *Populus fremontii*, *Salix gooddingii*, *Tamarix ramosissima*, and *Hymenoclea monogyra* occurrence in relation to groundwater depth along a perennial stream, Cherry Creek, Arizona, USA. Points represent plots with absences (0) and presences (1) of plant species; shaded areas are 95% confidence intervals. Models were significant and correctly predicted *Populus* presence in 75% of the observations (likelihood ratio, $P < 0.0001$; Hosmer-Lemeshow goodness-of-fit, $P = 0.8$), *Salix* presence for 77% of the observations (likelihood ratio, $P < 0.0001$; Hosmer-Lemeshow goodness-of-fit, $P = 0.2$), *Tamarix* presence in 63% of the observations (likelihood ratio, $P = 0.03$; Hosmer-Lemeshow goodness-of-fit, $P = 0.6$), and *Hymenoclea* presence in 80% of observations.

Vegetation and habitat relations

Bird surveys.—Overall, 59 species of birds were identified within the 20-m fixed-radius points. The most frequently sighted birds were the Yellow Warbler (*Dendroica petechia*), Wilson's Warbler (*Wilsonia pusilla*), Bell's Vireo (*Vireo bellii*), and Summer Tanager (*Piranga rubra*). Less common bird species observed only once included: Abert's Towhee (*Pipilo aberti*), Anna's Hummingbird (*Calypte anna*), Ash-throated Flycatcher (*Myiarchus cinerascens*), Black-headed Grosbeak (*Pheucticus melanocephalus*), Brewer's Sparrow (*Spizella breweri*), Brown-headed Cowbird (*Molothrus ater*), Bullock's Oriole (*Icterus bullockii*), Lucy's Warbler (*Vermivora luciae*), MacGillivray's Warbler (*Oporornis tolmiei*), Rock Wren (*Salpinctes obsoletus*), Song Sparrow (*Melospiza melodia*), Verdin (*Auriparus flaviceps*), Warbling Vireo (*Vireo gilvus*), and Yellow-rumped Warbler (*Dendroica coronata*).

Bird Habitat Index (BHI).—The most parsimonious BHI included seven variables (Table 1) quantifying diversity of vegetation height and size and foliage cover (PCA analysis; factors 1 and 2, $P = 0.05$). This model avoided collinearity and did not significantly differ from the full model of 15 variables ($r^2 = 0.98$, $P < 0.0001$). Habitat indices were significantly positively related to native riparian tree cover (Figs. 4–6), whereas indices showed no relation to nonnative tree and shrub cover (Fig. 5).

BHI was validated by having a significant positive association with bird community diversity, species richness, and abundance. None of the points with indices ≤ 0.3 had more than three species of birds observed during surveys, and many of these points had no species. Habitat indices ≥ 0.6 had bird species richness values averaging 4 to 6 and as high as 12.

DISCUSSION

Our BHI and models of groundwater and fluvial disturbance are unique in that we were able to predict changes in the spatial distribution of native riparian

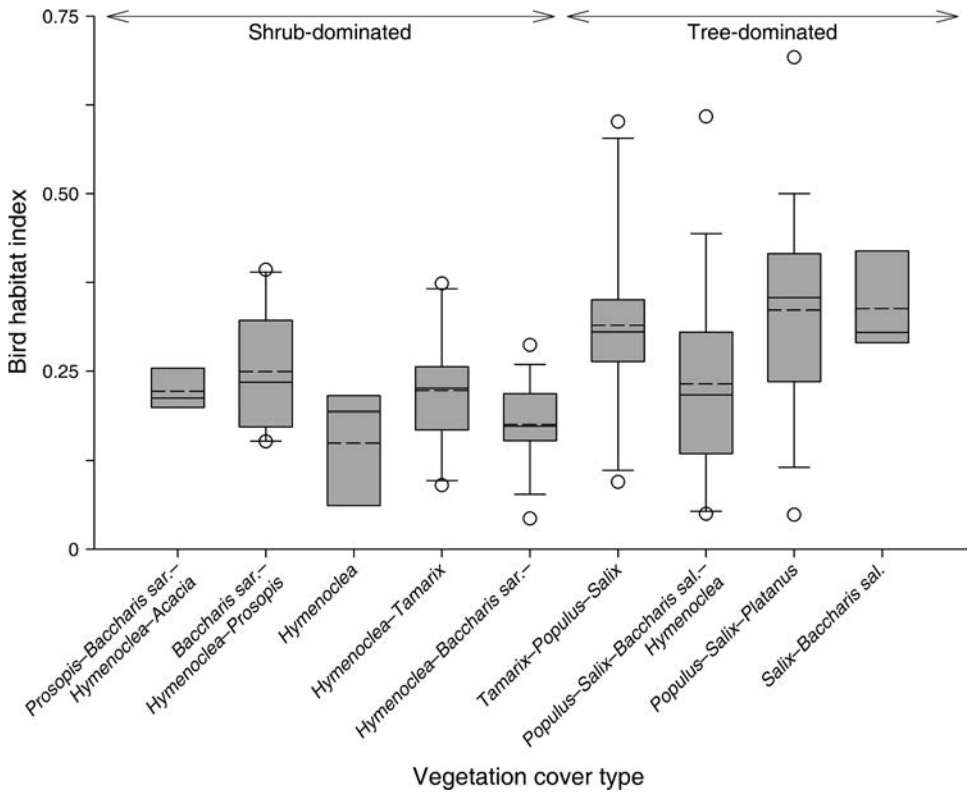

FIG. 4. Bird habitat index in nine vegetation cover types along a perennial stream, Cherry Creek, Arizona, USA. The boundary of the box nearest zero is the 25th percentile, the solid line within the box represents the median, dashed lines are the mean, and the boundary of the box farthest from zero represents the 75th percentile. Whiskers (error bars) above and below the box represent the 90th and 10th percentiles. Points lying outside of 90th and 10th percentiles are shown. Plant species *Baccharis sarothroides* is abbreviated as *Baccharis sar*. and *Baccharis salicifolia* is abbreviated as *Baccharis sal*. See *Vegetation and index development; BHI development*.

deciduous woodland, which is an important component of riparian bird habitat (Figs. 1 and 2). The most important findings relevant to riparian habitat and management of environmental flows were that: (1) habitat structural characteristics can be quantified in an index, (2) our index was validated by point count surveys of birds to quantify diversity, richness, and abundance, (3) the BHI is positively related to cover of native deciduous trees, and (4) predicted native tree cover declines by 88% when groundwater levels are lowered 2 m below base-level, effectively decreasing the extent of the floodplain available to provide structurally diverse habitat (Figs. 1, 2, and 8).

