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RESEARCH ARTICLE

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Removing invasive giant reed reshapes desert riparian butterfly and bird communities

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Abstract

Giant reed (*Arundo donax*) is a prevalent invasive plant in desert riparian ecosystems that threatens wildlife habitat. From 2008 to 2018, under a United States–Mexico partnership, prescribed burns and herbicide applications were used to remove giant reed and promote native revegetation along the Rio Grande—Río Bravo floodplain in west Texas, USA, and Mexico. Our goal was to explore the effects of the removal efforts on butterfly and bird communities and their habitat along the United States portion of the Rio Grande—Río Bravo floodplain in Big Bend National Park, Texas. During spring and summer, 2016–2017, we surveyed butterflies, birds, and their habitat using ground-collected and remotely sensed data. Using a variety of generalized linear and *N*-mixture modeling routines and multivariate analyses, we found that the initial giant reed removal efforts removed key components of riparian habitat leading to reduced butterfly and bird communities. Within several years following management, giant reed levels remained low, while riparian habitat conditions and butterfly and bird communities largely rebounded, including many disturbance-sensitive butterfly species and riparian-associated bird species. Butterflies were most consistently associated with forb and grass cover, and birds with a remotely sensed index of greenness (the normalized difference vegetation index), several vegetation cover types, and habitat heterogeneity, habitat elements that were most common in locations that had the longest time to recover following management actions. Our results suggest that prescribed burns and herbicide applications, when used following protocols to minimize risk to wildlife, can limit the spread of giant reed in desert riparian systems and introduce habitat conditions that support diverse and abundant butterfly and bird communities.

KEYWORDS

Arundo donax, Big Bend National Park, habitat management, image texture, invasive species, NDVI, prescribed fire, remote sensing

Riparian ecosystems are dynamic habitats that support high biodiversity and provide extensive ecosystem services (Gregory et al. 1991, Allan 2004, Riis et al. 2020). These ecosystems have also been subjected to intense human use, often leading to severely degraded conditions (Nilsson and Berggren 2000, Menuz and Kettenring 2013). One associated issue, the proliferation of invasive plants, has been especially intense in riparian systems (Richardson et al. 2007, Ringold et al. 2008, Osawa et al. 2013), leading to altered water flow dynamics (Lambert et al. 2010), adverse effects on native biodiversity (Bruno et al. 2019), reduced ecosystem services (Pejchar and Mooney 2009), and substantial costs for control and management (Commission for Environmental Cooperation [CEC] 2014*a*). In response, many projects worldwide have focused on the removal of invasive plants along river corridors to recover habitat for native plants and wildlife (Cooper et al. 2003, Rood et al. 2003, González et al. 2017, Modiba et al. 2017).

One of the largest and most biologically diverse rivers in the southwestern United States and northern Mexico is the Rio Grande (known in Mexico as the Río Bravo), with a substantial portion of the river flowing through the Chihuahuan Desert ecoregion. The most abundant invasive plant along much of the lower Rio Grande is the giant reed (*Arundo donax*), a globally significant invasive grass species (Lambert et al. 2010, Briggs et al. 2021). The giant reed was originally introduced to North America in the 1820s to control ditch erosion along irrigation channels and as building material (Bell 1997) and has since spread to most major riverine systems in the western United States, including the Rio Grande (Briggs et al. 2021). Large-statured and typically forming extensive, homogenous stands, giant reed can dominate near-riverbank vegetation, altering stream flows and lowering wildlife habitat heterogeneity (Dean and Schmidt 2011, Stover et al. 2018). For example, stands of giant reed are linked with lower ant and bird diversity than nearby uninvaded sites (Osbrink et al. 2017, Bruno et al. 2019), a reduction of riparian arthropods and macroinvertebrates (Herrera and Dudley 2003, Maceda-Veiga et al. 2016, Bruno et al. 2019), alteration of habitat use by mammalian carnivores (Hardesty-Moore et al. 2020), and introduced pests (Lambert and Dudley 2014). Giant reed invasion has clear and wide-ranging effects on animal habitat conditions. The impacts of management activities that remove giant reed and the subsequent response of wildlife are less well understood.

A bi-national consortium of conservation partners began using controlled burns and herbicide applications to suppress giant reed in riparian ecosystems along the Rio Grande in 2008 and continuing through 2018, focusing efforts along the 390-km continuous protected reach within Big Bend National Park (BIBE) and the Rio Grande Wild and Scenic River in the United States and the Santa Elena Canyon, Ocampo, and Maderas del Carmen protected areas in Mexico (CEC 2014*a*). The proposed vision for floodplain habitat included "desired future conditions," defined as a "diverse, patchy and discontinuous riparian plant community, where no specific non-native species is dominant" (CEC 2014*a*:6). Desired future conditions for wildlife were not rigidly defined but focused on maintaining the full complement of native wildlife species historically dependent on a diverse and dynamic mosaic of floodplain habitats (CEC 2014*b*). The sustained giant reed removal efforts have successfully reduced its abundance, with targeted burns initially removing most vegetation, and follow-up herbicide application controlling giant reed as other vegetation recovers (Briggs et al. 2021).

Our goal was to explore the effects of the giant reed removal efforts on butterfly and bird communities and their habitats during the initial 1 to 8 years after a prescribed burn. We focused our study on butterflies and birds because both taxa are abundant and diverse in the Rio Grande floodplain of BIBE (Wauer 1996, 2002) and are responsive to habitat change in riparian ecosystems (Rich 2002, Riparian Habitat Joint Venture 2004, Nelson 2007). Therefore, they are appropriate wildlife indicators of habitat recovery following management (Nelson 2007, Larsen et al. 2010, Dybala et al. 2018). To accomplish our goal, we used a space-for-time substitution sampling design where we characterized responses to giant reed removal by comparing locations throughout the floodplain that varied in their time since the last prescribed burn. As indicated above, following burns there were targeted herbicide applications to reduce the growth of giant reed. Prescribed burns, however, were the dominant removal method employed throughout BIBE, which is thus our management type of interest for this study. The management groups of our study included those with different times since burns (occurring within a 1–3, or a 4–8-year range) and unburned sites both with and without giant reed stands. Our study was thus designed to quantify the immediate effects of giant reed removal, and then the subsequent recovery of butterfly and bird communities and their habitat.

We had 2 objectives to support our goal. First, we quantified differences in habitat characteristics, butterfly and bird species compositions, and individual species abundance patterns in burned and unburned locations. We expected an initial reduction in habitat features and vegetation cover followed by partial recovery of non-reed vegetation and reduced giant reed abundance following prescribed burns, which has previously been described by Briggs et al. (2021) in the BIBE system. Further, we expected butterflies to respond rapidly following burns because early successional herbaceous plants should provide ample resource availability (Fiedler et al. 2012, Henderson et al. 2018). We also expected that birds would be slower to respond because woody vegetation, an important component of riparian bird habitat, would take at least several years to become established in burned areas (Kus 1998, Golet et al. 2008, Valente et al. 2019, Hall et al. 2020). For our second objective, we modeled associations between habitat characteristics and the abundance of butterfly and bird species that responded to the management efforts. We generally expected that butterfly species abundance would be positively associated with open areas within the floodplains and an abundance of herbaceous plants (Nelson 2007), and bird species abundance would be positively associated with vegetation greenness and increased levels of habitat heterogeneity (Riparian Habitat Joint Venture 2004, Mcfarland et al. 2012).

STUDY AREA

Big Bend National Park is situated in west Texas, located within the Chihuahuan Desert Ecoregion (Figure 1). The national park is approximately 3,200 km^2 in area and is characterized by Chihuahuan Desert flora and fauna in the lower elevation uplands, whereas the montane ecosystems are sky islands, which are isolated montane scrub and forests with higher precipitation, cooler temperatures, and distinctive flora and fauna from the surrounding desert (McCormack et al. 2009). The Rio Grande, which sits approximately 600 m above sea level throughout BIBE, marks the western, southern, and eastern boundaries of the national park. Its floodplain is diverse, containing scoured riverbed, gallery riparian forest, near-channel mesic shrubby vegetation, and xeric upper-floodplain scrub-shrub habitats, interspersed with rocky and cliff-dominated landscapes (Weber and Weber 2017). The dominant vegetation in the floodplain includes honey mesquite (*Prosopis glandulosa*), willows (*Salix* spp.), and seepwillow (*Baccharis salicifolia*), with many other plant taxa distributed throughout (Table 1). In addition to giant reed, common invasive plants in the floodplain include tamarisk (*Tamarix* spp.) and Bermuda grass (*Cynodon dactylon*).

