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Invasive giant reed shifts riparian habitat mosaics, with stronger effects on birds than butterflies across spatial scales

Heather L. Mackey · Lars Y. Pomara · Julie E. Coffey · Eric M. Wood

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Abstract Giant reed (*Arundo donax*) has invaded biologically diverse riparian ecosystems in warm and arid regions globally, yet its impacts on wildlife are still poorly understood. Resolving the multi-taxa, scale-explicit impacts of giant reed in the broader context of the riparian vegetation mosaics that support wildlife can help target ecological restoration efforts. We quantified effects of giant reed and other dominant riparian vegetation on bird and butterfly habitat occupancies at two spatial scales along the Rio Grande in west Texas, USA. Birds and butterflies are diverse in riparian systems and can be efficiently surveyed, making them useful indicator taxa. We surveyed 167 sites three times per year in 2016 and 2017, and used occupancy models to relate occupancy to cover proportions of dominant vegetation types derived from high-resolution aerial imagery at two scales (100 m and 500 m radii) to assess local vs. broader floodplain-scale effects. Five of 16 bird species (31%) showed negative giant reed associations at both scales, while two bird species (13%) showed positive giant reed associations and nine (56%) showed no direct effect. In contrast, no butterfly species showed direct negative associations with giant reed. However, positive associations for both butterflies and many bird species were primarily linked at both spatial scales to the vegetation types most displaced by giant reed and most likely to benefit from its control. Overall, vegetation effects were mostly at the local scale for birds, and the floodplain scale for butterflies, although negative effects of giant reed on birds persisted at the floodplain scale despite its confinement mainly to near-channel habitats. While giant reed directly impacted riparian habitat occupancy only for birds, control efforts are likely to affect both taxa positively by restoring mesic woody and herbaceous vegetation.

Keywords *Arundo donax* · Riparian habitat · Rio Grande · Río Bravo · Invasive plants · Wildlife

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H. L. Mackey
Yosemite National Park, 5083 Foresta Rd, El Portal, CA 95318, USA

L. Y. Pomara (✉)
Southern Research Station, USDA Forest Service, 200 WT Weaver Blvd, Asheville, NC 28804, USA
e-mail: lazarus.y.pomara@usda.gov

J. E. Coffey
UCI-Nature, University of California Irvine, Irvine, CA 92697-2525, USA

E. M. Wood
Department of Biological Sciences, California State University Los Angeles, 5151 State University Dr., Los Angeles, CA 90032-8201, USA

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Introduction

Invasive plants contribute to wildlife habitat degradation, displacing native vegetation and changing ecosystem structures and processes, which can impact wildlife food resources, predation risk, and reproductive sites (Gurevitch and Padilla 2004; Litt and Pearson 2013; Pimentel et al. 2005). Riparian ecosystems are especially vulnerable to plant invasions, in part because they are subject to intense and frequent disturbance from both natural and human causes, including periodic flooding, damming, water diversions, and conversion to agricultural land uses (Poff et al. 2011; Richardson et al. 2007; Ringold et al. 2008). Invasion vulnerability poses special risks in riparian ecosystems because these systems also support unusually high biological diversity, including abundant and diverse terrestrial wildlife (Carothers et al. 2020; Naiman et al. 1993).

Managing invasive plants to restore and improve riparian habitats is complicated by diverse habitat associations among wildlife species, variable habitat associations at different spatial scales, and consideration of the broader vegetation mosaics that constitute wildlife habitat (McMillan et al. 2023; Richardson et al. 2007). Because wildlife species show variable habitat associations across scales, they may be impacted by invasive plants differently at different spatial scales (Cozzi et al. 2008; Fletcher and Hutto 2008; Kral et al. 2018; Thornton et al. 2011). This may be related to the relative dominance of invasive plants and other vegetation in the same vegetation mosaics, and how this relationship changes with spatial scale (McMillan et al. 2023). In this study we address these concerns by asking how invasive giant reed (*Arundo donax*), and other riparian vegetation that it displaces, influence habitat occupancies by bird and butterfly species at two management-relevant spatial scales along a desert riparian floodplain. Birds and butterflies are useful indicators of riparian habitat use because they are species-rich in these systems—representing diverse trophic levels, resource needs, and responses to habitat variability both within and between these two taxonomic groups—and they can be surveyed efficiently (Nelson and Andersen 1999; Nelson 2007; Rich 2002). Assessing both groups therefore provides a fuller picture of the potentially diverse impacts of invasive plants on wildlife habitat.

