Projecting avian response to linked changes in groundwater and riparian floodplain vegetation along a dryland river: a scenario analysis

L. Arriana Brand,[1][*][†] Juliet C. Stromberg,[2] David C. Goodrich,[3] Mark D. Dixon,[4] Kevin Lansey,[5] Doosun Kang,[5] David S. Brookshire[6] and David J. Cerasale[7]

[1] *SAHRA Center, Department of Hydrology and Water Resources, University of Arizona, PO Box 210158-B, Marshall Building 530, Tucson, AZ 85721, USA*
[2] *School of Life Sciences, Arizona State University, Tempe, AZ 85287-4501, USA*
[3] *Agricultural Research Service, US Department of Agriculture, 2000 E. Allen Road, Tucson, AZ 85719, USA*
[4] *Department of Biology, University of South Dakota, Vermillion, SD 57069, USA*
[5] *Department of Civil Engineering and Engineering Mechanics, The University of Arizona, Tucson, AZ 85721, USA*
[6] *Department of Economics, University of New Mexico, 1 University of New Mexico, Albuquerque, NM 87131, USA*
[7] *Department of Ecology and Evolutionary Biology, Cornell University, Corson Hall, Ithaca, NY 14853, USA*

ABSTRACT

Groundwater is a key driver of riparian condition on dryland rivers but is in high demand for municipal, industrial, and agricultural uses. Approaches are needed to guide decisions that balance human water needs while conserving riparian ecosystems. We developed a space-for-time substitution model that links groundwater change scenarios implemented within a Decision Support System (DSS) with proportions of floodplain vegetation types and abundances of breeding and migratory birds along the upper San Pedro River, AZ, USA. We investigated nine scenarios ranging from groundwater depletion to recharge. In groundwater decline scenarios, relative proportions of tall-canopied obligate phreatophytes (*Populus/Salix*, cottonwood/willow) on the floodplain progressively decline, and shrubbier species less dependent on permanent water sources (e.g. *Tamarix* spp., saltcedar) increase. These scenarios result in broad shifts in the composition of the breeding bird community, with canopy-nesting and water-obligate birds declining but midstory nesting birds increasing in abundance as groundwater declines. For the most extreme draw-down scenario where all reaches undergo groundwater declines, models project that only 10% of the upper San Pedro floodplain would be comprised of cottonwood/willow (73% saltcedar and 18% mesquite), and abundances of canopy-nesting, water-obligate, and spring migrant birds would decline 48%, 72%, and 40%, respectively. Groundwater recharge scenarios were associated with increases in canopy-nesting birds particularly given the extreme recharge scenario (all reaches regain shallow water tables and perennial streamflow). Model outputs serve to assess the sensitivity of biotic groups to potential changes in groundwater and thus to rank scenarios based on their expected ecological impacts. Copyright © 2010 John Wiley & Sons, Ltd.

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INTRODUCTION

Rivers and streams are threatened worldwide with groundwater mining and appropriation of surface water runoff (Postel *et al.*, 1996; Richter *et al.*, 1997; Alley *et al.*, 2002). In arid and semiarid regions, ground- and surface-water are in high demand for municipal, agricultural, or industrial uses but are also needed to maintain riparian ecosystems (Stromberg *et al.*, 2007). Changes in hydrology can result in changes in physiognomy, abundance, and composition of riparian vegetation (Pettit *et al.*, 2001; Shaw and Cooper, 2008; Stromberg *et al.*, 1996). Given the biological importance of riparian corridors combined with the expectation that water scarcity will increase, an ability to predict the ecological impacts of alternative water management strategies is needed (Poff *et al.*, 2003; Richter *et al.*, 2003).

There is growing recognition that river conservation and restoration success hinges on hydrological conditions that support aquatic and riparian biota (Poff *et al.*, 1997; Shafroth *et al.*, 2008). Previous research has documented the hydrological requirements for the recruitment and survivorship of various southwestern riparian plant species, particularly cottonwood (*Populus fremontii*; Stromberg *et al.*, 1996; Scott *et al.*, 1999; Lytle and Merritt, 2004). In addition to the flood regimes needed to maintain successional dynamics (Richter and Richter, 2000), groundwater depth and its fluctuation are key mechanisms driving survivorship of shallow-rooted phreatophytes. In the American Southwest, Lite and Stromberg (2005) documented ranges of water table depth required to

* Correspondence to: L. Arriana Brand, US Geological Survey, Western Ecological Research Center, San Francisco Bay Estuary Field Station, 505 Azuar Drive, Vallejo, CA 94592, USA. E-mail: arriana_brand@usgs.gov
† Current address: US Geological Survey, Western Ecological Research Center, San Francisco Bay Estuary Field Station, 505 Azuar Drive, Vallejo, CA 94592, USA.

sustain various floodplain vegetation types, and these threshold relationships were applied in an assessment model that links riparian condition levels to surface and subsurface water availability (Stromberg *et al.*, 2006). Few studies, however, have provided a pro-active assessment of the potential effects of changing hydrological regime on riparian or wetland conditions, yet this is critical to guide water management efforts.

Assessment of groundwater change scenarios provides an important means to explore the potential impacts of human water use on riparian biota. Birds, in particular, have been used as indicators in the assessment of ecological condition in wetland and riparian systems and are often the target of restoration and conservation efforts (Rich, 2002; Scott *et al.*, 2003; Vaughan *et al.*, 2007; Sogge *et al.*, 2008). In the Florida Everglades, Curnutt *et al.* (2000) assessed potential responses of alternative water management plans on two bird species and the wading bird guild. In Australia, Schneider and Griesser (2009) assessed avian richness among water bodies with different hydrological regimes. On the upper San Pedro floodplain, Steinitz *et al.* (2003) assessed the potential for expansion of habitat for breeding southwestern Willow Flycatchers (*Empidonax traillii extimus*), given a range of water use options. Western riparian vegetation harbours some of the highest overall avian densities in North America (Krueper *et al.*, 2003; Sogge *et al.*, 2008), and many bird species respond strongly to changes in riparian vegetation composition and structure (Hunter *et al.*, 1987; Fleishman *et al.*, 2003; van Riper *et al.*, 2008). Yet, no studies have assessed the sensitivity of a broad group of avian species within southwestern riparian systems to potential water use scenarios.

In this article, we project the influence of alternative groundwater change scenarios on the proportion of the floodplain that supports different vegetation structure types and on bird abundances on the San Pedro River. We build upon previous research that includes a Decision Support System (DSS) that contains specific water use scenarios (Yalcin and Lansey, 2004) implemented with a recent groundwater model (Pool and Dickinson, 2007), an assessment model of riparian vegetation condition as a function of groundwater depth (Stromberg *et al.*, 2006), and estimated avian density responses to hydrological regime and riparian vegetation types on the San Pedro floodplain (Brand *et al.*, 2010). While continued efforts are underway to model vegetation changes that account for ongoing response to historic channel incision (Dixon *et al.*, 2009), we used an empirically based space-for-time substitution approach that could be implemented given existing models and data. Our results provide means to explore changes in the composition of the riparian floodplain vegetation, and the sensitivity of bird guilds and species, to a range of groundwater pumping, recharge, conservation, and augmentation scenarios. The results are broadly applicable to perennial and interrupted perennial rivers of the desert Southwest that supports tall-canopied forests in wetter reaches and shorter and more mesophytic species such as saltcedar in drier reaches.