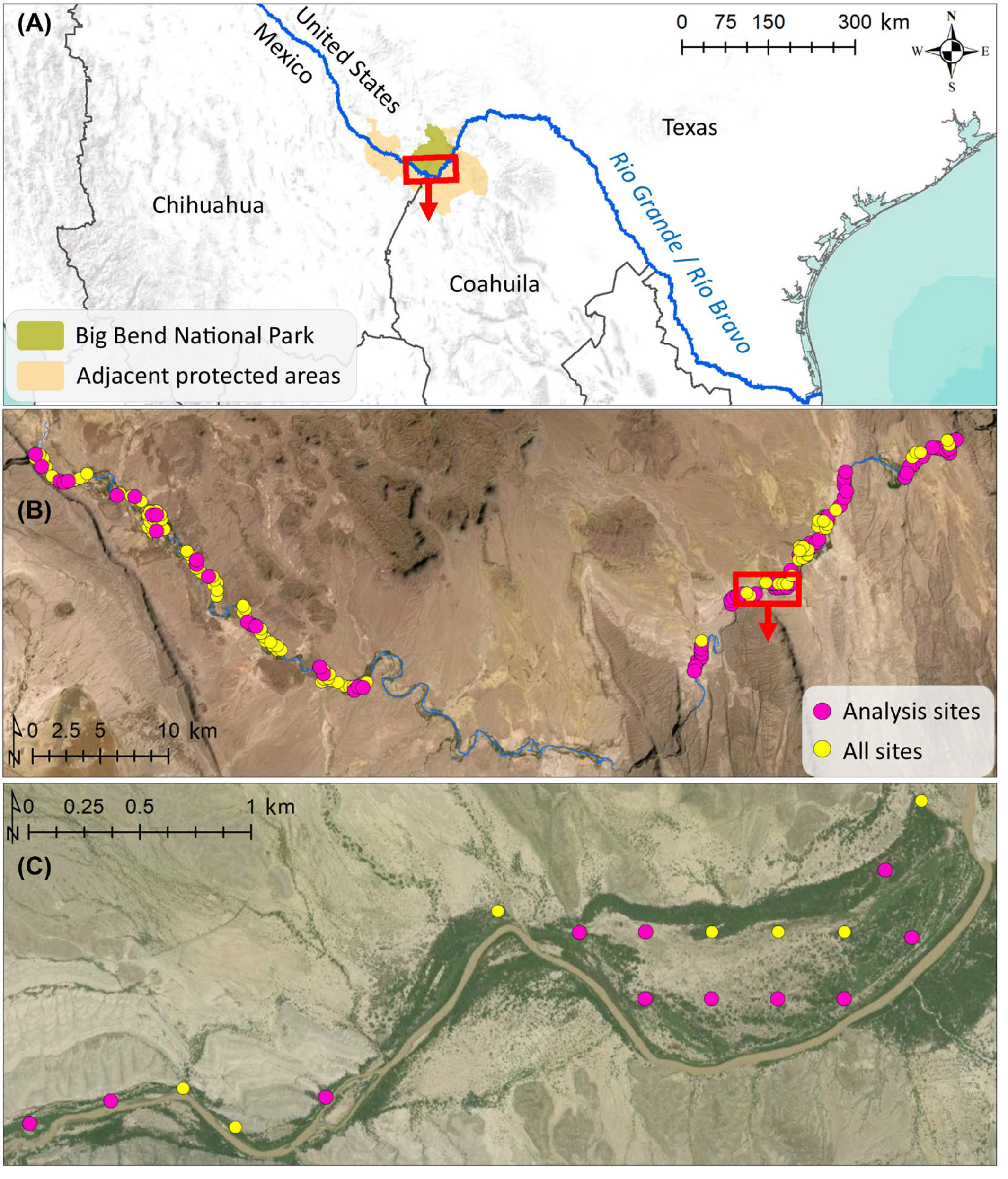

FIGURE 1 The study area within Big Bend National Park, Texas, USA, May to July 2016 and 2017, depicting A) the regional setting; B) 167 survey locations, including 73 (pink) sites used in analyses of management group differences and habitat associations of bird and butterfly species, and additional sites (yellow) included for estimating bird species abundance; and C) a typical floodplain reach with survey locations spaced 300 m apart.

The climate of BIBE includes hot summers (June–August) with monsoon rains (May–September), and cool to cold and dry late fall and winters (November–March; Weber and Weber 2017). The 30-year average for precipitation and temperature from May through July, when we completed fieldwork, for Brewster County where BIBE is situated was 32.53 mm and 27.11°C. The average precipitation and temperature for May through July in 2016 and 2017, which is the time of our study, were 34.15 mm and 27.26°C and 35.12 and 27.03°C, respectively

TABLE 1 Vegetation type classification within the Rio Grande floodplain in Big Bend National Park, Texas, USA, May to July 2016 and 2017, used to quantify vegetation cover at survey sites.

Vegetation class[a]	Description	Representative plant taxa[b]
Giant reed	Dense vegetation dominated by giant reed. Classification did not distinguish giant reed from common reed (*Phragmites australis*), a rare species in the study landscape.	Strongly dominated by giant reed; common reed rare (<1%)
Mesic tree or shrub	Dominated by species typical of mesic, occasionally inundated riparian areas. Excluded tall, closed gallery forest (bosques).	Willow spp., seepwillow, mesquite spp., tamarisk spp., tree tobacco (*Nicotiana glauca*), cottonwood (*Populus* spp.), giant reed
Xeric tree or shrub	Dominated by species typical of more xeric, less frequently inundated floodplain. Included large honey mesquite stands (bosques) and more open mixed tree and shrub stands.	Mesquite spp., acacia (*Acacia* spp.), retama (*Parkinsonia aculeata*), tree tobacco, tamarisk spp., guayacan (*Guaiacum angustifolium*), desert willow (*Chilopsis linearis*), creosote bush (*Larrea tridentata*)
Herbaceous (forb or grass)	Open areas dominated by a large number of herbaceous wildflower and forb species and native and non-native grasses. Excluded giant reed and common reed. Bermuda grass (*Cynodon dactylon*) was the primary non-native, mat-forming grass.	Nightshade (*Solanum* spp.), tansy aster (*Machaeranthera* spp.), sunflower (*Helianthus* spp.), trailing allionia (*Allionia incarnata*), globe-mallow (*Sphaeralcea* spp.), spiny aster (*Chloracantha spinosa*), Bermuda grass, Johnson grass (*Sorghum halepense*)

[a]These classes were generated from an analysis of a cloud-free, 1-m resolution National Agriculture Imagery Program (NAIP) air photo mosaic collected in 2016.

[b]Representative plant species and genera are not exhaustive but were commonly occurring. Bare ground or rock and open water pixels were classified as such and excluded from further analysis.

(PRISM Climate Group 2022). Thus, the rainfall was above average in both years of our study, whereas the temperature was similar to the long-term average.

METHODS

Controlled burns and herbicide applications

In collaboration with Mexican partners, the National Park Service targeted large giant reed stands in BIBE and adjacent Mexican lands with controlled burns and follow-up herbicide applications between 2008 and 2018 (Briggs et al. 2021). The burns were used to remove aboveground giant reed biomass, which, like in other systems, typically occurred in dense stands along the river channel (Stover et al. 2018). In this region, giant reed has thrived in mesic, near-channel sites that were historically disturbance-prone and supported mixed, low-stature vegetation, distinctive from the more stable gallery forest that also occurs in the floodplain (Briggs et al. 2021). Gallery forest contained little giant reed and was not a target for burning.