Stream flow, groundwater, and habitat maintenance

Multiple lines of evidence suggest that, because the alluvial groundwater is derived primarily from surface flow in Cherry Creek, reductions in stream flow (due to water development, climate change, or their combined effects) would have quantifiable negative consequences for riparian forest species and associated bird habitat characteristics and quality. Our data and other studies from this arid region suggest that the consequences of reduced stream flow include: reduction in spatial extent of potential habitat for dominant riparian forest species, conversion of complex riparian forest cover types to structurally and compositionally simple shrubland (Busch et al. 1992, Pockman and Sperry 2000), reductions in bird habitat structure (as reflected in the BHI), and reduced bird diversity and species richness (Fig. 2). The risk of such a conversion of complex riparian wildlife habitat to simplified habitat resembling adjacent terrestrial desert habitat increases as a function of stream flow reduction and associated groundwater decline (Fig. 1). Maintenance of high flows and associated fluvial disturbance is important for preventing encroachment and dominance by disturbance-intolerant shrubs.

Many of the riparian plant species responsible for high bird habitat complexity are considered obligate riparian species due to their reliance upon shallow water tables (Haney et al. 2008). Members of the Salicaceae are highly vulnerable to water stress which may result in leaf wilting, leaf loss, xylem cavitation, and branch or crown mortality and reduced cover when roots lose contact with groundwater (Tyree et al. 1994, Scott et al. 2000, Shafroth et al. 2000, Horton et al. 2001*a*). In arid regions, *Populus* depends on shallow floodplain groundwater

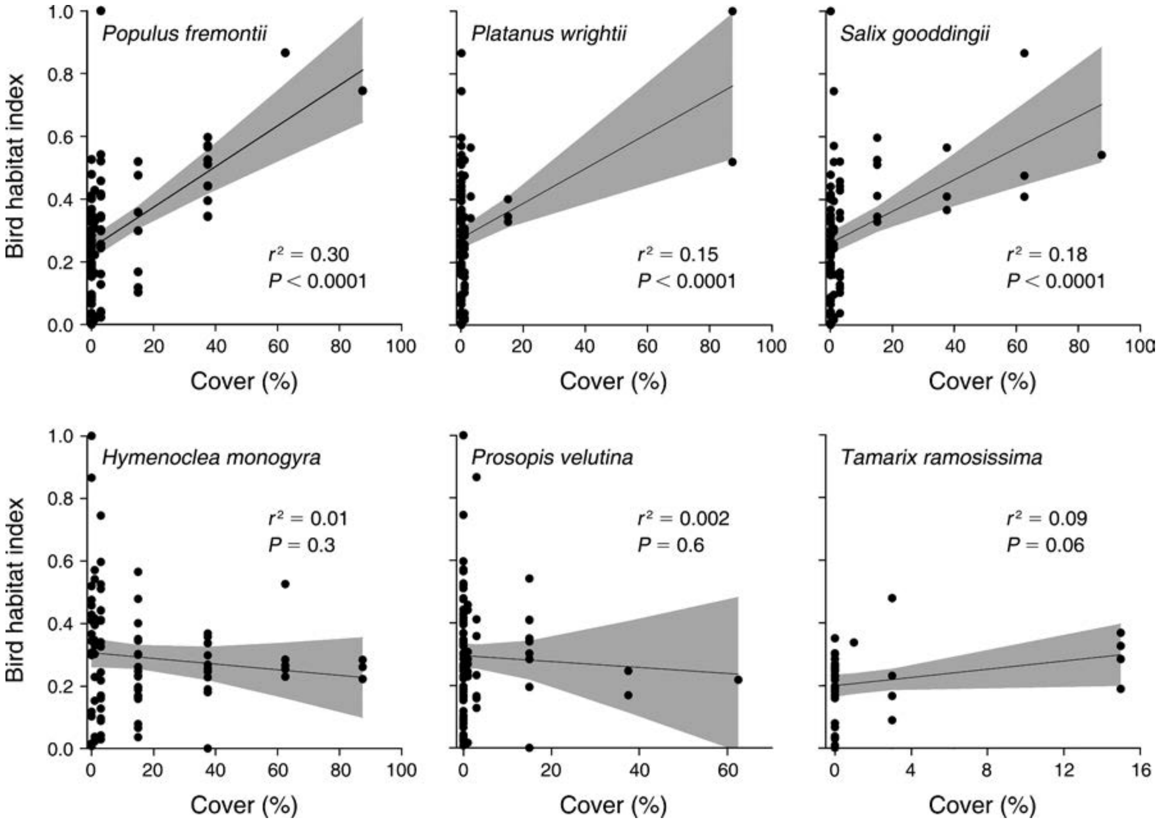

FIG. 5. Bird habitat index related to percent cover of *Populus fremontii* (in the absence of nonnative *Tamarix ramosissima*), *Salix gooddingii*, *Platanus wrightii*, *Hymenoclea monogyra*, *Prosopis velutina*, and *Tamarix ramosissima* (in the absence of *Populus fremontii*, *Salix gooddingii*, and *Platanus wrightii*) along a perennial stream, Cherry Creek, Arizona, USA. Shaded areas are 95% confidence intervals.

recharged by the adjacent stream, which makes individuals and forests particularly vulnerable to modifications of stream flow (Smith et al. 1991, Busch et al. 1992, Kolb et al. 1997). Indeed, riparian tree species were most abundant in areas along Cherry Creek where groundwater was within 2 m of the ground surface (Fig. 3).