METHODS

Study area

Our study area encompassed 60 km along the San Pedro Riparian National Conservation Area (SPRNCA) managed by the Bureau of Land Management (BLM; Figure 1). The San Pedro is one of the last unimpounded rivers in the Southwest that maintains large stretches of perennial surface water. The San Pedro River flows perennially in reach 2 and from reaches 4 through reach 7 and intermittently in the remainder of the river (Figure 1). The geology underlying the perennial reaches is composed of limestone and volcanic rock supporting impervious substrate. The saturated thickness of the regional aquifer under the perennial reaches is about 300–400 m thicker than other reaches. Streamflow is controlled by geology and the amount and location of groundwater pumping and recharge. As an example, reach 1 was a perennial prior to development but regional pumping has drawn down the groundwater levels resulting in a dry channel for much of the year.

Fremont cottonwood (*P. fremontii*) and Goodding willow (*Salix gooddingii*) forests are the predominant woody vegetation type in the floodplain of wet reaches of the San Pedro. Cottonwood and willow are obligate phreatophytes supported by shallow groundwater. These mature gallery floodplain forests generally form multi-layered stands with trees to 20 ± 5 m maximum height [mean $\pm$ standard deviation (SD)] and understories of shrubs, and herbaceous growth. In the drier stretches of river, depth-to-groundwater thresholds for cottonwood/willow survivorship are largely exceeded and the main pioneer species is saltcedar. In these drier sites, saltcedar forms a dense, shrub-layer canopy with 11 ± 4 m (mean $\pm$ SD) maximum height (Lite and Stromberg, 2005). Mesquite (*Prosopis* spp.) maintains smaller patches on the floodplain; it is a later successional species that like saltcedar can use a greater proportion of its water from precipitation or shallow flood water. While extensive riparian terraces occur along the San Pedro River, we restricted our study to woody vegetation types in the floodplain zone. We defined the lateral extent of the active floodplain using topography derived from high-resolution aerial photography and airborne light detection and ranging (Stromberg *et al.*, 2006).

Current conditions and future scenarios

We based our projection of current and future scenario conditions on an assessment model that specifies groundwater thresholds needed to maintain floodplain vegetation in three condition classes (Stromberg *et al.*, 2006). We used these published estimates of condition classes to represent current conditions within the 14 reaches of our study area; reaches were defined on the basis of relatively consistent stream geomorphology and hydrology (Figure 1). Condition class 3 reaches have shallow, stable alluvial groundwater, perennial or near perennial streamflow, and floodplain vegetation dominated by cottonwood/willow forests and woodlands (Table I).
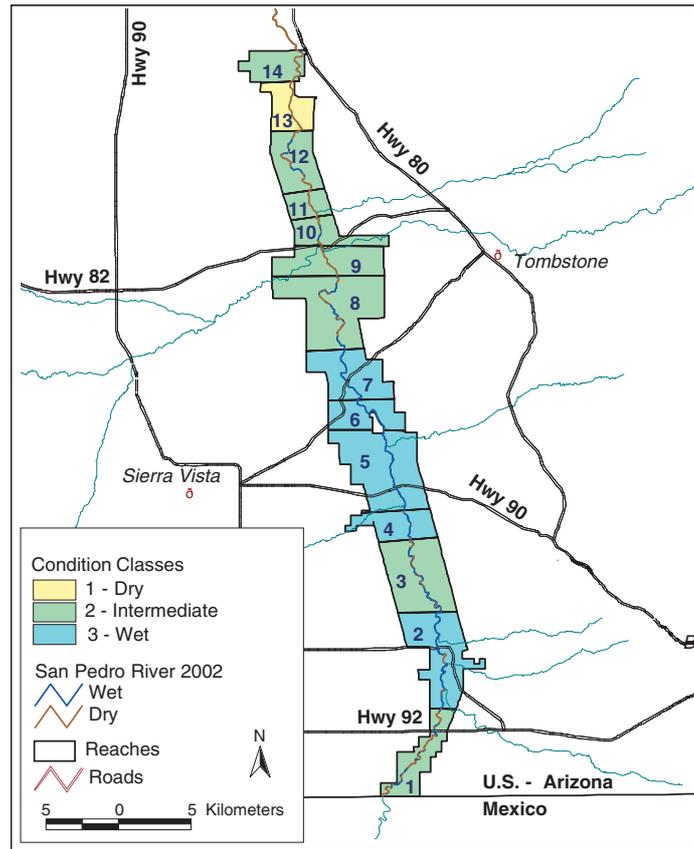
Figure 1. Map of the San Pedro National Riparian Conservation Area with condition classes for 14 reaches under current conditions (reproduced from Stromberg *et al*., 2006). Condition class 1, dry; condition class 2, intermediate; and condition class 3, wet.

Table I. Observed hydrological conditions of three riparian condition classes (reproduced from Leenhouts *et al*., 2006).

Condition class	Flow permanence (%)[a]	Dry seasonal maximum depth-to-groundwater (m)[b]	Groundwater fluctuation (m)[c]
1—Dry	<60 (highly intermittent)	>3·5 (deep)	>1 (large)
2—Intermediate	60–95 (intermittent)	2·5–3·5 (moderately shallow)	0·5–1 (moderate)
3—Wet	>95 (perennial or nearly perennial)	<2·5 (shallow)	<0·5 (small, stable)

[a] Percentage of year with surface water present; 100% = surface flow all year.
[b] Dry-season mean averaged across the floodplain.
[c] Difference between monthly maximum and minimum averaged across the floodplain.

Condition class 2 reaches have moderately shallow groundwater with moderate inter-annual fluctuation, intermittent streamflow, and vegetation characterized by cottonwood/willow but with higher proportions of saltcedar. Condition class 1 reaches have increased depth and seasonal fluctuation in groundwater, highly intermittent streamflow, and floodplain vegetation dominated by saltcedar shrublands with limited upper canopy cover.