Stands were burned once initially, and some were re-burned only if dense regrowth occurred in a subsequent year (Briggs et al. 2021). Giant reed is highly flammable, and burns were typically short-lived but intense, resulting in totally cleared areas lacking live vegetation within the targeted burn perimeters (Briggs et al. 2021). The floodplain area burned in a year ranged from 20–70 ha, with approximately 325 ha receiving ≥1 burn from 2008 to 2017. The mean burn size was 41 ha. Initial herbicide applications occurred in the spring following the first burn, with follow-up applications every year until giant reed was controlled. Stands received 1–6 applications (Briggs et al. 2021). The application was highly targeted—crews searched burned locations and applied herbicide (Imazapyr; Alligare, Opelika, AL, USA) on any remaining or resprouting giant reed stems or live, exposed roots. Further details on the prescribed burns and herbicide applications are in Briggs et al. (2021).

Sampling design

We used a space-for-time sampling design (Fontaine et al. 2009) because our study began after most giant reed removal efforts were completed and we did not have before-after sampling at individual sites (Briggs et al. 2021). This involved dense sampling within the available floodplain area to capture conditions in unburned locations with and without giant reed and burned locations at different times since the last burn. In 2016 we established a systematic sampling design in the floodplain within BIBE boundaries (Figure 1). We restricted field sampling to the United States side of the floodplain for logistical reasons, although giant reed management occurred on the Mexico and United States sides of the floodplain (Briggs et al. 2021). We used a high-resolution (1-m^2) National Agricultural Imagery Program (NAIP) aerial image mosaic captured in 2014 to delineate the floodplain. We used the 2014 image only for the establishment of our sampling design and not to quantify vegetation for analyses. We overlaid a 300-m^2 grid on the floodplain area and located a survey site (i.e., site) at each grid intersection. Our sampling design identified 167 sites distributed throughout the Rio Grande floodplain in BIBE, ranging from Santa Elena Canyon in the western portion of the park to Boquillas Canyon in the east (Figure 1).

As indicated above, prescribed burns were the dominant management method employed in BIBE to remove giant reed (Briggs et al. 2021). Therefore, we included both burned and unburned sites and the time since the last burn to examine the recovery of the system. We used the following criteria to assign sites into 4 management groups, which we used for the basis of our analyses. We used the group unburned giant reed (n = 17) for unburned sites with high giant reed cover (>13% cover within the 100-m survey site area, which was the highest quartile among all sites). We used this group to characterize pre-treatment habitat conditions (Figure 2). We used the group recent (n = 21) for sites burned ≤3 years before sampling. These were characterized by bare ground, sparse vegetation, and some resprouting giant reed (Figure 2). The group older (n = 19) described sites burned ≥4 years before sampling. These were characterized by the regrowth of riparian vegetation and some resprouting giant reed (Figure 2). We used the group unburned floodplain (n = 16) for unburned, non-forest sites without significant giant reed cover (<3% cover). We used this group to characterize typical non-forest floodplain conditions (Figure 2).

Of the original 167 sites, our analysis included 73 that met the above criteria. The additional 94 sites were primarily in more upland forested floodplain sites (principally honey mesquite gallery forest), which, as previously indicated, was not a target of the management activities. We opted to use quartiles defining giant reed cover thresholds to generate meaningfully different groups because we lacked data in this system for a single biologically justified threshold.

Butterfly and bird surveys

We surveyed birds and butterflies at each site from May to July 2016 and 2017. We conducted 3 counts at each site each year, with a fourth butterfly count in 2017 to capture mid-summer monsoonal activity. We used 5-minute point counts to record all birds detected by sight or sound within a 100-m radius (Hutto et al. 1986, Ralph et al. 1995). To survey butterflies, we established 10 × 100-m belt transects, centered at a bird point count location and oriented approximately parallel to the river. An observer slowly walked the centerline, recording butterflies within a 5-m grid of the observer (Brown and Boyce 1998).

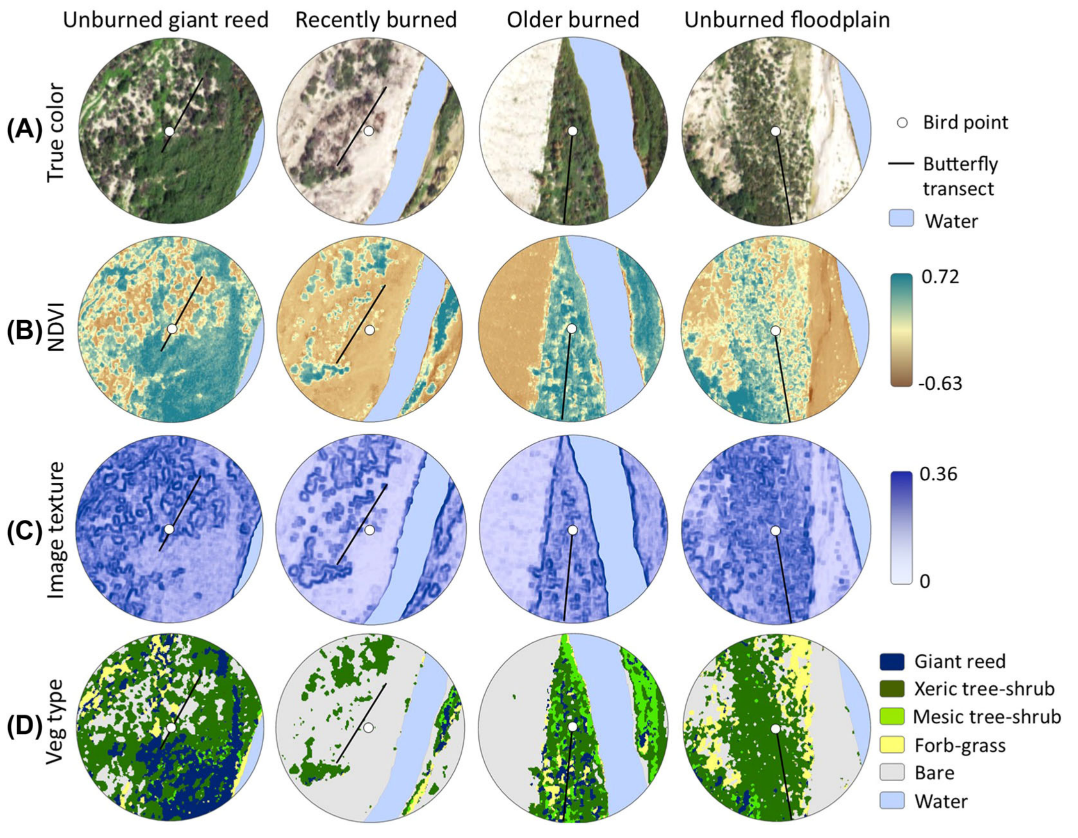

FIGURE 2 Remotely sensed habitat quantification within 100-m-radius survey sites, calculated from 1-m resolution, color-infrared National Agriculture Imagery Program (NAIP) imagery collected in 2016 for the floodplain of the Rio Grande in Big Bend National Park, Texas, USA, May to July 2016 and 2017. Butterfly 100-m survey transects are shown with black lines. Four example sites are shown, typical of the 4 management groups (columns). Rows: A) raw true-color image; B) normalized difference vegetation index (NDVI), indicating vegetation greenness; C) image texture, indicating horizontal habitat heterogeneity; and D) image classification to vegetation (veg) types. The main channel of the Rio Grande is shown in light blue. Mean NDVI is a unitless index ranging from −1 to 1, and image texture is a unitless, positive index.

We established walking routes consisting of 10–15-point count locations. Either JC or HM surveyed a walking route beginning a half hour before sunrise to conduct bird counts, then reversed direction to conduct butterfly surveys. We completed bird surveys by 1000 and butterfly surveys between 1000 and 1400. The 2 surveyors alternated visits to walking routes within and across the 2 study years, resulting in approximately equal visits to a site by each observer. We also alternated walking route directions between visits to balance the time-of-day when sites were surveyed.

Habitat characterization: remote sensing and field surveys

We quantified habitat characteristics in the floodplain using a cloud-free NAIP color-infrared air photo mosaic with 1-m^2 spatial resolution collected in 2016 (Figure 2). From this image, we computed a vegetation greenness index (the normalized difference vegetation index [NDVI]; Pettorelli et al. 2011), which is an important predictor of bird and insect richness and abundance (Seto et al. 2004, Wood et al. 2013). We calculated NDVI for each image pixel, then computed the mean value within each 100-m bird survey radius, excluding water pixels.