Colonization by nonnative giant reed has altered the structure and composition of vegetation in many riparian ecosystems in southern North America, with its largest impacts in southwestern desert riparian systems (Goolsby et al. 2023; Kato-Noguchi and Kato 2025; Lambert et al. 2010). This cane-like grass species typically grows 3 to 6 m high in the southwestern US, forms dense monospecific stands, and can also occur in mixed stands with other riparian vegetation (Goolsby et al. 2023). Giant reed can have wide-ranging effects including reduced plant, arthropod, and vertebrate abundance and diversity (Bruno et al. 2019; Cushman and Gaffney 2010; Herrera and Dudley 2003; Maceda-Veiga et al. 2016; Osbrink et al. 2017). Breeding birds may be impacted by the loss of foraging and nesting resources when giant reed displaces more diverse and structurally complex vegetation and suppresses arthropod abundances (Bruno et al. 2019; Giessow et al. 2011). Impacts on butterflies have not been well-studied, but the displacement of native herbaceous and shrub vegetation by giant reed may impact host plants and nectar availability (Hanula and Horn 2011; Kral-O'Brien et al. 2019; MacNally et al. 2004). In the Rio Grande floodplain in west Texas, multiple butterfly species showed their highest abundances at sites where native riparian vegetation had recovered after the removal of giant reed (Coffey et al. 2023).

Most studies reporting impacts of giant reed have focused on locally extensive monospecific stands. Such stands are typically concentrated where soil moisture is highest, including immediately along riverbanks (Briggs et al. 2021). At broader floodplain scales giant reed can be patchier, intermixing with other vegetation and constituting a lower proportion of total cover. It has been suggested that in such areas, localized impacts may be mitigated by other nearby vegetation, especially for highly mobile animals (Giessow et al. 2011). Management decisions may therefore depend on whether localized giant reed colonies have an outsized impact on landscape-scale habitat quality relative to other vegetation; how impacts at any scale may be mitigated by the presence of native vegetation; and how wildlife species respond to the vegetation types that benefit from giant reed control.

The objective of this study was to evaluate how invasive giant reed influences site occupancy by bird and butterfly species in desert riparian habitats, while

also accounting for the influence of other vegetation types, at different spatial scales relevant for habitat management. We assessed how impacts may vary across species and taxa by developing single-species occupancy models for multiple bird and butterfly species. We broadly expected that species occupancies would be lower at sites with higher giant reed cover, reflecting reduced resource availability for foraging and reproduction. We expected positive bird and butterfly associations with the mesic riparian vegetation that is displaced by giant reed, as these were floristically and structurally diverse, mostly native vegetation types. Further, we hypothesized that species that associate with other mesic vegetation types when giant reed cover is low may avoid those same types in areas that are more heavily invaded, suggesting an impact of giant reed beyond its immediate footprint. To test this, we examined interaction terms between giant reed and other mesic vegetation types in species occupancy models.

Since giant reed primarily occurs in near-riverbank portions of the floodplain, we expected the dominance of giant reed to decline relative to other vegetation components from the local patch to the floodplain-wide scale. We therefore also expected scale-dependency in giant reed impacts on species occupancies, with impacts declining at the floodplain scale, since floodplain-scale impacts might be more effectively mitigated by the influence of other vegetation types (Groom and Grubb, 2002; Rodewald and Bakermans 2006). To test this, we quantified major vegetation cover types, including giant reed, from high-resolution remotely sensed imagery at two spatial extents—local habitat within 100 m of survey locations, and broad-scale habitat within 500 m. The former acted as a measure of local vegetation associations for small-bodied wildlife species, and the latter approximated floodplain width in our study system to capture broader riparian vegetation context (Oneal and Rotenberry 2009).