We considered nine future scenarios linked with specific policy options for groundwater pumping or recharge (Table II and Figure 2). We based policy options on input from the Upper San Pedro Partnership (USPP; http://www.usppartnership.com), a consortium of 21 Non-Governmental Organizations, a private water company, and local, state, and Federal agencies (Richter *et al*., 2009). Options for pumping or recharge at specific locations within the regional aquifer were implemented

within a web-based DSS (Yalcin and Lansey, 2004). The DSS used a recent three-dimensional groundwater flow model (Pool and Dickinson, 2007) to develop unit response functions to estimate the effects of pumping or recharge at selected locations on the groundwater head for other locations of interest to decision makers and natural resource managers. The hydraulic conductivity of the streambed was adjusted in the numerical modelling to calibrate the flow rate between stream and aquifer using a lower conductivity for impervious streambed below perennial stream reaches. We evaluated linearity of the groundwater level response by comparing groundwater model forecasts from the full model with estimates using the response functions contained within the DSS. We found that the linear model provided good estimates

Table II. Description of DSS scenario assumptions and resulting hydrological change from current conditions[a] depicted in Figure 2.

Scenario	Municipal pumping	Agricultural pumping	Recharge	Other changes (conservation, urban runoff collection, CAP importation)	Resulting conditions
S1	Substantial increase in population growth of SV and unincorporated areas 1 and 2; additional pumping near reach 8 due to Tombstone and Whetstone growth	Unchanged from S0	Inactive SV wastewater recharge	Urban runoff recharge at upstream locations (recharge sites 1, 3, and 5)	0·5 m decrease in groundwater levels across all reaches
S2	Substantial increase in population growth of SV and unincorporated areas 1 and 2; additional pumping near reach 8 due to Tombstone and Whetstone growth	Unchanged from S0	Inactive SV wastewater recharge	None	1·0 m decrease in groundwater levels across all reaches
S3	Small decrease in population growth of SV and large decrease in all the three unincorporated areas	Unchanged from S0	Increased recharge at sites 7 and 8	Surplus CAP water used at recharge sites 1, 3, 4, and 5; collect and recharge SV urban runoff	0·5 m increase in groundwater levels across all reaches
S4	Very large increase in population growth in the unincorporated area 3	Double irrigated acreage near Palominas	None	None	Groundwater declines in southern SPRNCA
S5	Very large increase in population growth rates in Huachuca City, SV, and unincorporated areas 1 and 2. Increased pumping near reaches 8 and 9 due to Tombstone and Whetstone growth	Unchanged from S0	None	Additional basin recharge at two locations provided by CAP importation (recharge sites 1 and 3)	Groundwater declines in the lower Babocomari and northern SPRNCA
S6	Large decreases in population growth rates of Bisbee and the three unincorporated areas	Unchanged from S0	Increased recharge at sites 7 and 8	Import CAP water to reduce SV pumping; surplus CAP water used at recharge sites 1, 3, 4 and 5; collect and recharge SV urban runoff	Large increases in groundwater levels due to recharge and conservation efforts in SV and Bisbee
S7	Very large increases in population growth rates of Huachuca City, SV, and unincorporated areas 2 and 3	Double irrigated acreage near Palominas	None	None	Groundwater declines in the southern and northern portions of the SPRNCA
S8	Extremely large increase in population growth rates in SV, large increase in Huachuca City, and very large increase in the three unincorporated areas	Double irrigated acreage near Palominas	Eliminate SV wastewater recharge	None	Driest—all reaches with deep groundwater and highly intermittent flow
S9	Large decrease in population growth rate in Bisbee, and very large decrease in all three unincorporated areas	Unchanged from S0	Increased recharge at sites 7 and 8	Import CAP water to reduce SV pumping; surplus CAP water used at recharge sites 1, 3, 4 and 5; collect and recharge SV urban runoff; adopt extreme conservation initiatives	Wettest—all reaches with shallow groundwater and perennial flow

SV, Sierra Vista; SPRNCA, San Pedro Riparian National Conservation Area; CAP, Central Arizona Project. Pumping and recharge locations are shown in Figure 3.
[a] Current conditions reflect closure of a large farm near Palominas in 2007.
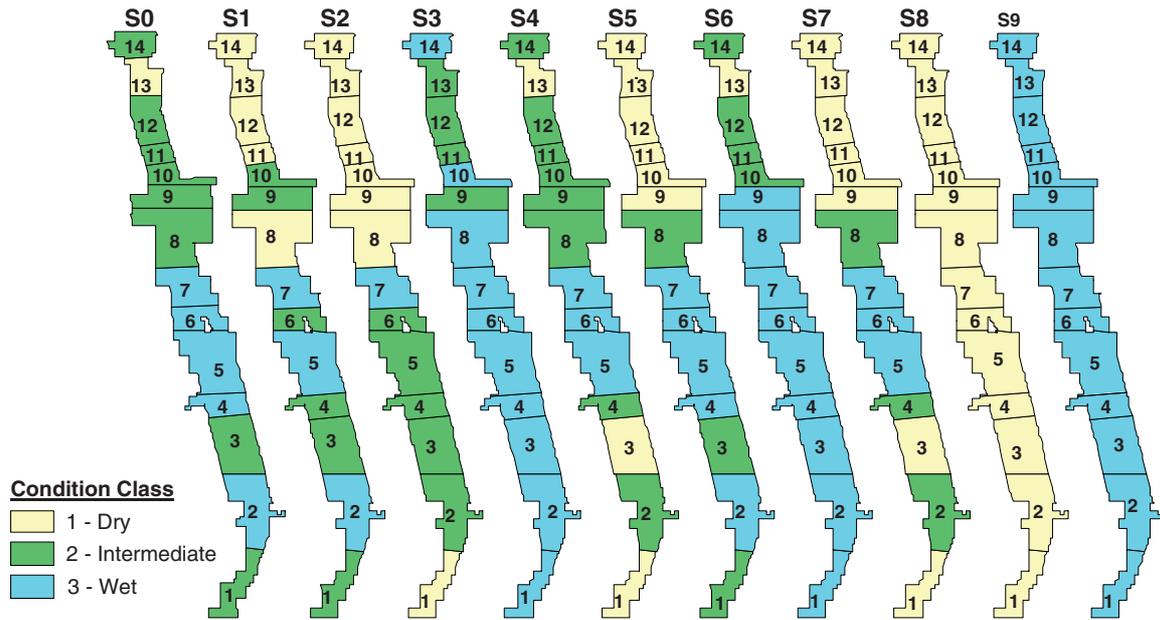[b] Whetstone is located at the intersection of Hwys 82 and 90.

Figure 2. Current conditions and nine groundwater change scenarios applied to 14 reaches on the San Pedro River. Condition class 1, dry; condition class 2, intermediate; and condition class 3, wet. Scenarios are defined in Table II.

for the range of changes in pumping and recharge that we considered. Thus, the DSS enabled the projections of groundwater depth along the riparian corridor following user-specified pumping or recharge at one or more locations.