We also computed image texture, an index of habitat heterogeneity (Wood et al. 2012), which is a useful predictor of bird occurrence, diversity, and abundance (St-Louis et al. 2006, 2009; Bellis et al. 2008; Culbert et al. 2012; Wood et al. 2012, 2013) but is untested in its capability to predict butterfly abundance. We computed image texture as the second-order standard deviation of NDVI, capturing the variability in pixel value greenness across a defined area (Wood et al. 2012). We first calculated the standard deviation of pixel values within a 5 × 5-pixel moving window and assigned this value to the center pixel. We then calculated the standard deviation of those values within the 100-m survey radius (Wood et al. 2013). We computed the NDVI and habitat heterogeneity calculations using the image analysis and focal stats tools in ArcGIS 10.5.1 (Esri, Redlands, CA, USA).

To quantify the cover of vegetation classes from the NAIP image, we first defined 4 classes that broadly characterized floodplain vegetation and were relevant for giant reed management and for quantifying riparian wildlife habitat use (Nelson and Andersen 1999, Brand et al. 2008). These classes were giant reed, xeric woody vegetation, mesic woody vegetation, and low herbaceous vegetation (i.e., forbs and grasses, excluding giant reed; Table 1). While a diverse mix of woody species occurred in the floodplain, a fundamental distinction can be made between more mesic and more xeric formations, influenced largely by soil moisture, with distinctive composition and structure. The mesic and xeric woody classes distinguished these.

We delineated these 4 classes through image segmentation and supervised classification of the NAIP image in ArcGIS 10.5.1 (Mountrakis et al. 2011). We included the original image bands (infrared, red, green, blue) and our image texture layer for classification. The classification training sample consisted of selected pixels within survey areas, assigned to classes using field-collected vegetation data and visual image interpretation. Once all pixels were classified, we smoothed the image to reduce pixel mixing, using a 3 × 3-pixel moving window and assigning the majority class to the center pixel. Finally, we calculated cover proportions within the 100-m bird survey areas for each class (Figure 2).

For the accuracy assessment of the classified image, we developed an error matrix (Congalton 1991) by auto-generating 500 points distributed randomly across the 100-m-radius survey areas. Independent of the classified image, we assigned these points to classes through visual inspection of 1-m raw imagery, supported with another 0.5-m air photo mosaic from the same period. We excluded points that we could not assign to a class with certainty. At the resulting 232 validation points, we then compared assignments to the supervised classification, resulting in 93.5% accuracy across classes (the lowest accuracy was for giant reed [88.1%] and the highest was for bare ground [100%]). We excluded water and bare ground pixels from further analysis because our focus was on vegetation features following management. We used the accuracy assessment tool in the ArcGIS image analyst toolbox for these calculations (Esri).

The cover of grass and forb vegetation are important butterfly habitat features (Pickens and Root 2008) that were difficult to distinguish from one another with remote sensing. Therefore, we included these 2 ground-based habitat measures in butterfly analyses, replacing the image-based herbaceous cover estimates. We estimated the proportional cover of forbs and grasses (excluding giant reed) within the butterfly transects by visual estimation in the field using a relevé method (Minnesota Department of Natural Resources 2007). Observers walked the length of each transect and sketched the cover of grass and forb vegetation within the 5-m gridded rectangular outline of the transect, from which we estimated cover.

Statistical analyses

Habitat, butterfly, and bird responses to burns

Before analysis related to objective 1, we accounted for imperfect bird species detectability by fitting single-season *N*-mixture models to estimate species-specific, site-specific abundance, using the unmarked package in R (Royle 2004, Kéry et al. 2009, Fiske and Chandler 2011). We included site visits during both years to build a detection history across all 6 visits. We included the full set of sites ($n = 167$) to maximize the robustness of detection coefficients to improve site-level abundance estimates at the 73 sites that were included in 1 of the 4 management groups. We estimated the local abundance (N_i) of bird species as a function of the intercept (i.e., the mean), with a Poisson error distribution (Kéry et al. 2009). We modeled detection probability as a function of observer and year. This allowed detection probability estimates to vary between the 2 observers and the 2 years with potentially differing survey conditions. To derive site-specific species abundance estimates at the 73 sites, we estimated the posterior distribution of latent abundance from the *N*-mixture models using empirical Bayes methods with the function ranef (Fiske and Chandler 2011). *N*-mixture models fit using count data from repeat visits have been criticized for being non-identifiable (i.e., not precise; Barker et al. 2018). Nevertheless, a follow-up screening test of 137 bird data sets, many of which are similar to our point count methodology, suggested that parameter estimates under Poisson *N*-mixture models, which was our method, were identifiable and thus precise (Kéry 2018).

We estimated butterfly species abundance as the maximum raw abundance observed on any single visit to a site, among the 7 total visits. We did not use *N*-mixture models for butterflies because many species had few detections, leading to unreliable estimates. Further, the closure assumption is a challenge with butterfly data because many have variable flight periods, multiple generations, or distinct movement patterns (e.g., migration). Thus, the unmodeled maximum abundance is a conservative estimate of butterfly relative abundance among sites. We included only butterfly species with ≥5 observations in the analyses. For both the bird and butterfly abundance estimation, when burning or herbicide application occurred between the 2 survey years, which occurred at 8 sites, we only included survey data for the first year. Overall, 21 butterfly species and 23 bird species met our abundance estimation criteria and were included in objective 1 analyses (Tables 2 and 3).

To address our first objective of quantifying differences in habitat characteristics, butterfly and bird species compositions, and individual species abundance patterns among management groups, we completed 2 analyses. First, we used multivariate, non-metric multidimensional scaling (NMDS) and associated tests to assess differences among management groups in habitat characteristics and species compositions (McCune et al. 2002). We quantified site-site differences in species composition for butterflies and birds separately, using the Bray-Curtis dissimilarity index (McCune et al. 2002) on the raw (butterflies) or estimated (birds, using *N*-mixture models) abundance data, and visualized group differences graphically using NMDS. We then tested for differences among and between management groups in habitat characteristics and butterfly and bird composition, using permutational analysis of variance (PERMANOVA) on distance matrices, followed by pairwise tests with correction for multiple comparisons (Anderson 2001). We also examined site-site variation in butterfly and bird species composition or habitat characteristics within management groups using the betadisper test for homogeneity of within-group dispersions, followed by pairwise tests between groups. The betadisper test addressed whether burned sites resulted in a wider variety of conditions, with different habitat characteristics, butterfly species compositions, or bird species compositions, than existed among unburned sites.

Second, we examined associations of individual butterfly and bird species abundances with management groups to understand which species were most responsible for management group differences using indicator species analysis (ISA) with permutational significance tests (De Cáceres and Legendre 2009). We tested for associations with one management group or more than one management group, using the indicator value as the measure of strength of association, and examining permutation-based *P*-values to weigh evidence for the significance of the relationship (De Cáceres et al. 2010). Indicator species analysis provided an additional, species-level characterization of community compositional differences related to management groups. To aid the interpretation of ISA statistical results, we separately characterized all bird species included in our analysis in terms of desert riparian habitat associations documented in the literature (obligate, preferential, or facultative; Carothers et al. 2020). We were unaware of comparable information in the literature for butterflies. Nevertheless, we assigned the disturbance susceptibility score (DSS) to all butterfly species in our analysis. The DSS was developed specifically for butterfly monitoring to indicate habitat quality in southwestern desert riparian systems, especially during restoration activities (Nelson and Andersen 1994). High DSS values indicated strong disturbance sensitivity,

TABLE 2 The 21 butterfly species of the community-level analysis, with management group associations from indicator species analysis (ISA), and disturbance susceptibility scores (DSS). Our study was focused within the Rio Grande floodplain in Big Bend National Park, Texas, USA, May to July 2016 and 2017.