The study was situated within a floodplain corridor along the Rio Grande (known in Mexico as the Río Bravo) in Big Bend National Park (BIBE) in the southwestern United States. The Rio Grande floodplain is a regional hotspot for biological diversity including high bird and butterfly species diversity (Carothers et al. 2020; Leslie 2016). This binational floodplain along the US-Mexico border is protected from development along the reaches we studied, but colonization by giant reed has nonetheless been heavy in recent decades. This study builds on efforts to inform riparian habitat management with an improved understanding of giant reed impacts on wildlife, in landscape context with other managed vegetation. Previous work in this system demonstrated community-level shifts in birds and butterflies following giant reed control efforts (Coffey et al. 2023) but less is known about how individual species respond to the presence of giant reed in relation to other vegetation types and across spatial scales.

Methods

Study area

The Rio Grande floodplain is surrounded by Chihuahuan Desert uplands and sits approximately 600 m above sea level at BIBE, marking the western, southern, and eastern boundaries of the park, and the international border between the United States and Mexico (Fig. 1). Outside of steep canyon reaches, the floodplain includes a mosaic of scoured riverbed, near-channel mesic shrubby and grassy-herbaceous vegetation, gallery riparian forest, and xeric upper-floodplain shrubby habitats, interspersed with rocky and bare soil areas (Weber and Weber 2017). Floodplain vegetation is diverse (Table 1), varying with patch disturbance history, floodplain position, and other factors. Non-native invasive plants of management concern include giant reed, tamarisk (*Tamarix* spp.), and Bermuda grass (*Cynodon dactylon*). As a fraction of total riparian vegetation, giant reed cover varies with floodplain morphology, soil moisture, and disturbance history (Fig. 2). Stands reach considerable size and density but are more fragmented than the most heavily invaded reaches in North America, along the lower Rio Grande in south Texas and coastal rivers in California (Everitt et al. 2005; Goolsby et al. 2023). Control efforts were implemented along some reaches we studied in years prior to our site sampling, with the goal to restore a diverse mix of native riparian plants through targeted prescribed fire and herbicide applications (Briggs et al. 2021). The response of birds and butterflies to those treatments and the associated native vegetation recovery has been reported elsewhere, using a subset of the study sites included here (Coffey et al. 2023). The