We considered scenarios that ranged from realistic to extreme using a variety of adjustments in the DSS (Table II). We varied municipal pumping and population growth rates in four incorporated areas and three unincorporated areas (Figure 3). We also varied the locations and quantity of pumping for irrigated agriculture. Recharge options were assessed that included large-scale rainwater harvesting in Sierra Vista and water importation via an extension of the Central Arizona Project. We also considered the influence recharge sites including six located on the river and two located far from the river that would eventually impact groundwater levels on the San Pedro (recharge sites 1–8 on Figure 3). The two extreme scenarios (S8 and S9) required large variation in DSS settings compared with current conditions (e.g. large increase or decrease in population growth rates), with all other scenarios lying between these two extremes. We constructed scenarios S1, S2, and S3 to illustrate the effects of uniform changes across reaches in groundwater levels from the current conditions (0·5 and 1·0 m declines and 0·5 m groundwater increase, respectively), whereas scenarios S4 through S7 illustrate the effects of spatially variable changes in groundwater depths. We assumed that all combinations of pumping or recharge options within each scenario were activated in year 2008 and carried out simulations to 2050.

Vegetation areas and transitions

We represented current vegetation areas using a geographic information system vegetation coverage based on manual interpretation of aerial photography accurate to 2–5 m resolution (U.S. Army Topographic Engineering Center, 2001). Vegetation was initially classified using the National Vegetation Classification System then collapsed into broad categories that included cottonwood/willow, saltcedar, and mesquite that comprised 526, 159, and 114 ha on the floodplain, respectively (total of 798 ha). These three woody vegetation types are the most abundant types in the floodplain.

The current relative proportions of these three floodplain vegetation types varied substantially by condition class. In reaches classified within the 'dry' condition class (those with deep groundwater and highly intermittent flow), cottonwood/willow comprised $10 \pm 6\%$, saltcedar $72 \pm 5\%$, and mesquite $18 \pm 5\%$ of the floodplain area [mean $\pm$ standard error (SE)]. In reaches classified within the 'intermediate' condition class, cottonwood/willow increased to $51 \pm 12\%$, whereas saltcedar decreased to $23 \pm 10\%$ with mesquite comprising $25 \pm 6\%$ of the floodplain area. In 'wet' reaches (those with shallow groundwater and perennial flow), 86 ± 6 and $14 \pm 6\%$ of the floodplain were covered by cottonwood/willow and mesquite, respectively; no perennial reaches contained stands of saltcedar. When considering the two pioneer vegetation types on the floodplain for spring migrant birds (685 total ha), relative proportions of cottonwood/willow versus saltcedar changed by condition class, respectively, with 11 ± 6 versus $89 \pm 6\%$ in dry reaches, 67 ± 13 versus $33 \pm 13\%$ in intermediate reaches, and 100 versus 0% in wet reaches.

Changes in groundwater levels derived from the scenarios were in turn used to project changes in riparian habitat condition class from biohydrological relationships (Lite and Stromberg, 2005; Leenhouts *et al.*, 2006; Stromberg *et al.*, 2006; Table I). We used the relative
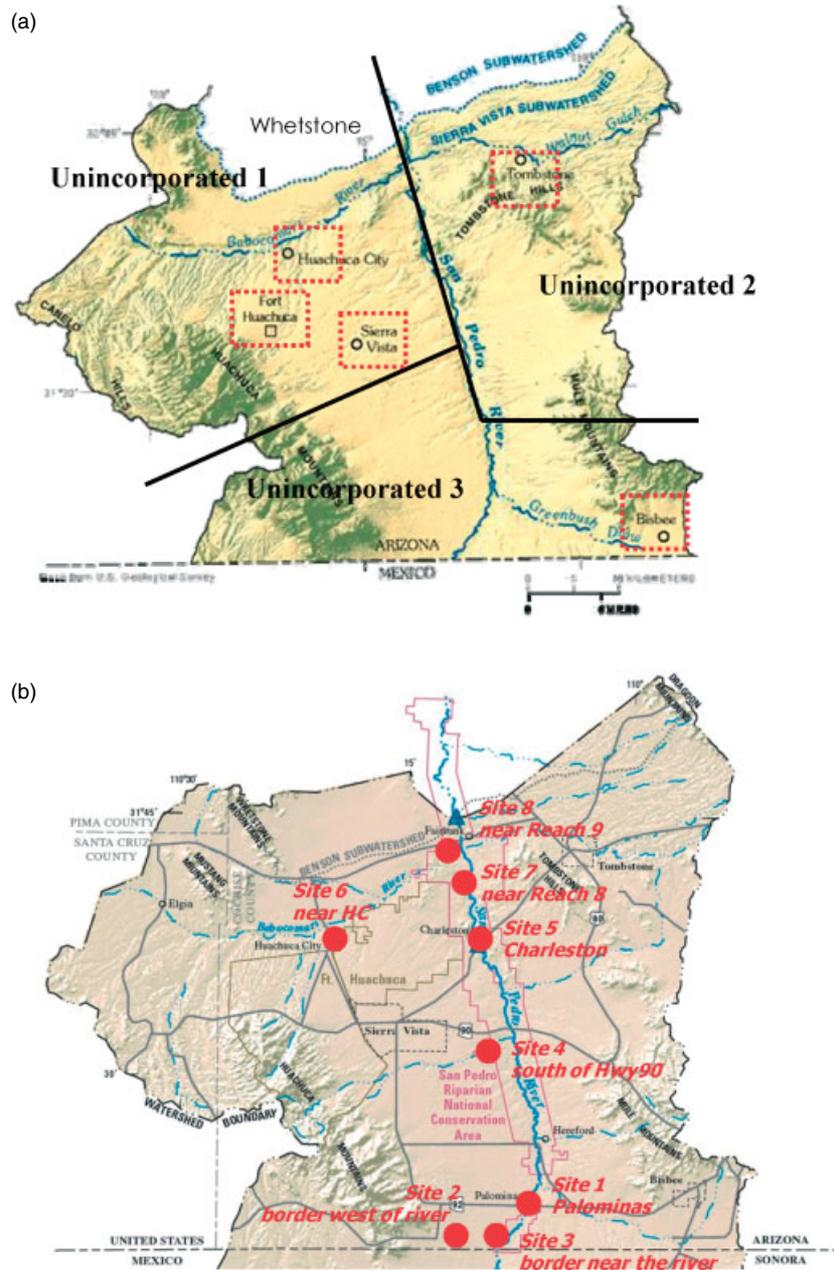
Figure 3. Location of (a) cities and unincorporated areas in the Sierra Vista subwatershed of the San Pedro and (b) eight potential recharge sites.

proportion of floodplain vegetation types within each condition class to project vegetation transitions across scenarios using space-for-time substitution (Michener, 1997; Fukami and Wardle, 2005) under the assumption that stands would replace each other based on mortality followed by recruitment (Figure 4). We estimated the mean and SE of the proportions of cottonwood, saltcedar, and mesquite on the floodplain by reach. Proportions across reaches provided the replication to reflect the average and variability about the vegetation attributes within hydrological classes. Within current conditions, there were 5, 8, and 1 reaches of condition classes 3 (dry), 2 (intermediate), and 1 (wet), respectively (Figure 1). To estimate variability for condition class 1, we subdivided this reach into five equal length sub-reaches; while this may underestimate variation for this condition class, we felt it was

most important to use data from the upper San Pedro to avoid bias in the estimation of mean proportions. We then used the mean and SE of the vegetation proportions by condition class to project expected vegetation areas under different groundwater change scenarios. We assumed that the floodplain area remained constant between current and scenario conditions.