Common name	Scientific name	Obs[a]	ISA[b]	DSS[c]
Queen	*Danaus gilippus*	258	0.29(C)	12
Fatal metalmark	*Calephelis nemesis*	25	0.37(C)	11*
Sleepy orange	*Abaeis nicippe*	378	0.42(C)	10
Marine blue	*Leptotes marina*	35		9
Phaon crescent	*Phyciodes phaon*	13		9*
Pipevine swallowtail	*Battus philenor*	11		8
Clouded skipper	*Lerema accius*	19		8*
Large orange sulphur	*Phoebis agarithe*	20	0.44(C)	8*
Orange skipperling	*Copaeodes aurantiaca*	14		7.5
American snout	*Libytheana carinenta*	44		7.5
Western pygmy-blue	*Brephidium exilis*	12		7
Painted crescent	*Phyciodes picta*	13	0.35(A)	7*
Orange sulphur	*Colias eurytheme*	29		6
Dainty sulphur	*Nathalis iole*	103		6
Black swallowtail	*Papilio polyxenes*	20		6
Checkered white	*Pontia protodice*	1,048		6
Southern dogface	*Zerene cesonia*	23		6
Reakirt's blue	*Echinargus isola*	135	0.29(C,D)	5
Lyside sulphur	*Kricogonia lyside*	837		5
Variegated fritillary	*Euptoieta claudia*	39		4
Gray hairstreak	*Strymon melinus*	52		4

[a]Total observations across all surveys at all sites.

[b]If a species was a significant indicator for ≥1 management groups at the alpha = 0.10 level, the ISA value and the groups are shown. A = unburned giant reed; B = recently burned; C = older burned; D = unburned floodplain (no giant reed).

[c]Table organized in decreasing order of DSS (Nelson and Anderson 1994). Higher DSS indicates lower disturbance tolerance. Species with an asterisk did not have published scores, so we scored them using the criteria in Nelson and Anderson (1994).

which we assumed suggested the use of the older or unburned management groups. We used the vegan package for the NMDS, PERMANOVA, and betadisper analyses, and the indicspecies package for the ISA analysis, all within the R statistical programming environment (De Cáceres and Legendre 2009, Oksanen et al. 2017, R Core Team 2017).

Butterfly and bird habitat associations

To address our second objective of modeling the associations between habitat characteristics and the abundance of butterflies and birds, we fitted generalized linear models for butterflies and *N*-mixture models for birds.

TABLE 3 The 23 bird species of the community-level analysis, with management group associations from indicator species analysis (ISA), and general riparian habitat associations for birds in the Rio Grande floodplain in Big Bend National Park, Texas, USA, May to July 2016 and 2017.

Common name	Scientific name	Obs[a]	ISA[b]	Riparian[c]
Blue grosbeak	*Passerina caerulea*	299		O
Common yellowthroat	*Geothlypis trichas*	135	0.43(A)	O
Lucy's warbler	*Oreothlypis luciae*	43		O
Painted bunting	*Passerina ciris*	817	0.27(C+D)	O
Summer tanager	*Piranga rubra*	125		O
Yellow-billed cuckoo	*Coccyzus americanus*	109		O
Yellow-breasted chat	*Icteria virens*	782	0.36(A+C)	O
Bell's vireo	*Vireo bellii*	1,448	0.50(A+C+D)	P
Black-tailed gnatcatcher	*Polioptila melanura*	288		P
Common ground-dove	*Columbina passerina*	101	0.36(A)	P
Ladder-backed woodpecker	*Dryobates scalaris*	72	0.33(B+D)	P
Lesser goldfinch	*Spinus psaltria*	42		P
Mourning dove	*Zenaida macroura*	228	0.40(A+D)	P
Northern cardinal	*Cardinalis cardinalis*	312	0.28(B+C)	P
Pyrrhuloxia	*Cardinalis sinuatus*	97	0.30(C+D)	P
Verdin	*Auriparus flaviceps*	274	0.40(C+D)	P
White-winged dove	*Zenaida asiatica*	395	0.42(A+D)	P
Ash-throated flycatcher	*Myiarchus cinerascens*	348	0.36(B+D)	F
Black-throated sparrow	*Amphispiza bilineata*	207	0.52(D)	F
Canyon wren	*Catherpes mexicanus*	36		F
Greater roadrunner	*Geococcyx californianus*	353	0.29(A+B+D)	F
House finch	*Haemorhous mexicanus*	86	0.30(C)	F
Varied bunting	*Passerina versicolor*	15		F

[a]Total observations across all surveys at all sites.

[b]If a species was a significant indicator for ≥1 management groups at the alpha = 0.10 level, the ISA value and the groups are shown. A = unburned giant reed; B = recently burned; C = older burned; D = unburned floodplain (no giant reed).

[c]Table organized in decreasing order of riparian association: O = obligate; P = preferential; F = facultative.

We intended to understand habitat associations specifically for species that responded to the prescribed burns, so we included only the species identified as indicator species in the ISA. Given the butterfly count data, we examined the suitability of Poisson and negative binomial generalized linear models. We assessed assumptions for each fitted model, including normality, heteroscedasticity, and independence. Finding high variance relative to the mean for all butterfly indicator species, we used generalized linear models with a negative binomial error distribution (Zuur et al. 2011). We fitted generalized linear models using the MASS package in R (Venables and Ripley 2002, R Core Team 2017). For birds, we used *N*-mixture models, which differed from those used in the initial abundance estimation (described above) because the habitat-association models included habitat covariates, and they used only the 73 sites included in management groups. *N*-mixture modeling methods were otherwise similar.

We used a model selection framework to rank models relative to one another within a set using Akaike's Information Criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002). We created 2 distinct model sets for model selection, one composed of independent variables predicting butterfly species abundances and another for birds. For butterfly models, we examined 7 independent variables: mean NDVI, habitat heterogeneity, and the percent cover of giant reed, xeric woody vegetation, mesic woody vegetation, forbs, and grasses. For birds, we examined 6 independent variables: mean NDVI, habitat heterogeneity, and the percent cover of giant reed, xeric woody vegetation, mesic woody vegetation, and herbaceous vegetation (forbs and grasses, excluding giant reed). To avoid overly complex models and reduce their number, we only examined models with ≤2 habitat variables and did not include interactions. We initially examined collinearity among variables, using a Pearson correlation coefficient of 0.60 as a threshold (Dormann et al. 2013) and determined that xeric woody vegetation should not be included in the same model with either NDVI (positive correlation) or habitat heterogeneity (negative correlation). Under those constraints, the 2 model sets (for butterflies and birds) included 26 and 19 models, respectively (Tables S1 and S2, available in Supporting Information). We quantified habitat variable importance for a given species as the summed Akaike weights (Σw_i) for all models containing the variable (Burnham and Anderson 2002).

RESULTS

Habitat, butterfly, and bird responses to burns

The NMDS results suggested that the butterfly and bird species compositions in the 2 burned groups did not necessarily reflect an obvious trajectory from (or towards) either of the unburned groups (Figure 3). Our results indicated that the giant reed management and post-burn vegetation recovery provided conditions that supported novel bird and butterfly species compositions (Figure 3).

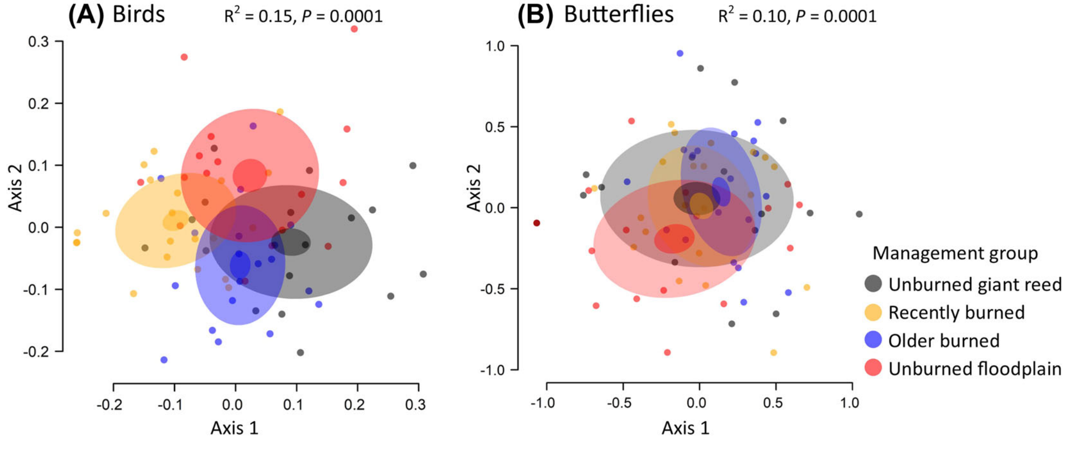

FIGURE 3 Non-metric multidimensional scaling (NMDS) ordination of sites based on species composition of A) 23 bird species and B) 21 butterfly species at 73 survey sites, which are shown in colors indicating management groups, in the floodplain of the Rio Grande in Big Bend National Park, Texas, USA, May to July 2016 and 2017. Large and small ellipses indicate the standard deviation of points and the standard error of management group centroids, respectively. We present R^2 and P-values for management group differences, from analysis of variance on distance matrices (PERMANOVA).