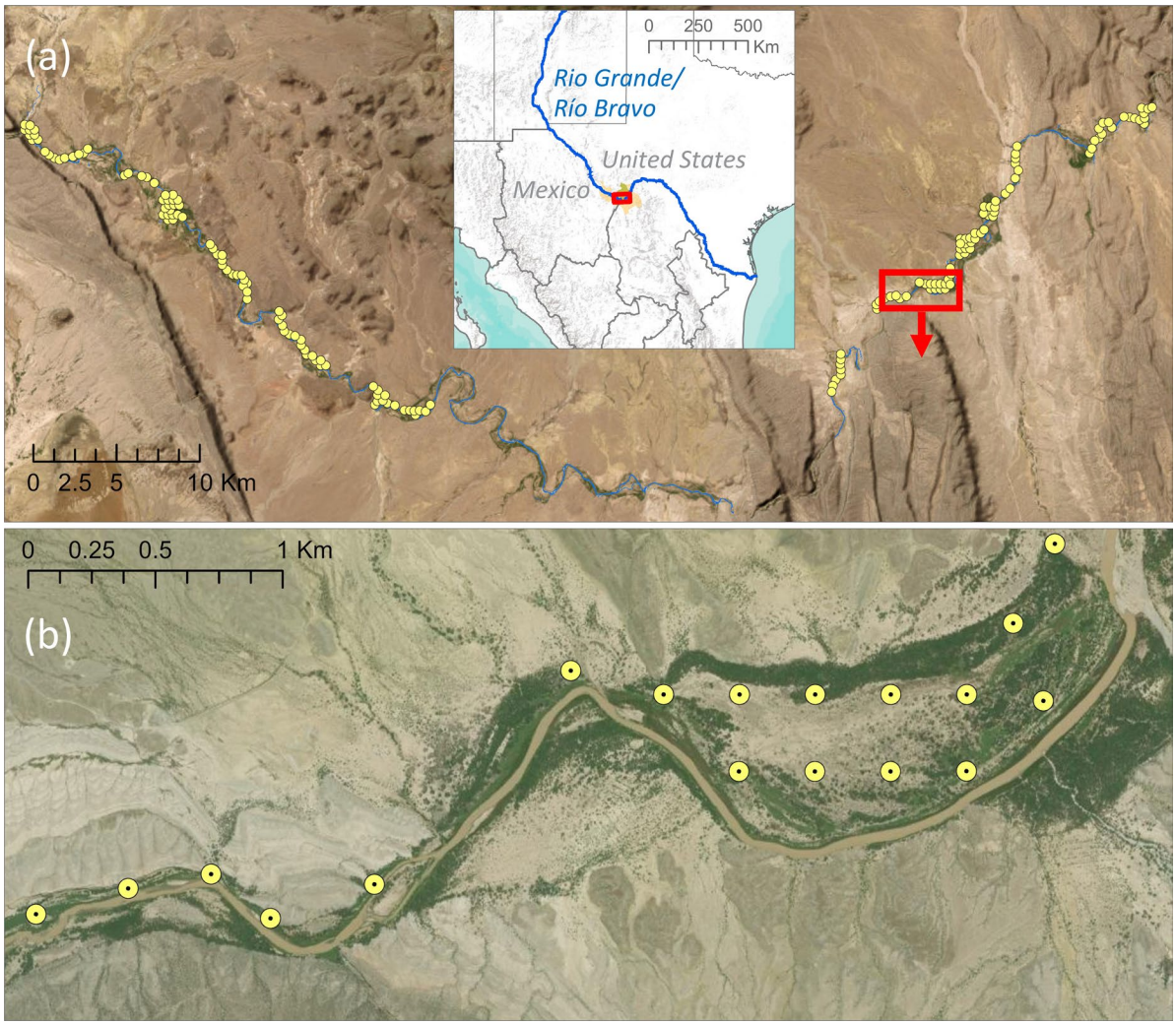

Fig. 1 Bird and butterfly survey locations in desert riparian habitat along the United States side of the Rio Grande/Río Bravo in west Texas. **a** 167 sites (yellow dots) along the river in Big Bend National Park. **b** A river reach showing sites within the floodplain, separated by at least 300 m

current study builds on this effort with broader coverage of the floodplain including many untreated sites, to quantify the influence of giant reed and other vegetation types on birds and butterflies separate from any treatment effects.

Bird and butterfly surveys and vegetation cover measurement

We established a systematic sampling design in the floodplain within BIBE (Fig. 1). For logistical reasons, field sampling was restricted to the U.S. side of the floodplain, but vegetation cover patterns are broadly similar in Mexico's portion 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 (not used for vegetation analysis), overlaid a 300 × 300 m grid, and placed candidate survey sites at grid intersections. Subsequent field-based selection to ensure accessibility resulted in 167 sites (Fig. 1).

We surveyed birds and butterflies at each site from May to July in 2016 and 2017. We conducted three counts at each site each year, with a fourth butterfly

Table 1 Vegetation type classification within the Rio Grande floodplain in BIBE, generated from analysis of a cloud-free, 1 m resolution national agriculture imagery program (NAIP) air photo mosaic collected in 2016

Vegetation class	Description	Representative plant taxa
Giant reed	Dense vegetation dominated by giant reed. Classification did not distinguish *A. donax* from *Phragmites australis* (common reed), a rare species in the study landscape	Strongly dominated by *A. donax*; *P. australis* rare (< 1%)
Mesic tree or shrub	Dominated by species typical of mesic, occasionally inundated riparian areas. Excluded tall, closed gallery forest (mesquite bosques)	*Salix* spp., *Baccharis salicifolia*, *Prosopis* spp., *Tamarix* spp., *Nicotiana glauca*, *Populus* spp., *A. donax*
Xeric tree or shrub	Dominated by species typical of xeric, less frequently inundated floodplain. Included large *Prosopis* stands (mesquite bosques), and more open mixed tree and shrub cover	*Prosopis* spp., *Acacia* spp., *Parkinsonia aculeata, N. glauca*, *Tamarix* spp., *Guaiacum angustifolium*, *Chilopsis linearis*, *Larrea tridentata*
Herbaceous (forb or grass)	Open areas characterized by many herbaceous wildflower and forb species and native and non-native grasses. Excluded *A. donax* and *P. australis*. *Cynodon dactylon* was the primary non-native, mat-forming grass	*Solanum* spp., *Machaeranthera* spp., *Helianthus* spp., *Allionia incarnata*, *Sphaeralcea* spp., *Chloracantha spinosa*, *C. dactylon*, *Sorghum halepense*