Bird density estimation

We drew breeding bird density estimates by vegetation type and hydrological regime for four breeding bird guilds and representative species from Brand *et al.* (2010) to model expected avian response to the various groundwater scenarios. In that study, distance sampling and regression analyses were used to estimate the mean and
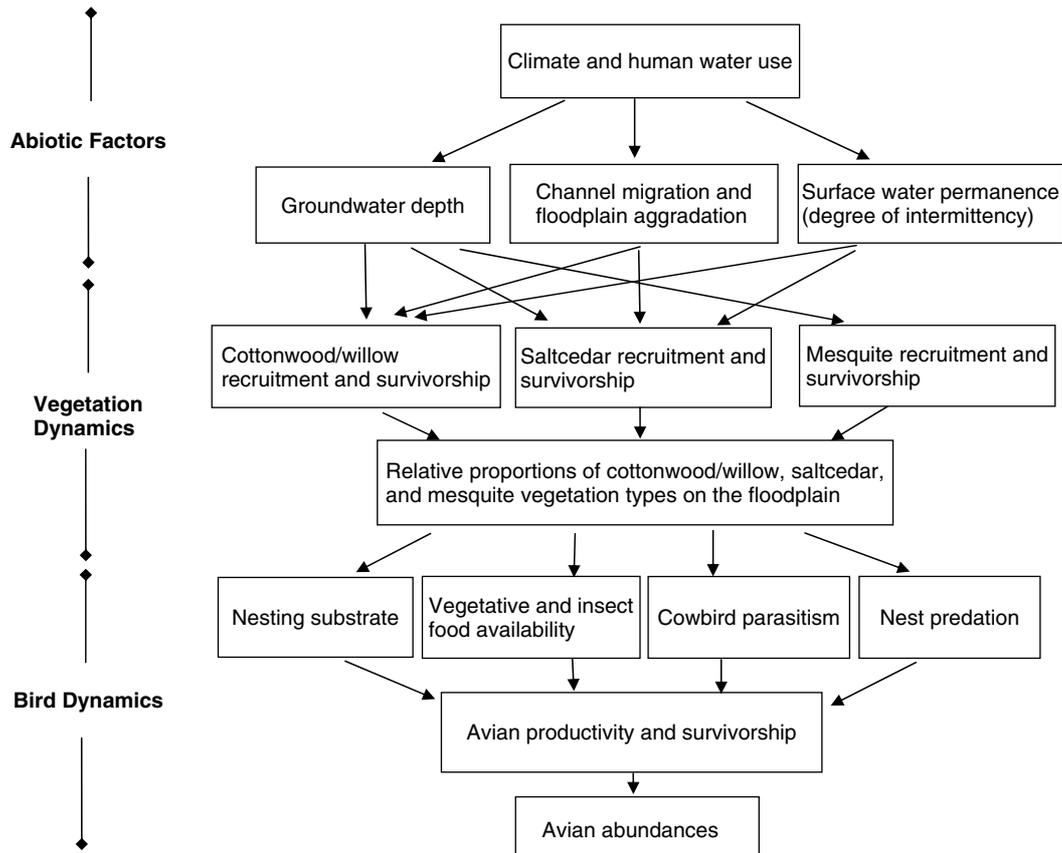
Figure 4. Conceptual diagram of the relationship between abiotic factors, vegetation dynamics, and avian dynamics on the San Pedro floodplain.

SE of densities for understory nesting, midstory nesting, canopy-nesting, and water-obligate birds sampled at 23 sites on the upper and lower San Pedro River during the 1998–2001 avian breeding seasons (15 May to 32 July). These estimates were computed for seven vegetation/hydrological classes relevant for this study: cottonwood/willow in intermediate and wet reaches (condition classes 2 and 3), saltcedar in dry and intermediate reaches (condition classes 1 and 2), and mesquite in all three hydrological conditions. To capture avian response to changes in vegetation structure, Brand *et al*. (2010) classified breeding birds based on average nesting height as understory nesters (0–2 m), midstory nesters (2–4 m), and canopy nesters (>4·5 m) based on observed nesting heights and regional information from species accounts in the Birds of North America (Poole, 2005). To capture expected changes in surface water intermittency, the water-obligate bird category included swimming, wading, shorebirds, and songbirds dependent on surface water in the Southwest (Poole, 2005; Brand *et al*., 2010).

Because of the importance of the San Pedro as a migratory corridor, we analysed a supplemental dataset to estimate densities for spring migrant birds (Cerasale, 2004). For that study, a single, experienced observer sampled point transects within 3 h of sunrise during spring migration season (7 April to 20 May 2003) on the SPRNCA. Forty point transects from eight sites, each sampled six to seven times, were classified as cottonwood/willow or saltcedar dominant vegetation (no spring migration data were available for mesquite). We used program Distance 5·0 (Thomas *et al*., 2006) to estimate detection probabilities for each bird species or guild within each vegetation type. We included species that only migrate through the San Pedro and those that migrate and also breed during the summer months, but excluded resident species based on Poole (2005) and personal observations (L. A. B. and D. J. C). We considered a set of detection functions that included two factor covariates: vegetation type and detection rank (high, medium, or low ease of detection), and selected the best detection function for each species in each vegetation type using Akaike's Information Criterion (AIC) model selection (Burnham and Anderson, 2002). We accounted for differing survey effort by incorporating a multiplier in the analysis (Buckland *et al*., 2001) and used detection probabilities combined with grouped species' mean counts to estimate density and the SE of density for each vegetation type.