TABLE 4 Differences among management groups in habitat characteristics (including all habitat variables) and butterfly and bird species composition in the Rio Grande floodplain in Big Bend National Park, Texas, USA, May to July 2016 and 2017.

Group comparison	*F*	R^{2}[a]	*P*
Habitat characteristics			
Unburned floodplain vs. older burned	20.28	0.381	0.001
Unburned floodplain vs. unburned giant reed	6.59	0.175	0.001
Unburned floodplain vs. recent burned	8.00	0.186	0.003
Older burned vs. unburned giant reed	13.41	0.283	0.001
Older burned vs. recent burned	2.50	0.062	0.082
Unburned giant reed vs. recent burned	9.26	0.205	0.001
Butterfly species composition			
Unburned floodplain vs. older burned	4.94	0.130	0.001
Unburned floodplain vs. unburned giant reed	1.16	0.036	0.302
Unburned floodplain vs. recent burned	2.50	0.067	0.015
Older burned vs. unburned giant reed	2.42	0.066	0.015
Older burned vs. recent burned	2.28	0.057	0.020
Unburned giant reed vs. recent burned	2.07	0.054	0.031
Bird species composition			
Unburned floodplain vs. older burned	3.32	0.092	0.003
Unburned floodplain vs. unburned giant reed	2.76	0.082	0.029
Unburned floodplain vs. recent burned	4.54	0.115	0.002
Older burned vs. unburned giant reed	3.09	0.083	0.004
Older burned vs. recent burned	5.11	0.118	0.001
Unburned giant reed vs. recent burned	5.94	0.142	0.001

[a]The permutational analysis of variance (PERMANOVA) on distance matrices tests were based on Euclidean distance for habitat variables, and Bray-Curtis distance for species compositions. Higher R^2 values indicate greater dissimilarity between groups.

The 4 management groups differed in their habitat characteristics (PERMANOVA: $R^2 = 0.28$, $P < 0.01$), with a general trend of the unburned groups being dissimilar in their habitat conditions from the burned groups (Table 4; Figure 4). The greatest dissimilarity in habitat characteristics between management groups was the older burned and unburned floodplain groups (PERMANOVA: $R^2 = 0.32$, $P < 0.01$; Table 4). The only management groups that had similar habitat conditions were the recently burned and older burned groups (PERMANOVA: $R^2 = 0.05$, $P = 0.12$; Table 4). Both the recently burned and older burned groups had low levels of giant reed, suggesting that giant reed does not return to high densities following management (Figure 4).

Butterfly community composition differed among the management groups (PERMANOVA: $R^2 = 0.10$, $P < 0.01$; Table 4). The patterns in the overall dissimilarities of the butterfly community among management groups were influenced by differences between the older and the unburned floodplain groups (PERMANOVA: $R^2 = 0.13$, $P = 0.001$; Figure 3). Butterfly communities were least dissimilar between the unburned floodplain and unburned giant reed groups (PERMANOVA: $R^2 = 0.04$, $P = 0.30$; Table 4; Figure 3). Bird composition was also dissimilar among

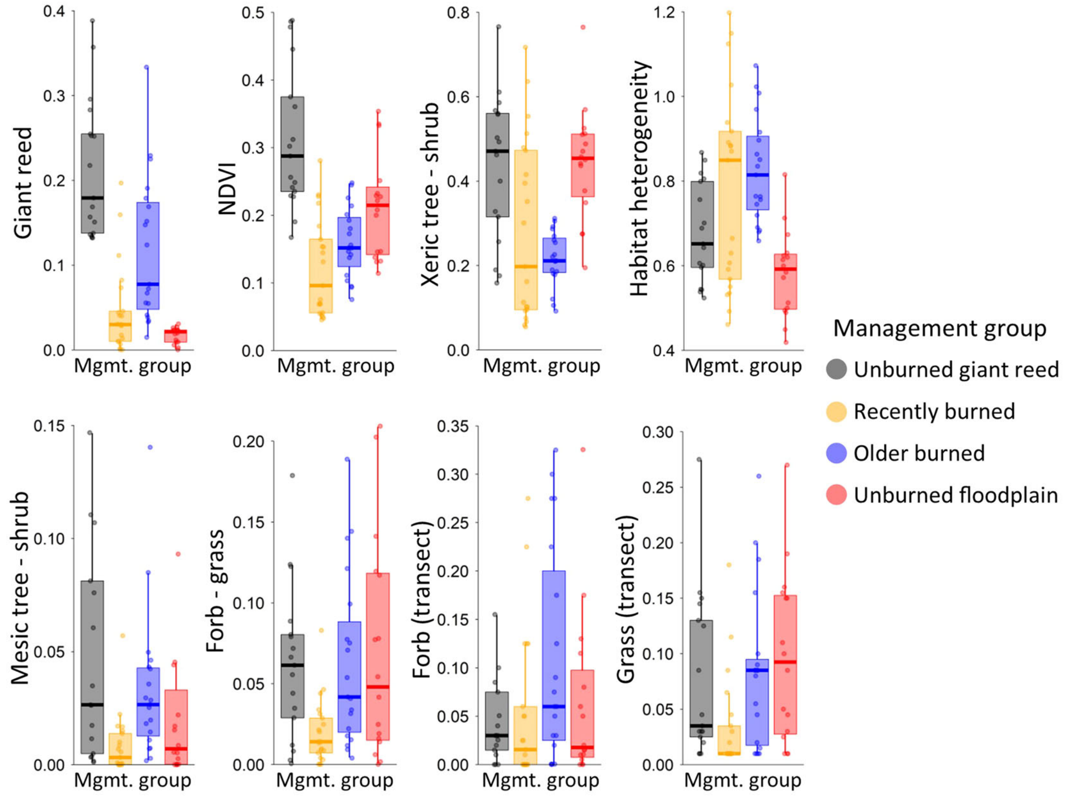

FIGURE 4 Habitat characteristics among the 4 management (mgmt.) groups in the floodplain of the Rio Grande in Big Bend National Park, Texas, USA, May to July 2016 and 2017. Boxplots indicate the group median (bar), first and third quartiles (box), and range. Points indicate the individual survey sites. Forb (transect) and grass (transect) cover data were collected along the 100-m butterfly survey transects; all others were derived from 1-m, 2016 National Agriculture Imagery Program imagery and summarized at the 100-m-radius bird survey extent. All units are site cover proportions except those for normalized difference vegetation index (NDVI) and horizontal habitat heterogeneity (i.e., image texture), each of which is a unitless index.

the 4 management groups ($R^2 = 0.15$, $P < 0.01$; Table 4). In general, avifaunal communities were distinct between the recently burned group and all other groups (Table 4), which was indicative of the lack of avian habitat immediately following prescribed burns.

The variability in butterfly and bird species compositions among sites within the management groups was similar for all 4 management groups (betadisper analysis; Figure 3). The results for birds suggested similar within-group variation across management groups ($F = 0.33$, $P = 0.81$), whereas butterflies suggested possible differences ($F = 2.54$, $P = 0.06$). The 95% confidence intervals (standard deviation) overlapped 0 for all pairwise management-group comparisons.