Both low and high flows are important for riparian tree establishment and maintenance. Sufficient low flows capable of supporting shallow water tables can increase the likelihood of disturbance-adapted regenerants and support root development, growth, and survival to reproductive age (Mahoney and Rood 1998, Horton and Clark 2001). High flows create bare, exposed sites for recruitment by disturbance-adapted species (e.g., *Populus*, *Salix gooddingii*, *S. exigua*, *Platanus*). Our results showed that riparian forest species had affinities to both highly disturbed habitats and those with shallow water tables, whereas shrubs were only excluded from areas of high fluvial disturbance, regardless of water table depth (Fig. 1b). Molles et al. (1998) found that high flows serve to exclude upland species from riparian areas, recharge and maintain alluvial groundwater levels, and support biochemical processes on the floodplain. Variation in flow regime through time (timing, magnitude, frequency, and sequencing of high and low flow) can foster heterogeneity by providing opportunities for different species to become established at different times, creating variation in the age- and size-class structure of vegetation and the heterogeneity of habitat.

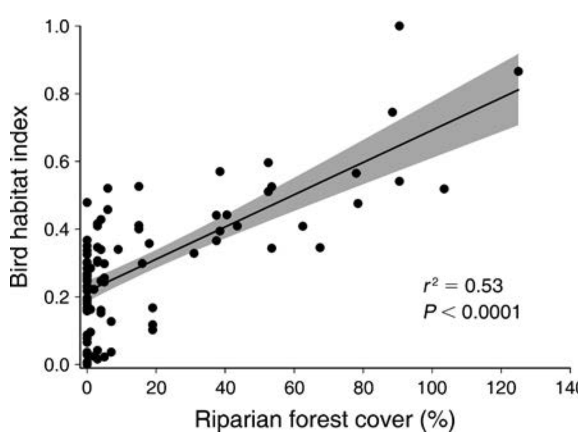

FIG. 6. Bird habitat index related to cover of native riparian forest species (*Populus fremontii*, *Salix gooddingii*, and *Platanus wrightii*) along a perennial stream, Cherry Creek, Arizona, USA. Shaded areas are 95% confidence intervals.

Plate 1. (Upper left) Riparian forest dominated by *Populus fremontii*, *Platanus wrightii*, and *Salix gooddingii* along Cherry Creek, Arizona, USA. This forest had bird habitat index (BHI) values of 0.6 or greater and bird species richness as high as 12. (Upper right) Yellow Warbler (*Dendroica petechia*), which prefers riparian forest. (Lower right) Shrublands, which are dominated by *Prosopis velutina*, *Baccharis sarothroides*, *Hymenochlea monogyra*, and *Tamarix ramosissima* in xeroriparian areas. Xeroriparian shrublands along Cherry Creek had BHI scores of less than 0.3, and bird species richness never exceeded 3. (Lower left) Phainopepla (*Phainopepla nitens*), which prefers xeroriparian shrubland habitat. Photo credits: landscapes, D. M. Merritt; birds, Brendon Grice.

Many desert shrubs have an advantage over native riparian species. This is due in part to their greater potential rooting depth (Busch and Smith 1995, Stromberg et al. 1996, Horton et al. 2001*a*, *c*) and adaptations for functioning at lower water potentials that are lethal to most native phreatophytes (Cleverly et al. 1997, Pockman and Sperry 2000). Few species have the ability to function and maintain dominance under both water-stressed and flooded conditions; this is an energetic trade-off for most native species (Horton et al. 2001*a*, *b*, c). Reduced high and low stream flow and subsequent groundwater decline has more of an impact on native riparian species than on desert shrubs and nonnative riparian species such as *Tamarix ramosissima* (Cleverly et al. 1997, Pockman and Sperry 2000, Horton et al. 2001*c*, Merritt and Poff 2010). Our work associates increases in shrub-dominated cover types with lower bird habitat quality, and suggests that desert shrubs are less sensitive to depth to groundwater on floodplains but are excluded from near-channel habitats by fluvial disturbance.

Bird habitat

Structurally and compositionally heterogeneous vegetation is an important component of wildlife habitat, through providing a variety of food resources and shelter (Arnold 1988, MacNally 1990, McElhinny et al. 2005). Vertical structure provides a wider variety of habitat niches, increasing potential bird species diversity (MacArthur and MacArthur 1961, Woinarski et al. 1997, McElhinny et al. 2005). Riparian habitats, with their exceptional structural and compositional diversity, provide a variety of resources not found in adjacent upland habitats (Powell and Steidl 2000, 2002, Palmer and Bennett 2006, Kirkpatrick et al. 2009). This difference in structure is one important reason why bird species composition differs between upland and riparian habitats (Finch 1989, Doyle 1990, Ellis 1995). Kirkpatrick et al. (2009) found that bird numbers and richness of bird communities increased 75% and 68%, respectively, in riparian areas compared to areas 200 m from stream channels along southwestern Arizona streams. This aggregation near riparian areas is also due in part to the presence of standing water (Brand et al. 2008).