Bird abundance by current and scenario conditions

We used vegetation areas multiplied by avian densities by vegetation type as the basis for estimating bird abundances ($\hat{N}$) for current and future scenario conditions. We used bird density estimates for five bird guilds and the most common species per guild. We assumed that avian densities appropriately reflected avian recruitment and survivorship (Bock and Jones, 2004; Figure 4). We
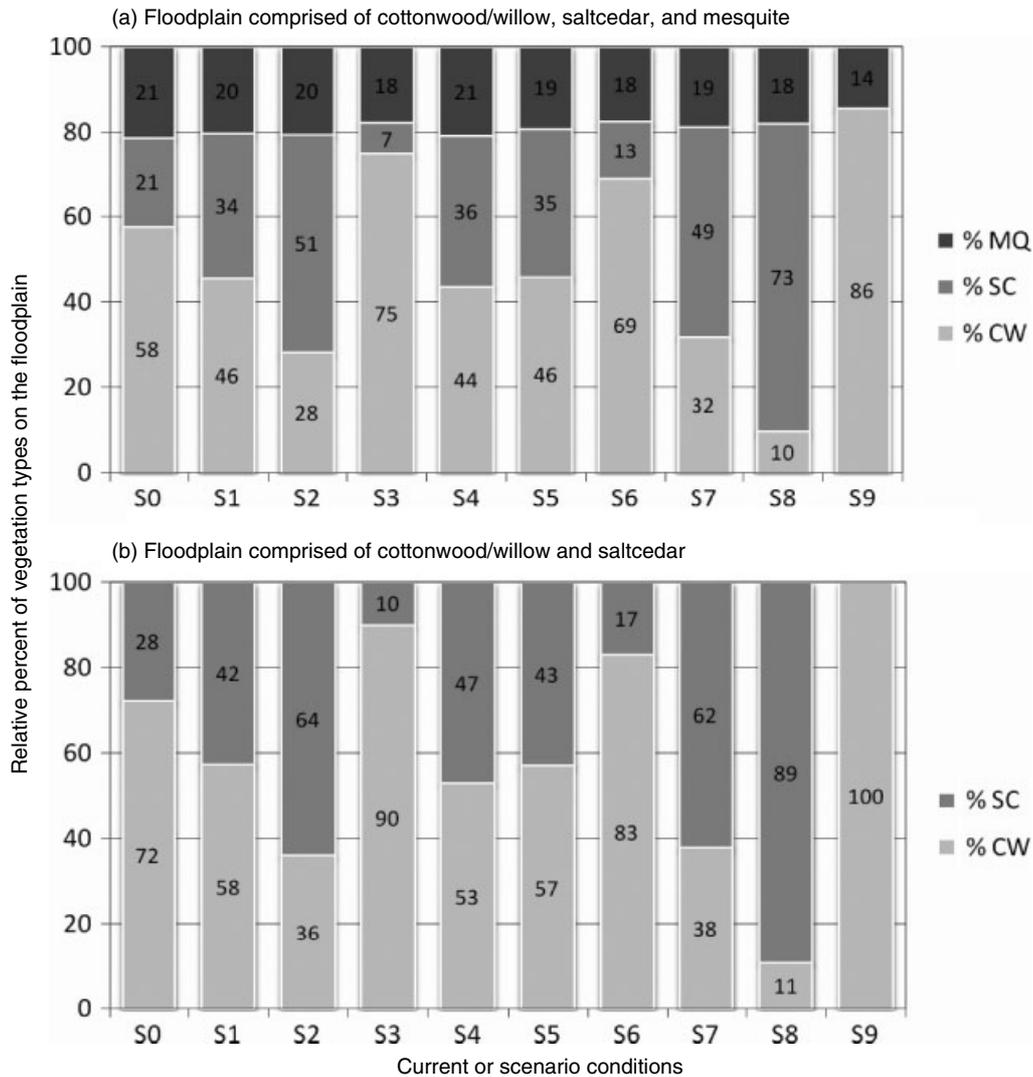
Figure 5. Proportion of patch types comprised (a) cottonwood/willow (CW), saltcedar (SC), and mesquite (MQ) and (b) cottonwood/willow and saltcedar on the SPRNCA floodplain for current conditions and nine groundwater change scenarios.

defined the reach area (A_r) equal to the sum of cottonwood, saltcedar, and mesquite areas within the floodplain. We modelled the impact of a groundwater change scenario (s) through changes in condition classes (c) by reach which then altered the proportions of each vegetation type. Estimates for the vegetation type proportions ($\hat{P}$) for different condition classes were obtained from available reach data sorted by condition class then averaged over reaches. We defined bird abundance (number of birds) by scenario as:

$$\hat{N}_s = \sum_{r=1}^{r=14} A_r \sum_{v=1}^{v=3} \hat{P}_{vc(r,s)} \hat{D}_{vc(r,s)} \quad (1)$$

where r = reach (1–14), v = vegetation type (cottonwood, saltcedar, or mesquite), and c = condition class (1–3, defined in terms of reach and scenario).

For current conditions, we assumed that vegetation areas were known with negligible error and thus the SE estimates of bird abundance projection stemmed from bird density errors only. When estimating the SE of abundance for scenario conditions (N_s), however, we

used the delta method (Powell, 2007) to incorporate estimated errors from both vegetation type proportions and bird densities. We set $\alpha = 0\cdot1$ to minimize the probability of a type II error and interpreted meaningful differences in avian abundances by scenario in terms of non-overlapping 90% confidence intervals. Because we only had data for spring migrant birds in cottonwood and saltcedar (not mesquite), we altered the above methods accordingly for these two vegetation types for spring migrants.

RESULTS

Groundwater decline scenarios

Our models indicate that groundwater decline scenarios would cause broad shifts in the vegetation and avian communities across the study area (Figures 5–7). The proportion of cottonwood/willow forest declined from 58% in current conditions to 44–46% of the floodplain area for the milder draw-down scenarios (scenarios 5, 1, and 4), and to 32–10% of the floodplain for the more

extreme draw-down scenarios (scenarios 7, 2, and 8). Along with these changes in vegetation composition and structure, the canopy-nesting guild declined significantly (17–48%) across all draw-down scenarios. All four canopy-nesting species showed similar patterns, with significant declines in abundance for Yellow Warbler, Lesser Goldfinch, and Summer Tanager in the more extreme draw-down scenarios.

The proportion of saltcedar increased from 21% in current conditions to 34–36% of the floodplain area for the milder draw-down scenarios (scenarios 5, 1, and 4) and to 49–73% of the floodplain for the more extreme draw-down scenarios (scenarios 7, 2, and 8). The midstory nesting guild increased significantly (19–31%) with the more extreme groundwater declines. All four midstory nesting species showed similar patterns but with significant increases in abundance only for Lucy's Warbler across all scenarios. As a group, the understory nesting guild had no significant changes for any of the scenarios we examined, but individual species responded strongly. The two non-water obligate understory nesting birds, Bell's Vireo and Yellow-breasted Chat, increased in abundance with groundwater draw-down as saltcedar became the more dominant floodplain vegetation type. Both understory nesting species that were also water-obligates, Common Yellowthroat and Song Sparrow, declined with groundwater draw-down. As a group, water-obligate birds declined across all draw-down scenarios, with a significant reduction in abundance of 72% in the most extreme scenario. Spring migrants declined in all draw-down scenarios with significant declines in the three more extreme scenarios. Individual spring migrants, Yellow Warbler and Wilson's Warbler, showed similar patterns (Figures 6 and 7).