Indicator species analysis resulted in 6 butterfly indicator species of the 21 examined, and 15 bird indicator species of the 23 examined (Tables 2 and 3; Figure 5). Butterfly indicator species were mainly associated with the older burned group, including 5 of the 6 species: the large orange sulphur (*Phoebis agarithe*), the sleepy orange (*Abaeis nicippe*), the fatal metalmark (*Calephelis nemesis*), the queen (*Danaus gilippus*), and the Reakirt's blue (*Echinargus isola*). The Reakirt's blue was also associated with the unburned floodplain group. The painted crescent (*Phyciodes picta*) was the only butterfly indicator for unburned giant reed. The recently burned group was the only management group with no butterfly indicator species. For birds, all 4 management groups harbored indicator

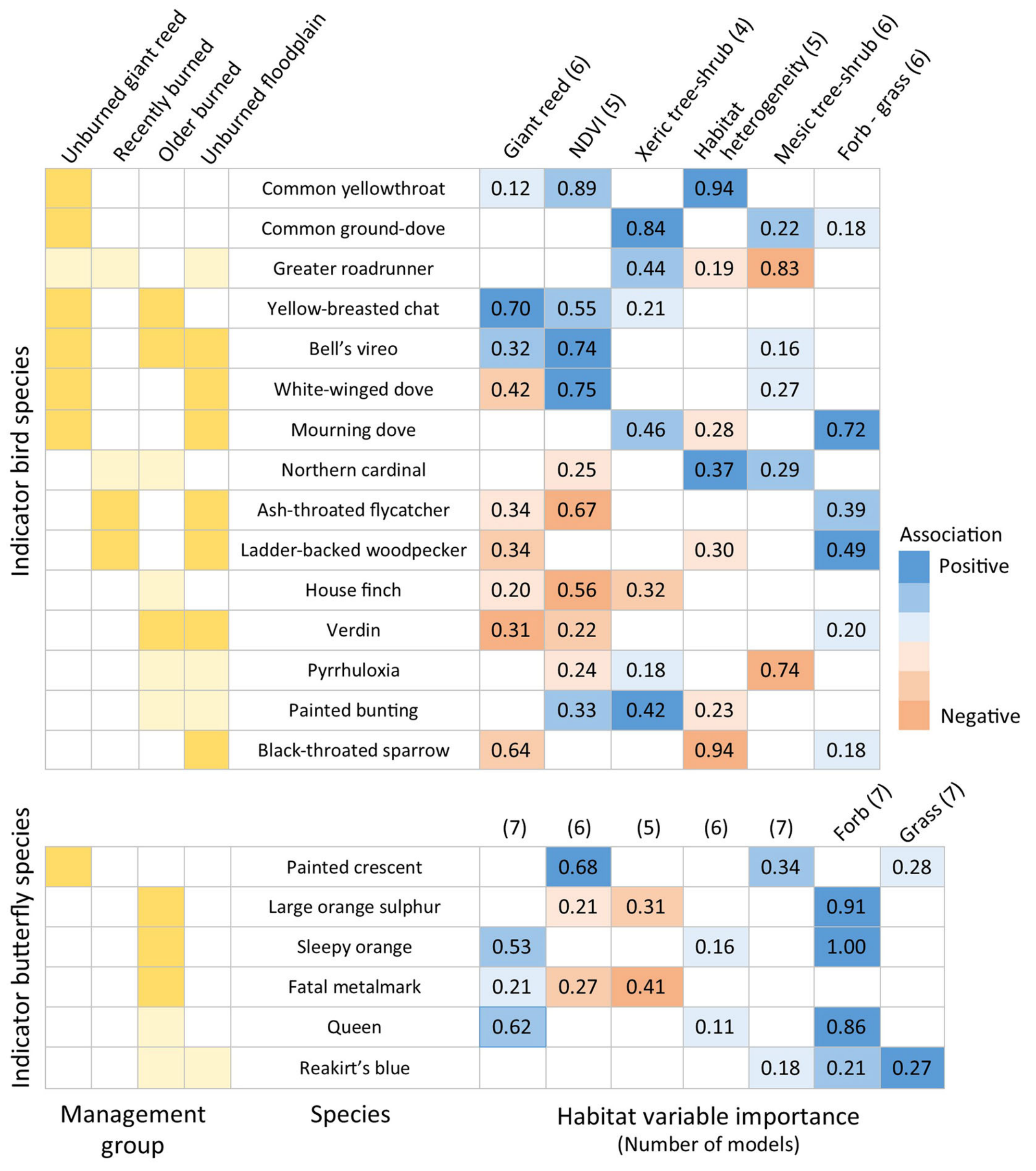

FIGURE 5 Management group indicator bird and butterfly species identified through indicator species analysis, shown with habitat variables found to be associated with species abundances in model selection for species in the floodplain of the Rio Grande in Big Bend National Park, Texas, USA, May to July 2016 and 2017. A species was an indicator for the management group(s) highlighted by darker or lighter yellow, denoting an associated *P*-value < 0.05 or *P*-value < 0.10, respectively. Habitat variables are shown with their importance value (i.e., the summed Akaike weights; Σw_i) for all models containing the variable, for a given species. The number of models containing the variable is shown in parentheses. Full model sets included 19 models for each bird species and 26 for butterfly species. The 3 most important habitat variables are shown for each species. NDVI = normalized difference vegetation index.

species, the unburned floodplain group having the most (10 species), and the recently burned group having the fewest (4 species; Figure 5). The older burned group and the unburned floodplain group had the most indicator species in common (4 bird species and 1 butterfly species), and the most indicator species overall (12 species for older burned and 11 species for unburned floodplain; Figure 5).

Butterfly and bird habitat associations

The most important habitat variable explaining butterfly indicator species abundance was forb cover (Figure 5; Table S3, available in Supporting Information). Forb cover was positively associated with the abundance of 4 butterfly indicator species (i.e., large orange sulphur, sleepy orange, queen, and Reakirt's blue) and was the most important variable for 3 of those (Figure 5; Table S3). As indicated above, these species were indicators of the older burned group, which had the highest forb cover (Figure 4). Mean NDVI was the most important variable (positive association) for the painted crescent, the one butterfly indicator species for the unburned giant reed group (Figure 5), and mean NDVI was highest in that group (Figure 4). Giant reed cover was positively associated with 3 butterfly species (sleepy orange, fatal metalmark, queen), but the importance of the relationship was overshadowed by forb cover (Figure 5).

The most important habitat variable in explaining bird indicator species abundance, overall, was NDVI (Figure 5). Riparian-affiliated species such as the common yellowthroat (*Geothlypis trichas*) and the Bell's vireo (*Vireo bellii*) were positively associated with NDVI, while birds that generally use open spaces, such as the house finch (*Haemorhous mexicanus*) and the ash-throated flycatcher (*Myiarchus cinerascens*) were negatively associated with NDVI (Figure 5). Habitat heterogeneity was positively or negatively associated with 7 species, which generally reflected their breeding and foraging habitat niches within the floodplain (Figure 5). For example, the common yellowthroat, a shrub-affiliated breeding species, was positively associated with habitat heterogeneity, while the black-throated sparrow (*Amphispiza bilineata*) was negatively associated with habitat heterogeneity, and they are typically associated with sparsely vegetated xeric scrub (Figure 5). The association of giant reed with bird species abundance was positive in 3 cases and negative in 6 (Figure 5).

DISCUSSION

Our results suggest that removing giant reed using prescribed burns and targeted herbicide applications, even without active replanting of native vegetation, positively affects butterfly and bird communities in the Rio Grande floodplain of BIBE. We predicted that habitat conditions and butterfly and bird communities would respond positively to giant reed management activities, which is mostly what we found. Habitat changes associated with the management activities included the suppression of giant reed and the presence of riparian habitat elements over the 8 years following management activities. Butterflies and birds appeared to respond to those changing conditions, with a large proportion of the species included in our study showing variations in their abundance among the management groups (i.e., the indicator species we identified), which influenced overall species composition differences. Positive responses occurred primarily after the initial 3 post-management years; more indicator species were associated with the older management group than with any other group, and these species were among the most disturbance-intolerant species detected during the study (for butterflies; Nelson and Andersen 1994) and included several obligate and preferential riparian-associated species (for birds; Carothers et al. 2020). Taken together, our study indicates that the removal of giant reed carried out in BIBE and adjacent lands is a viable approach if the goal is to promote habitat conditions favoring diverse and abundant butterfly and bird communities (CEC 2014*b*).