Representative plant taxa are not exhaustive but were common. adapted from Coffey et al. (2023)

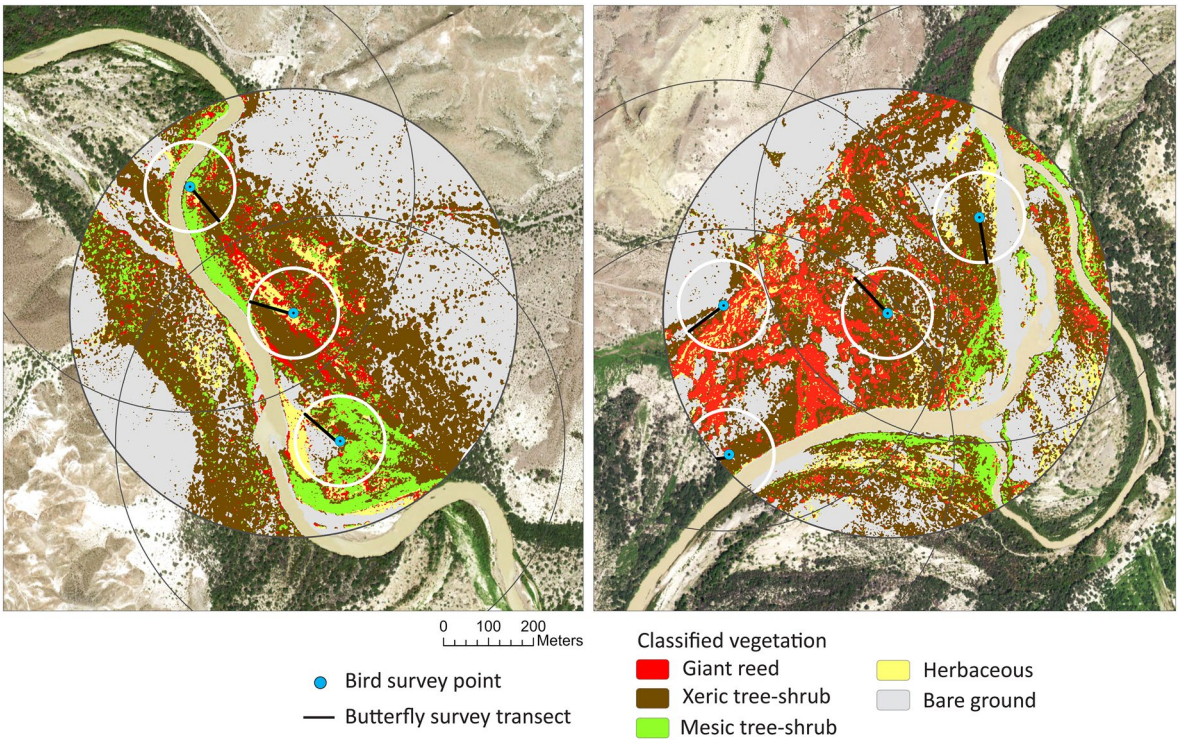

Fig. 2 Study site examples with vegetation cover classification overlaying the NAIP 1.0 m air photo mosaic that was used for the classification. The study design allowed analysis of relationships between the multiple vegetation types (including giant reed) and site occupancy by bird and butterfly species, analyzed at the 100 m radius (white circles) and 500 m radius (gray circles) scales, centered on each of the 167 survey sites