Groundwater recharge scenarios

The groundwater recharge scenarios were generally more similar to current conditions and had smaller impacts on both vegetation proportions and bird abundances compared with draw-down scenarios (Figures 5–7). Relative proportions of cottonwood/willow increased from 58% in current conditions to 69, 75, and 86% of the floodplain when considering the three vegetation types for scenarios 6, 3, and 9, respectively. While bird abundance patterns were generally the converse of those observed for groundwater draw-down scenarios, models project no significant bird abundance changes for the two mild recharge scenarios. However, for restoration of all reaches to perennial flow conditions (scenario 9), the canopy-nesting bird guild significantly increased and Brown-headed Cowbird abundance significantly decreased in abundance by 46%.

DISCUSSION

The first step in achieving ecologically sustainable water management is to estimate key aspects of river hydrology needed to sustain desired biota (Richter *et al.*, 2003). Our study contributes to this goal by assessing linked changes
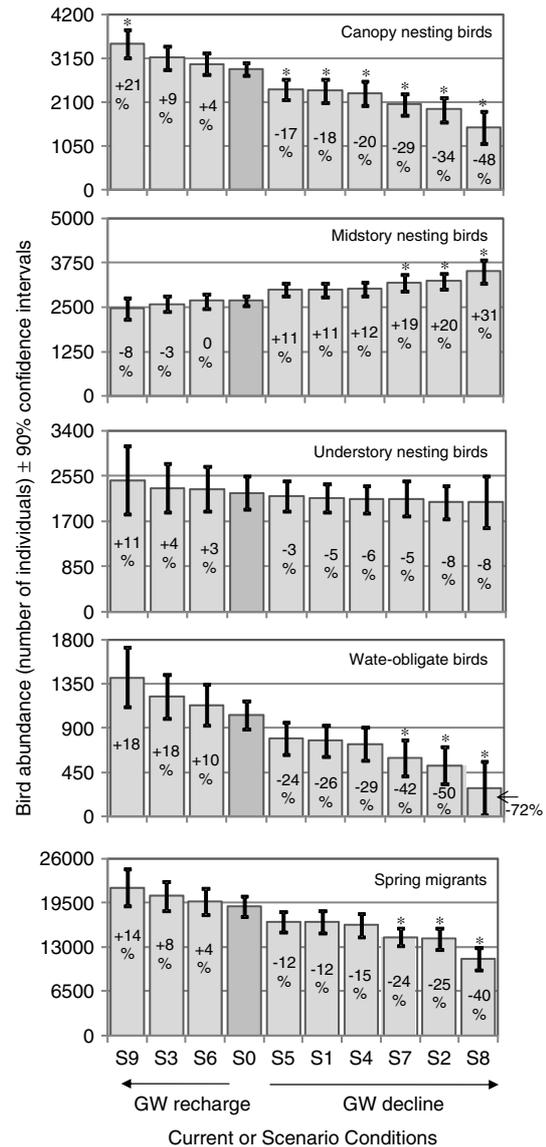

Figure 6. Projected bird abundances by avian guild for current conditions and groundwater change scenarios applied to the San Pedro River. Each scenario shows the expected percentage change in bird abundance from current conditions. Scenarios are in the order from wettest (left) to driest (right). An '*' indicates significant differences between scenario and current conditions based on non-overlapping 90% confidence intervals.

in the composition and structure of woody vegetation types and avian populations to groundwater change on a river of the desert Southwest. Many of the avian changes are a response to the shift in vegetation structure that occurs with groundwater decline, as tall, broadleaf forests (cottonwood and willow) give way to shorter and shrubbier species (e.g. saltcedar and mesquite) that are less reliant on permanent groundwater sources. Our projections of altered vegetation and avian abundance by scenario highlight the importance of managing land and water use throughout the watershed to sustain desired streamflow regimes.

Not all avian taxa responded similarly to changes in groundwater. Canopy-nesting birds maintain highest density in tall-tree vegetation such as cottonwood/willow that are sustained by shallow groundwater (Hunter *et al.*,
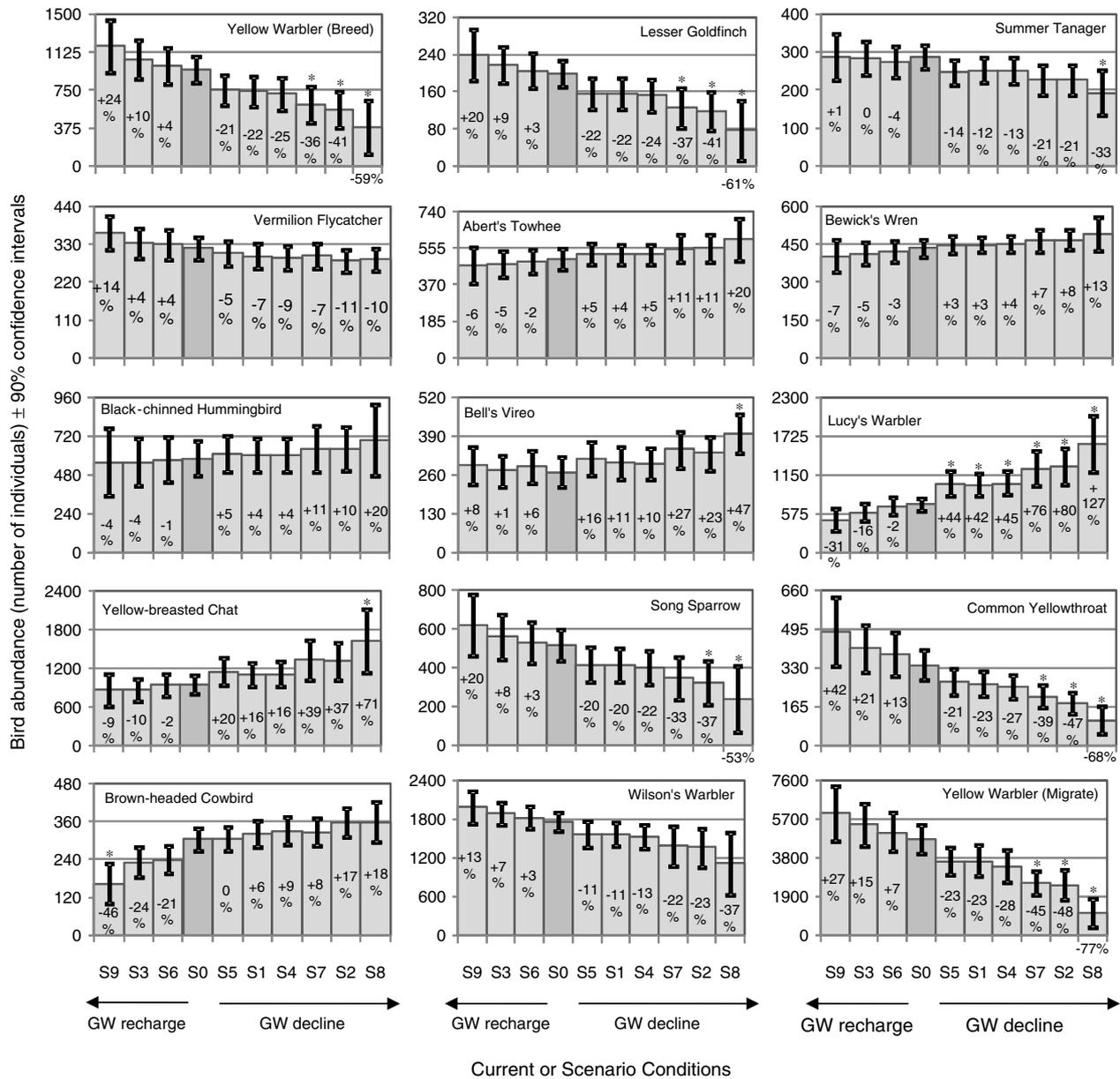
Figure 7. Projected bird abundances for 15 species for current conditions and groundwater change scenarios applied to the San Pedro River. Each scenario shows the expected percentage change in bird abundance from the current conditions. Scenarios are order from wettest (left) to driest (right). An '*' indicates significant differences between scenario and current conditions based on non-overlapping 90% confidence intervals.