We expected that diverse habitat conditions would largely recover following the management efforts, with a lower cover of giant reed and a higher cover of mostly native, riparian vegetation. While we did not measure plant species-level responses to the removal efforts other than giant reed (Briggs et al. 2021), our work does lend support to the expectation that aspects of butterfly and bird habitat, such as higher forb cover and increased habitat heterogeneity, appear to recover following prescribed burns to remove giant reed. Our results are not unlike what was found in the Segura River basin in the Southeast Iberian Peninsula, Spain, where riparian vegetation and associated wildlife communities rebounded 4 years following the management and removal of giant reed (Bruno et al. 2019). Further, our observations of increasing NDVI, habitat heterogeneity, mesic woody cover, and forb and grass cover at our older burned sites compared with recently burned sites reinforce findings from another study in BIBE that documented the recovery of early successional, primarily native, riparian vegetation after the application of prescribed burn and herbicide treatments (Briggs et al. 2021). In other regions of the southwestern United States, floodplain vegetation responded quickly to giant reed removal, with increased native herbaceous plant richness and woody shrub establishment within 2 years after removal and management efforts (Giessow et al. 2011, Racelis et al. 2012, Howe 2014). Our results support the conclusion that aggressive management of large, monodominant giant reed stands can allow the establishment of riparian vegetation not dominated by giant reed.

We predicted that butterfly and bird communities would largely respond to the giant reed removal efforts because of the introduction of novel wildlife habitat conditions. Our results supported our predictions, albeit with somewhat weaker-than-expected responses. For example, differences in butterfly species composition among the management groups were small compared to differences in habitat measures and differences in bird species composition. This suggests that generalist species, such as the checkered white (*Pontia protodice*) and the lyside sulphur (*Kricogonia lyside*), were present throughout our system. These were the 2 most frequently detected butterfly species across all sites, they were not ISA indicator species for any management group, and they had among the lowest DSS scores. Further, our analysis did not reveal butterfly indicator species in recently burned sites but did so in the older burned sites. The older burned sites had the most indicator species, which contrasted with our expectation that butterflies would rapidly colonize recently burned sites likely in response to an abundance of floral resources (Pickens and Root 2008, Curtis et al. 2015). Rather, our results align with butterfly DSS scores (Nelson and Andersen 1994, 1999), suggesting that sites burned at least 4 years before our surveys supported the highest diversity and abundance of disturbance-sensitive butterfly species, such as the queen, the fatal metalmark, and the sleepy orange. In some xeric systems, butterfly community recovery after a burn can occur more rapidly (Serrat et al. 2015) in response to the openness of treated habitat even before herbaceous plants and nectar resources are fully established (Waltz and Covington 2004). In our desert riparian system, our results suggested that butterfly habitat requires several years of recovery, which might especially be true in areas where herbicide applications were used, which was the case at our managed study sites (Briggs et al. 2021).

For birds, the distinctive species compositions among all 4 management groups suggested that the prescribed burns and herbicide applications introduced unique avian habitats at different post-disturbance successional stages. The giant reed removal efforts initially produced open and patchy areas within the burn footprints (Briggs et al. 2021). Some indicator species avoided these conditions, while others, such as the northern cardinal (*Cardinalis cardinalis*), the ash-throated flycatcher, and the ladder-backed woodpecker (*Dryobates scalaris*) had higher abundances at the recently burned sites. Possibly these 3 indicator species used the newly formed habitat for foraging in burned vegetation (the woodpecker), the open areas with perches (the flycatcher), or the ground for seeds (the cardinal; Billerman et al. 2021). The larger number of indicator bird species for the older burned group compared with the recently burned group suggests a stronger recovery of bird communities over the longer term but with a species composition that was distinctive from the unburned floodplain. Several species that are riparian specialists within the region were identified as ISA indicators for the older burned group, including the yellow-breasted chat (*Icteria virens*), the Bell's vireo, the northern cardinal (an indicator for both burned groups), and the painted bunting (*Passerina ciris*; Carothers et al. 2020). Given that we sampled only up to 8 years after burns, it is not clear whether burned sites will eventually become more like the unburned floodplain or will instead remain on a distinctive trajectory. Nevertheless, our findings regarding bird community responses are generally in line with those from the Segura River basin (Bruno et al. 2019) and broadly support other riparian management projects that found the removal of invasive vegetation subsequently leads to woody species recovery that supports riparian-affiliated avifauna (Kus 1998, Valente et al. 2019, Hall et al. 2020).

Unexpectedly, 6 indicator species had positive associations with giant reed. We suggest that the associations we found likely had little to do with the plant and more to do with where the plant grows—typically along the river's edge. The river's edge locations also harbor riparian conditions that many of the indicator species are associated with, such as the yellow-breasted chat, the common yellowthroat, and the Bell's vireo, which were all positively associated with giant reed. An addition to our sampling design could have included a use versus availability design, where we directly compared use (e.g., bird foraging or nesting, butterfly pollination, or host-plant use) with the availability of plants among the management groups (Gabbe et al. 2002, Wood et al. 2012, Cole et al. 2020). Such a design would yield important information on the direct interactions of bird and butterfly species with giant reed, and other plants in the system, which is something our study cannot offer. We suggest such a design would be a valuable approach for future giant reed removal and habitat recovery research.

Our work employed remote sensing methods—some, very common (NDVI), and others that are novel (image texture)—to characterize habitat conditions following management efforts (Wood et al. 2012, Pettorelli et al. 2014). In addition to accurately characterizing habitat conditions, NDVI (greenness) and image texture (habitat heterogeneity) were important predictors of the abundance of many bird and butterfly species in the years following giant reed suppression (Figure 5). Our results support the use of high-resolution remotely sensed data sources to characterize broad vegetation classes (Pettorelli et al. 2014) and to monitor the cover of plant species of management interest, at least when those species are sufficiently abundant and stand-forming, as is the case for giant reed (He et al. 2011). Additionally, the relationships we observed between habitat heterogeneity and bird abundance patterns are consistent with reports of bird habitat selection along the Trinity River in California, USA (Rockwell and Stephens 2018). Using field measurements, Rockwell and Stephens (2018) reported that restored and reference riparian systems with more complex vegetation structure supported nesting territories of yellow-breasted chats and yellow warblers (*Setophaga petechia*). Remote sensing methods do not provide the same level of detail as strictly field-based monitoring. The approaches employed in our analysis, however, provided a variety of data sufficient for broad habitat characterization, including some that are not readily measured in the field (e.g., NDVI greenness), and across areas where it may not be possible to conduct field sampling (e.g., crossing international borders). Thus, our work supports an extension of the remote sensing approaches used in the analysis for future invasive plant management restoration projects and research.

RESEARCH IMPLICATIONS

Given our results, we offer the following research implications regarding the effects of large-scale invasive plant removal efforts on butterfly and bird communities. Invasive plant removal efforts using prescribed burning do not replace natural disturbances in desert riparian floodplains. Nevertheless, our results suggest that this form of active management can favor a variety of habitat conditions that promote diverse and abundant butterfly and bird assemblages. Both natural flooding and fire regimes have been strongly altered in most southwestern desert riparian systems. In this context, continuing an active prescribed fire management program if invasive species control remains a concern can also likely play a role in maintaining a diverse, disturbance-dependent riparian habitat mosaic. This should be weighed against any role fire may play in opening habitat for new invasive species colonization, which did not appear to be a primary concern in our study system.

Aggressive habitat management approaches such as those required to remove giant reed also restructure bird and butterfly communities, and we observed variable species responses both within and between these 2 taxa. Even for species with modest responses, given the scale of the treatments along several hundred kilometers of the Rio Grande within BIBE and in Mexico, this represents a significant impact within the region. Our study was far from a complete multi-taxa effort, but even our limited scope revealed that no one species or group is likely to provide full information about the responses of other groups. For large-scale invasive plant removal programs with ecosystem-level impacts, monitoring a diversity of taxa can provide information about complex dimensions of system recovery.

Remote sensing methods enabled us to quantify habitat at a management-relevant spatial scale and could readily be extended to multi-temporal change analysis, timed with management activities. Further, high-resolution image classification proved more useful for quantifying giant reed cover at the floodplain scale than our field effort could have achieved. Considering the relative ease and accuracy of using NDVI, image texture, and image classification to characterize giant reed and other important wildlife habitat features at scale, integrated management and monitoring efforts can benefit from similar methods to assess change over management-relevant timescales and spatial domains.

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CONFLICTS OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All surveys were carried out under National Park Service research permit BIBE-2016-SCI-0037. No animals were handled during this work.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.31zcrjdqn.

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