The relationship between birds and habitat has been well evaluated. Habitat structural complexity has long been known to positively influence bird species richness and abundance in general (MacArthur and MacArthur 1961, Willson 1974, Roth 1976, Cody 1981) and in riparian areas in particular (Emmerich and Vohs 1982, Finch 1989, Knopf and Samson 1994, Sanders and Edge 1998, Powell and Steidl 2002). Riparian habitats have more horizontal structure and vertical layering of habitat and are composed of plant species not generally found in adjacent upland areas (Sabo et al. 2005,

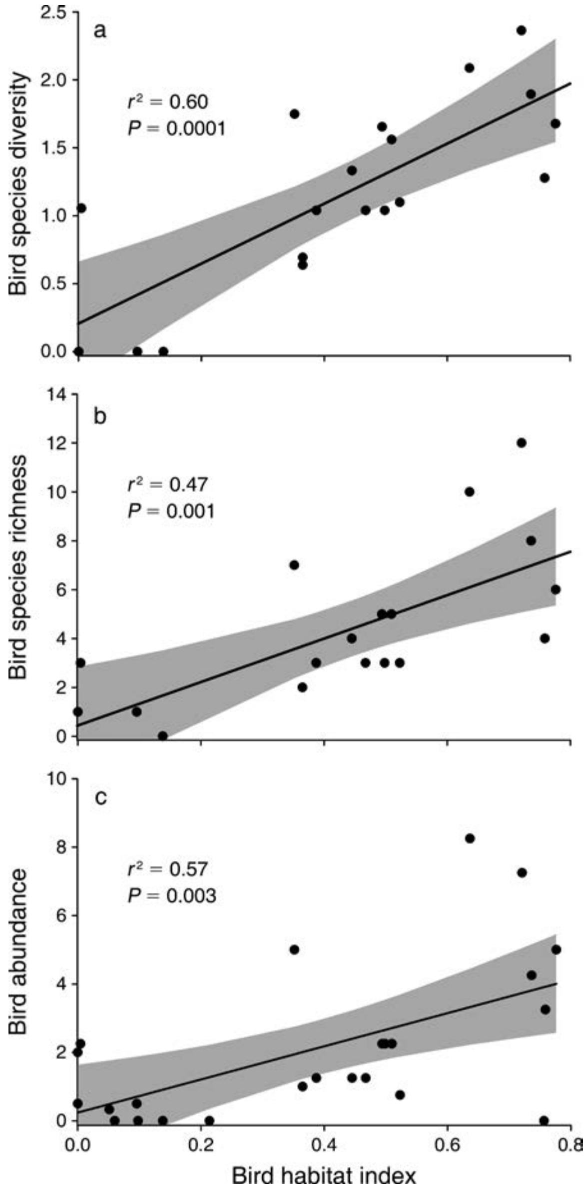

FIG. 7. Relationships between bird habitat index scores (which represent structural and provisional heterogeneity) and (a) measurements of bird community diversity (Simpson diversity index), (b) bird species richness, and (c) bird abundance along a perennial stream, Cherry Creek, Arizona, USA. Shaded areas are 95% confidence intervals.

Palmer and Bennett 2006). Within the American Southwest, >50% of breeding birds are dependent upon riparian habitats at some time during their life cycle (Knopf et al. 1988, Kirkpatrick et al. 2009). Maintenance of these riparian forests has been shown to require perennial stream flow in desert landscapes. Reduction in stream flow and stream flow intermittency may result in declines in forest structure, loss of mature *Populus* stands, and conversion of forest to shrub or grassland–shrubland system (Boggs and Weaver 1994, Stromberg et al. 2005, Stromberg et al. 2007, Merritt and Poff 2010).

Along Cherry Creek, habitat indices showed a significant positive relationship with native plant cover because plants such as *Populus*, *Salix*, and *Platanus* likely contribute to basal area and diameter of woody species, variables included in the BHI (Table 1, Figs. 5–7). *Populus* and other large-diameter trees are important resources for woodpecker and sapsucker species that excavate cavities (Brenowitz 1978, Sedgwick 1997), which are later used as nesting and roosting sites for other birds and mammals (Jones et al. 1994, Martin and Eadie 1999). Maintaining a diversity of tree and shrub species can contribute to the heterogeneity of foliage layers, another important variable included in our index. Within the arid Southwest, Powell and Steidl (2002) conclude that long-term conservation of songbirds requires maintenance of native riparian tree and shrub species, and Brand et al. (2011) agree that a reduction of native trees from dewatering stream scenarios will lead to losses in canopy-nesting bird species. Similarly, habitat indices along Cherry Creek were lowest in xeroriparian areas composed of upland shrubs (e.g., *Hymenoclea*), which are more abundant farther from the stream channel, and nonnative shrubs (e.g., *Tamarix*).

Simulated groundwater decline and bird habitat

It is likely that riparian forest extent along Cherry Creek has expanded and contracted in response to wetter periods of time with increased stream flow and prolonged periods of drought, respectively. Lowering of alluvial water tables can be caused by reduced flow from upstream (caused by climate change or water extraction), channel incision (caused by headcutting, downcutting, or sand and gravel mining), groundwater pumping, and localized stream flow diversion (Stromberg et al. 1996, Kondolf 1997). Simulated incremental declines in surface and groundwater levels were predicted to cause frequency of *Populus*-dominated riparian forest habitat to decline from its current 35% cover at an average rate of 4%/dm decline in groundwater level from the modeled base flow (Figs. 1 and 2). Depending upon the severity and persistence, incremental reductions in surface water and groundwater levels increase the likelihood of conversion of riparian forest to shrubland, the migration of the riparian forest–xeroriparian edge nearer to the stream channel, and the reduction in extent or complete loss of riparian forest. These shifts in vegetation would likely result in shifts in the bird community from cavity- and canopy-nesting species, i.e., Gila Woodpecker, *Melanerpes uropygialis*; Yellow Warbler, *D. petechia*; Summer Tanager, *P. rubra*, to middle-level nesting species, i.e., Abert's Towhee, *P. aberti*; Bell's Vireo, *V. bellii*; Yellow-breasted Chat, *Icteria virens* (Brand et al. 2011) (see Plate 1).