1987; Scott *et al*., 2003). While species that are able to nest in the lower canopy (such as Vermilion Flycatcher and Summer Tanager) may be less impacted, others that nest in the uppermost canopy layer, or require large trunk or branch bearths such as cavity nesters or raptors, are likely most sensitive to loss of mature cottonwood and willow trees (Hunter *et al*., 1987; Brand *et al*., 2010). Overall, canopy-nesting birds are largely dependent on mature cottonwood/willow and declined with all groundwater draw-down scenarios that we considered, which supports use of this guild as one indicator of riparian condition in western riparian systems (Rich, 2002). On the contrary, our models projected that midstory nesting and some understory nesting species would increase with groundwater decline and corresponding increases in saltcedar coverage. Other studies have also documented

increasing densities of shrub-nesting birds with increasing saltcedar, such as Yellow-breasted Chat and Abert's Towhee (Brown and Trosset, 1989; Ellis, 1995). Still other shrub-nesting species that nest readily in terrace vegetation types, such as Lucy's Warblers in mesquite (Brand *et al*., 2010), may be less sensitive to changes occurring in the floodplain.

Avian densities generally provide a strong indication of habitat quality, yet disconnects between density and demographic parameters can occur and may be more likely in exotic vegetation types that are evolutionarily novel (Bock and Jones, 2004). Birds nesting in saltcedar associated with groundwater declines may be particularly vulnerable, although avian demographic information is limited in southwestern riparian systems (Sogge *et al*., 2008). Parasitism by brown-headed cowbirds is

an important mechanism that reduces productivity of host species in southwestern riparian systems including Bell's Vireo on the San Pedro (Chace *et al.*, 2005; Brand *et al.*, 2010). Our results suggest that parasitism rates may be associated with flow regime because Brown-headed Cowbird densities increased with groundwater decline, and decreased significantly by 46% on the San Pedro floodplain with restoration of perennial conditions in all reaches. Thus, restoration of hydrological conditions may serve as a tool to reduce parasitism risk and enhance avian populations in southwestern riparian systems.

As one of the last unimpounded rivers in the region that maintains significant stretches of perennial surface water, the San Pedro River provides insights into the groundwater needed to maintain riverine habitat for water-obligate birds. The general pattern of declining abundance of water-obligate birds with groundwater draw-down scenarios is likely due to the strong linkages that exist between groundwater and surface water on many rivers including the San Pedro (Alley *et al.*, 2002; Lite and Stromberg, 2005). Many of the water-obligate birds also are responding to the riparian vegetation (Brand *et al.*, 2010). For example, Song Sparrows on the San Pedro had highest densities in cottonwood regardless of hydrological regime, although Common Yellowthroats had significantly higher densities in cottonwood with perennial versus intermittent flow. Other, rarer species that responded strongly to both vegetation and surface water availability included Yellow-billed Cuckoo, Great-blue Heron, Mallard, Killdeer, and Black Phoebe (Brand *et al.*, 2008). Some of these species have been locally extirpated from dewatered rivers in the region; for example, Great-blue Herons no longer occur on the Lower Rio Grande (Wauer, 1977). Similarly, our results indicate that with the more extreme draw-down scenario on the San Pedro, densities of some water-obligate birds could be locally extirpated.

Lowland riparian areas in the Southwest constitute less than 1% of the landscape but provide critical stopover resources for many spring migrant bird species (Skagen *et al.*, 1998; Kelly and Hutto, 2005). In their study of spring migration patterns across southwestern North America, Skagen *et al.* (2005) found riparian forest cover was critical for many spring migrants obligate to this vegetation type. Our results further highlight the importance of adequate groundwater, and a high proportion of tall, broadleaf forests to maintain high abundances of spring migrant birds on the San Pedro. We found extremely high spring migrant densities on the San Pedro similar to those observed by Skagen *et al.* (1998), illustrating the importance of this habitat to a substantial number of individual birds that likely fan out to breeding grounds over the western USA (Skagen *et al.*, 2005). Thus, declining groundwater, and subsequent reduction in stopover resources for spring migrants that funnel through the San Pedro riparian corridor, could ultimately contribute to future population declines in breeding birds at a much broader scale (Ohmart, 1994; Moore *et al.*, 1995).

There are a number of inherent limitations in the modelling approach that we used. As is common with space-for-time substitution, we used existing spatial variance within condition classes as a surrogate for the temporal variance that occurs over a hydrological change scenario (Fukami and Wardle, 2005). In addition, we assumed that the characteristics that we see today are likely to hold in the future. Although the multi-age structure of cottonwood/willow stands would likely be maintained over the next half-century on the San Pedro, over longer time periods the relative abundance of all the pioneer trees is expected to decline as part of a long-term response to historic river entrenchment which set in motion a century of pioneer forest infill (Dixon *et al.*, 2009). Thus, our results should be interpreted in terms of the sensitivity of species and guilds to changes in groundwater, rather than to exact quantitative predictions.

Despite its limitations, space-for-time substitution is one of the most powerful techniques available to assess potential future conditions (Michener *et al.*, 1997). The problem of confounding variation can be ameliorated, in part, by basing changes on abiotic drivers (Fukami and Wardle, 2005), such as that used in this study. Attempts to develop scenarios that link physical, biological, and human components can be limited by basing scenarios on economic foundations, because of degree of uncertainty in the human endeavour can be too high to draw meaningful conclusions (Nilsson *et al.*, 2003). On the contrary, we based our scenarios on groundwater characteristics with associated policy options, and in turn, played the expected changes in hydrology through the vegetation and avian changes. We feel that this approach has merit; although it is uncertain how future land development and population growth will affect the upper San Pedro basin and other rivers in the region, our approach serves to assess the sensitivity of biotic groups to the range of possible hydrological changes and thus to rank scenarios based on their expected ecological impacts (Peterson *et al.*, 2003).

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