Shrub-dominated vegetation cover types had lower habitat indices and were similar to upland habitats. Though riparian forest dominants such as *Populus*,

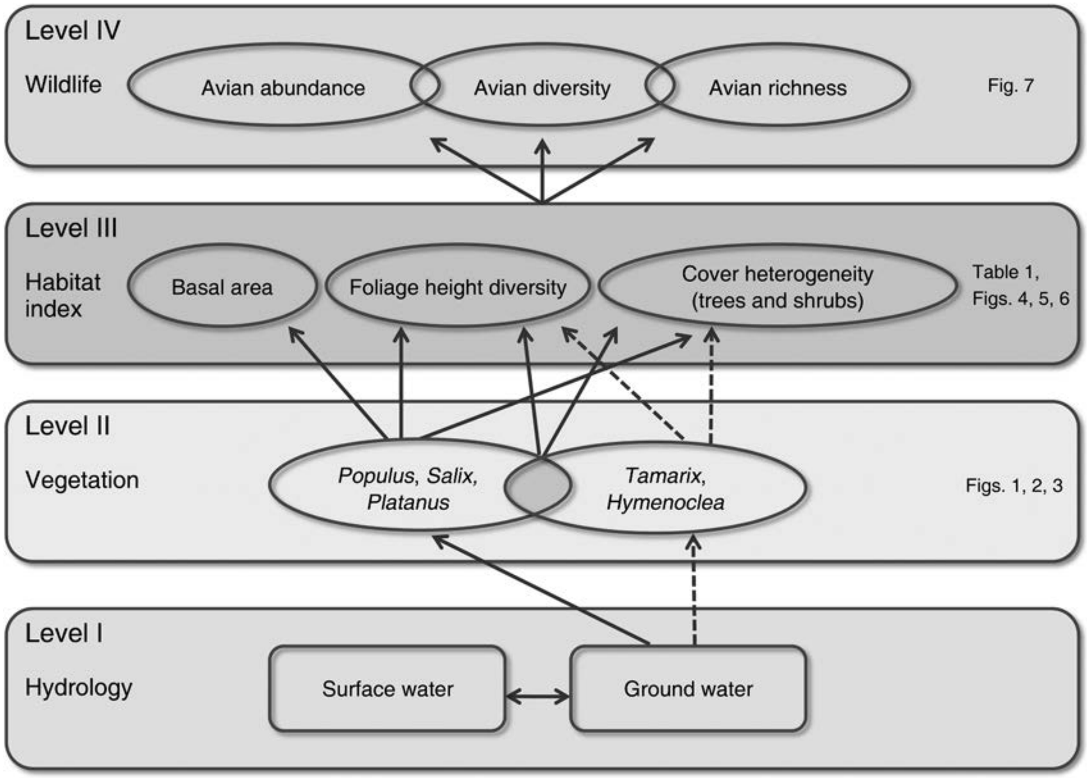

Fig. 8. We developed a systematic approach to evaluate the trade-offs between changes in stream flow and groundwater regimes and biotic characteristics of an arid riparian system. We determined the relationships among hydrology (level I), riparian plant communities (level II), habitat index (level III), and the bird community (level IV) along Cherry Creek in Arizona, USA. Solid arrows indicate a positive relationship or strong influence of one component on another. Dashed arrows indicate a negative relationship or weak influence of one component on another. Note the zone of overlap between two vegetation communities that contribute to the habitat index and the index itself contributing to bird community parameters.

Salix, and *Platanus* may persist for some time along streams with reduced high flows, depleted low flows and reduced interannual variability in flows can cause forests to be sparse, of low age class diversity, and lack desired wildlife benefits (Stromberg et al. 1996). *Tamarix* is not particularly competitive against *Populus* and *Salix* under well-watered conditions (Sher et al. 2000). Furthermore, *Tamarix* does poorly under *Populus* canopy (Lesica and Miles 2001) and under other native trees (e.g., *Acer negundo* [Dewine and Cooper 2008]); therefore maintenance of flows that support native forest species is key to preventing nonnative shrub dominance in riparian areas (Merritt and Poff 2010).

Conclusions

Our work along Cherry Creek and the extensive literature from the American Southwest suggest that reductions in stream flow would increase the risk of riparian vegetation transitioning from forest to shrub dominated, and result in degradation of bird habitat. Incremental reductions in stream flow would result in an increased likelihood of shifts from high-quality riparian habitat (*Populus*, *Salix*, and *Platanus*-dominated riparian forest) to lower-quality habitat dominated by native desert and xeroriparian shrubs such as *Hymenoclea*, *Baccharis sarothroides*, *Prosopis*, and nonnative *Tamarix* along Cherry Creek (Figs. 1, 2, and 4). The most certain means of maintaining wildlife habitat along Cherry Creek is continuation of historical patterns of low flows, high flows, timing and sequencing of flows, and the maintenance of a range of variability in seasonal and interannual flows. The degree of deviation from these historic stream flow patterns will determine the magnitude and trajectory of vegetation change in response to altered flow regimes (Figs. 1 and 2; see also Davis et al. 2005).

Our approach provides a risk assessment of the extent and biological consequences of riparian forest decline as a function of groundwater depletion and altered fluvial disturbance. We have presented a systematic approach to determination and evaluation of the trade-offs between changes in stream flow, groundwater regimes, fluvial disturbance, and biotic characteristics of sites. Our approach (Fig. 8) has applications for other arid stream systems. We first determined the relationships between surface and groundwater and identified sources of moisture to the organisms supporting bird habitat–riparian vegetation (level I of Fig. 8). We then developed realized niche models of several riparian plant species that represent different vegetation cover types (level II of Fig. 8). Attributes of these cover types were then used to quantify habitat attributes of importance to the wildlife taxa of interest (in this case birds), and to summarize them as a habitat index (BHI; level III in Fig. 8). Such attributes could be defined and quantified for other taxonomic groups such as mammals and herpetiles. We then validated our BHI through field inventories to calculate bird diversity, richness, and abundance (level IV in Fig. 8). From this, we were able to model responses of key habitat elements to realistic human-caused flow alterations due to extraction or climate change. Through this systematic approach and the construction of response curves (Fig. 1), managers, decision makers, and the public are better able to evaluate the consequences and trade-offs of changes to flow and disturbance regimes. Rather than provide a minimum flow or single set of flow recommendations, these response curves provide a continuum from which to evaluate acceptable levels of change.

As with many other areas worldwide, demands on freshwater resources in Arizona and throughout the American Southwest are projected to increase, while water supplies are projected to decrease due to climate change (Hawkins and Ellis 2010). Indeed, arid regions throughout the world are projected to become warmer and drier in the future, leading to higher frequency and intensity of drought (IPCC 2007). The population of the basin within which Cherry Creek drains is expected to double by 2050, and freshwater supplies are projected to decline (Marshall et al. 2010). Because surface and groundwater are managed under different regulatory frameworks in the state of Arizona, and groundwater use is unregulated, continued conversion of streams from perennial to intermittent throughout the region is inevitable. Our work, and the work of others in the region (Brand et al. 2011), suggests that groundwater losses will negatively influence the distribution, characteristics, and quality of riparian forests and associated resident and migratory bird habitat.

Riparian areas and habitats are not currently recognized by law as "legitimate users of water," nor are they given equal status with human water demands (sensu Naiman et al. 2002). As a consequence, conflicts over providing water to support wildlife habitat over human existence are expected to intensify (Poff et al. 2003). The development of tools to quantify the effects of surface and groundwater depletion and to relate these changes to consequences in biotic communities are critical (Fig. 8). In the American West, $<1\%$ of the landscape supports riparian vegetation (Knopf et al. 1988, Knopf and Samson 1994), yet these areas provide habitat for more species of breeding birds than any other vegetation type (Knopf and Samson 1994). To this end, we suggest that maintaining variation in high- and low-flow events in perennial streams, particularly in arid regions, can aid in the maintenance and conservation of avifauna and their habitats.

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Literature Cited

Arnold, G. W. 1988. The effects of habitat structure and floristics on the densities of bird species in Wandoo Woodland. Australian Wildlife Research 15:499–510.

Bateman, H. L., M. J. Harner, and A. Chung-MacCoubrey. 2008. Abundance and reproduction of toads (*Bufo*) along a regulated river in the southwestern United States: importance of flooding in riparian ecosystems. Journal of Arid Environments 72:1613–1619.

Bibby, C. J., B. N. Phillips, and A. J. E. Seddon. 1985. Birds of restocked conifer plantations in Wales. Journal of Applied Ecology 22:619–633.

Boggs, K., and T. Weaver. 1994. Changes in vegetation and nutrient pools during riparian succession. Wetlands 14:98–109.

Brand, L. A., J. C. Stromberg, D. C. Goodrich, M. D. Dixon, K. Lansey, D. Kang, D. S. Brookshire, and D. J. Cerasale. 2011. Projecting avian response to linked changes in groundwater and riparian floodplain vegetation along a dryland river: a scenario analysis. Ecohydrology 4:130–142.

Brand, L. A., J. C. Stromberg, and B. R. Noon. 2010. Avian density and nest survival on the San Pedro River: importance of vegetation type and hydrologic regime. Journal of Wildlife Management 74:739–754.

Brand, L. A., G. C. White, and B. R. Noon. 2008. Factors influencing species richness and community composition of breeding birds in a desert riparian corridor. Condor 110:199–210.

Braun-Blanquet, J. 1965. Plant sociology: the study of plant communities. C. D. Fuller and H. S. Conard, translators and editors. Hafner, London, UK.

Brenowitz, G. L. 1978. Gila Woodpecker agonistic behavior. Auk 95:49–58.

Busch, D. E., N. L. Ingraham, and S. D. Smith. 1992. Water uptake in woody riparian phreatophytes of the southwestern United States: a stable isotope study. Ecological Applications 2:450–459.

Busch, D. E., and S. D. Smith. 1995. Mechanisms associated with decline of woody species in riparian ecosystems of the southwestern U.S. Ecological Monographs 65:347–370.

Canterbury, G. E., T. E. Martin, D. R. Petit, L. J. Petit, and D. F. Bradford. 2000. Bird communities and habitat as ecological indicators of forest condition in regional monitoring. Conservation Biology 14:544–558.

Carothers, S. 1974. Breeding ecology and time-energy budget of male Vermilion Flycatchers and comments on the social organization of southwestern riparian birds. Dissertation. University of Illinois, Chicago, Illinois, USA.

Cleverly, J. R., S. D. Smith, A. Sala, and D. A. Devitt. 1997. Invasive capacity of *Tamarix ramosissima* in a Mojave desert floodplain: the role of drought. Oecologia 111:12–18.

Cody, M. L. 1981. Habitat selection in birds: the roles of vegetation structure, competitors and productivity. BioScience 31:107–113.

Curtis, R. O., and D. D. Marshall. 2000. Why quadratic mean diameter? Western Journal of Applied Forestry 15:137–139.

Davis, M. A., et al. 2005. Vegetation change: a reunifying concept in plant ecology. Perspectives in Plant Ecology Evolution and Systematics 7:69–76.

Dewine, J. M., and D. J. Cooper. 2008. Canopy shade and the successional replacement of Tamarisk by native box elder. Journal of Applied Ecology 45:505–514.

Doyle, A. T. 1990. Use of riparian and upland habitats by small mammals. Journal of Mammalogy 71:14–23.

Ellis, L. M. 1995. Bird use of saltcedar and cottonwood vegetation in the Middle Rio Grande Valley of New Mexico, U.S.A. Journal of Arid Environments 30:339–349.

Emmerich, J. M., and P. A. Vohs. 1982. Comparative use of four woodland habitats by birds. Journal of Wildlife Management 46:43–49.

Finch, D. M. 1989. Habitat use and habitat overlap of riparian birds in three elevational zones. Ecology 70:866–880.

Freemark, K. E., and H. G. Merriam. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. Biological Conservation 36:115–141.

Gore, J. A., and F. D. Shields. 1995. Can large rivers be restored? BioScience 45:142–152.

Haney, J. A., D. S. Turner, A. E. Springer, J. C. Stromberg, L. E. Stevens, P. A. Pearthree, and V. Supplee. 2008. Ecological implications of Verde River flows. A report by the Arizona Water Institute, The Nature Conservancy, and the Verde River Basin Partnership, Arlington, Virginia, USA.

Hawkins, T. W., and A. W. Ellis. 2010. The dependence of streamflow on antecedent subsurface moisture in an arid climate. Journal of Arid Environments 74:75–86.

Hill, M. O., and P. Šmilauer. 2005. TWINSPAN for Windows version 2.3. Centre for Ecology and Hydrology and University of South Bohemia, Huntingdon, UK and Ceske Budejovice, Czech Republic.

Horton, J. L., and J. L. Clark. 2001. Water table decline alters growth and survival of *Salix gooddingii* and *Tamarix chinensis* seedlings. Forest Ecology and Management 140:239–247.

Horton, J. L., T. E. Kolb, and S. C. Hart. 2001*a*. Physiological response to groundwater depth varies among species and with river flow regulation. Ecological Applications 11:1046–1059.

Horton, J. L., T. Kolb, and S. C. Hart. 2001*b*. Leaf gas exchange characteristics differ among Sonoran desert riparian tree species. Tree Physiology 21:233–241.

Horton, J. L., T. E. Kolb, and S. C. Hart. 2001*c*. Responses of riparian trees to interannual variation in ground water depth in a semi-arid river basin. Plant Cell and Environment 24:293–304.

Hutto, R. L., S. M. Pletschet, and P. Hendricks. 1986. A fixed-radius point count method for nonbreeding and breeding season use. Auk 103:593–602.

IPCC. 2007. Climate change 2007: the physical science basis. *In* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averiyt, M. Tignor, H. L. Miller, editors. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69:373–386.

Kirkpatrick, C., C. J. Conway, and D. LaRoche. 2009. Surface water depletion and riparian birds. Final report submitted to Arizona Game and Fish Department by USGS Arizona Cooperative Fish and Wildlife Research Unit, Tucson, Arizona, USA.

Kissling, W. D., R. Field, and K. Boehning-Gaese. 2008. Spatial patterns of woody plant and bird diversity: functional relationships or environmental effects? Global Ecology and Biogeography 17:327–339.

Knopf, F. L., R. R. Johnson, T. Rich, F. B. Samson, and R. C. Szaro. 1988. Conservation of riparian ecosystems in the United States. Wilson Bulletin 100:272–284.

Knopf, F. L., and F. B. Samson. 1994. Scale perspectives on avian diversity in western riparian ecosystems. Conservation Biology 8:669–676.

Kolb, T. E., S. C. Hart, and R. Amundson. 1997. Boxelder water sources and physiology at perennial and ephemeral stream sites in Arizona. Tree Physiology 17:151–160.

Kondolf, G. M. 1997. Hungry water: effects of dams and gravel mining on river channels. Environmental Management 21:533–551.

Legendre, P., and L. Legendre. 1998. Numerical ecology. Second English edition. Elsevier, Amsterdam, The Netherlands.

Lesica, P., and S. Miles. 2001. Tamarisk growth at the northern margin of its naturalized range in Montana, USA. Wetlands 21:240–246.

Lite, S. J., and J. C. Stromberg. 2005. Surface water and ground-water thresholds for maintaining *Populus-Salix* forests, San Pedro River, Arizona. Biological Conservation 125:153–167.

MacArthur, R. H. 1964. Environmental factors affecting bird species diversity. American Naturalist 98:387–397.

MacArthur, R. H., and J. W. MacArthur. 1961. On bird species-diversity. Ecology 42:594–605.

MacNally, R. 1990. The roles of floristics and physiognomy in avian community composition. Australian Journal of Ecology 15:321–327.

Mahoney, J. M., and S. B. Rood. 1998. Streamflow requirements for cottonwood seedling recruitment—an integrative model. Wetlands 18:634–645.

Marshall, R. M., M. D. Robles, D. R. Majka, and J. A. Haney. 2010. Sustainable water management in the southwestern United States: reality or rhetoric? PLoS One 5.

Martin, K., and J. M. Eadie. 1999. Nest webs: a community-wide approach to the management and conservation of cavity-nesting forest birds. Forest Ecology and Management 115:243–257.

McElhinny, C., P. Gibbons, C. Brack, and J. Bauhus. 2005. Forest and woodland stand structural complexity: its definition and measurement. Forest Ecology and Management 218:1–24.

Merritt, D. M., H. L. Bateman, and C. D. Peltz. 2010. Instream flow requirements for maintenance of wildlife habitat and riparian vegetation: Cherry Creek, Tonto National Forest, Arizona. Report prepared for Tonto National Forest, Phoenix, Arizona, USA.

Merritt, D. M., and N. L. Poff. 2010. Shifting dominance of riparian *Populus* and *Tamarix* along gradients of flow alteration in western North American rivers. Ecological Applications 20:135–152.

Molles, M. C., C. S. Crawford, L. M. Ellis, H. M. Valett, and C. N. Dahm. 1998. Managed flooding for riparian ecosystem restoration. BioScience 48:749–756.

Naiman, R. J., S. E. Bunn, C. Nilsson, G. E. Petts, G. Pinay, and L. C. Thompson. 2002. Legitimizing fluvial ecosystems as users of water: an overview. Environmental Management 30:455–467.

Nilsson, C., and K. Berggren. 2000. Alterations of riparian ecosystems caused by river regulation. BioScience 50:783–792.

Palmer, G. C., and A. F. Bennett. 2006. Riparian zones provide for distinct bird assemblages in forest mosaics and south-east Australia. Biological Conservation 130:447–457.

Pockman, W. T., and J. S. Sperry. 2000. Vulnerability to xylem cavitation and the distribution of Sonoran desert vegetation. American Journal of Botany 87:1287–1299.

Poff, N. L., D. J. Allen, M. A. Palmer, D. D. Hart, B. D. Richter, A. H. Arthington, K. H. Rogers, and J. A. Stanford. 2003. River flows and water wars: emerging science for environmental decision making. Frontiers in Ecology and the Environment 1:298–306.

Powell, B. F., and R. J. Steidl. 2000. Nesting habitat and reproductive success of Southwestern riparian birds. The Condor 102:823–831.

Powell, B. F., and R. J. Steidl. 2002. Habitat selection by riparian songbirds breeding in southern Arizona. Journal of Wildlife Management 66:1096–1103.

Roth, R. R. 1976. Spatial heterogeneity and bird species-diversity. Ecology 57:773–782.

Sabo, J. L., R. Sponseller, M. Dixon, K. Gade, T. Harms, J. Heffernan, A. Jani, G. Katz, C. Soykan, J. Watts, and A. Welter. 2005. Riparian zones increase regional species richness by harboring different, not more, species. Ecology 86:56–62.

Sanders, T. A., and W. D. Edge. 1998. Breeding bird community composition in relation to riparian vegetation structure in the western United States. Journal of Wildlife Management 62:461–473.

SAS. 2011. SAS Stat 9.3. SAS Institute, Cary, North Carolina, USA.

Scott, M. L., G. C. Lines, and G. T. Auble. 2000. Channel incision and patterns of cottonwood stress and mortality along the Mojave River, California. Journal of Arid Environments 44:399–414.

Scott, M. L., P. B. Shafroth, and G. T. Auble. 1999. Responses of riparian cottonwoods to alluvial water table declines. Environmental Management 23:347–358.

Sedgwick, J. A. 1997. Sequential cavity use in a cottonwood bottomland. Condor 99:880–887.

Shafroth, P. B., J. C. Stromberg, and D. T. Patten. 2000. Woody riparian vegetation response to different alluvial water table regimes. Western North American Naturalist 60:66–76.

Sher, A. A., D. L. Marshall, and S. A. Gilbert. 2000. Competition between native *Populus deltoides* and invasive *Tamarix ramosissima* and the implications for reestablishing flooding disturbance. Conservation Biology 14:1744–1754.

Smith, S. D., A. B. Wellington, J. L. Nachlinger, and C. A. Fox. 1991. Functional responses of riparian vegetation to streamflow diversion in the eastern Sierra Nevada. Ecological Applications 1:89–97.

Stromberg, J. C., K. J. Bagstad, J. M. Leenhouts, S. J. Lite, and E. Makings. 2005. Effects of stream flow intermittency on riparian vegetation of a semiarid region river (San Pedro River, Arizona). River Research and Applications 21:925–938.

Stromberg, J. C., J. A. Boudell, and A. F. Hazelton. 2008. Differences in seed mass between hydric and xeric plants influence seed bank dynamics in a dryland riparian ecosystem. Functional Ecology 22:205–212.

Stromberg, J. C., S. J. Lite, and M. D. Dixon. 2010. Effects of stream flow patterns on riparian vegetation of a semiarid river: implications for a changing climate. River Research and Applications 26:712–729.

Stromberg, J. C., S. J. Lite, R. Marler, C. Paradzick, P. B. Shafroth, D. Shorrock, J. M. White, and M. S. White. 2007. Altered stream-flow regimes and invasive plant species: the Tamarix case. Global Ecology and Biogeography 16:381–393.

Stromberg, J. C., R. Tiller, and B. Richter. 1996. Effects of groundwater decline on riparian vegetation of semiarid regions: the San Pedro, Arizona. Ecological Applications 6:113–131.

Tews, J., U. Brose, V. Grimm, K. Tielborger, M. C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31:79–92.

Tyree, M. T., K. J. Kolb, S. J. Rood, and S. Patino. 1994. Vulnerability to drought induced cavitation of riparian cottonwoods in Alberta: a possible factor in the decline of the ecosystem? Tree Physiology 14:455–466.

USGS. 1988. Guidelines for determining flood flow frequency, Bulletin 17-B. Bulletin #17B PB86 157278/AS. United States Geological Survey, Department of the Interior, Washington, D.C., USA.

Waddle, T. J., and K. D. Bovee. 2009. Environmental flows studies of the Fort Collins Science Center, U.S. Geological Survey: Cherry Creek, Arizona. U.S. Geological Survey, Reston, Virginia, USA.

Wiens, J. A. 1974. Habitat heterogeneity and avian community structure in North American grasslands. American Midland Naturalist 91:195–213.

Willson, M. F. 1974. Avian community organization and habitat structure. Ecology 55:1017–1029.

Woinarski, J. C. Z., H. F. Recher, and J. D. Majer. 1997. Vertebrates of eucalypt formations. Pages 303–341 *in* J. E. Williams and J. C. Z. Woinarski, editors. Eucalypt ecology: individuals to ecosystems. Cambridge University Press, Cambridge, UK.

Zar, J. H. 1996. Biostatistical analysis. Third edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Supplemental Material

Appendix A

Location of the Cherry Creek study reach in the Tonto National Forest, the USGS stream flow gage used for hydrologic analyses, and the location of the Salt River, Arizona, USA (*Ecological Archives* A022-106-A1).

Appendix B

The configuration of 95 113-m^2 vegetation plots along Cherry Creek, Arizona, USA. Cherry Creek flows from top to bottom (*Ecological Archives* A022-106-A2).

Appendix C

Correlation matrix for vegetation variables considered for the bird habitat index (*Ecological Archives* A022-106-A3)