count in 2017 to capture mid-summer monsoonal activity. We used 5-min point counts to record all birds detected by sight or sound within a 100 m radius (Hutto et al. 1986; Ralph et al. 1995). We established a 10×100 m butterfly survey belt transect at each site, as close as possible to the point count location and oriented approximately parallel to the river. An observer slowly walked the centerline, recording butterflies within a 5 m grid (Brown and Boyce 1998). We established walking routes consisting of 10 to 15 survey sites each. One of two trained observers surveyed a walking route beginning 30 min before sunrise to conduct bird counts, then reversed direction to conduct the butterfly counts. We completed bird counts by 10:00 and butterfly counts between 10:00 and 14:00. The two surveyors alternated visits to routes and alternated walking route directions between visits to balance surveyor effort and time of day across sites. Surveys were not conducted during inclement weather.

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 (Fig. 2). To quantify the cover of vegetation classes from the NAIP image, we first defined four classes that broadly characterized floodplain vegetation and that were relevant for giant reed management and wildlife habitat management (Brand et al. 2008; Nelson and Andersen 1999). These classes were giant reed, xeric tree-shrub vegetation, mesic tree-shrub vegetation, and low herbaceous vegetation (i.e., forbs and grasses, excluding giant reed). While a diverse mix of woody tree and shrub species occurred in the floodplain, a basic distinction can be made between more mesic and more xeric formations influenced largely by soil moisture, with distinctive composition and structure (Hannon et al. 2009; Wauer 1973). The mesic and xeric tree-shrub classes distinguished these formations (Table 1).

We delineated these four classes through image segmentation and supervised classification of the NAIP image in ArcGIS 10.5.1 (ESRI 2017; Mountrakis et al. 2011). The training sample consisted of selected pixels within survey areas, assigned to classes using field-collected vegetation data and visual assessment, and visual image interpretation. The four classes were sufficiently broad that they were readily visually discernable both in the field—on the basis of the gross structural and floristic properties given in Table 1—and in high-resolution imagery. 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. Classification accuracy was 93.5% for a validation sample of 232 points (Coffey et al. 2023). The validation points were randomly distributed across classes, with the following sample sizes and accuracies: bare ground (n = 57; 100%); xeric tree-shrub (n = 72; 94%); mesic tree-shrub (n = 23; 91%); herbaceous (n = 42; 90%); giant reed (n = 42; 88%). Finally, we calculated cover proportions for each class within 100 m and 500 m radii around each bird survey location. The cover proportions excluded open water but accounted for bare ground as part of the total cover—the four vegetation class proportions therefore summed to less than 1.0 (Fig. 2).

Occupancy modeling

We used occupancy models to estimate species' site occupancies and relate these to site characteristics. Occupancy modeling allows for unbiased estimation of species-habitat relationships, relying on multiple site visits to estimate occupancy probability when detection probability is less than 1.0 (MacKenzie et al. 2018). We initially filtered all species detected during surveys by four criteria for inclusion in the analysis (Table S1). Only (1) riparian-obligate or riparian-affiliated bird species with (2) breeding populations in the study area were included, since we were interested in the potential impacts of giant reed on riparian habitat occupancy by species that depend on that habitat (Carothers et al. 2020). We were not aware of any similar classification of butterfly species by riparian habitat affiliation in the southwestern United States, but in general, butterfly abundances in southwestern desert habitats are strongly concentrated in riparian corridors, so we included all detected butterfly species for the first two criteria. Further, we only included species that were (3) detected on at least ten separate occasions and (4) whose initial intercept-only models converged. Flyover-only detections were also removed for all bird species, which effectively removed several species from the analysis including hawk, vulture, and swallow species.

We fitted single-season occupancy models to estimate species-specific, site-specific occupancy probability, using the *unmarked* package version 1.4 in

R version 4.3.0 (Fiske and Chandler 2011; MacKenzie et al. 2018; R Core Team 2023). We included site visits during both years to build a detection history across all six visits for birds, and all seven visits for butterflies. We modeled detection probability with observer and year as visit-level covariates. This allowed estimates to vary between the two observers with potentially different detection abilities, and the two years with differing conditions. If burning or herbicide application for giant reed control had occurred between the two survey years, which occurred at eight sites, we only included survey data for the first year (2016). In those cases, the 2017 visits were entered as no-data, which is accommodated by occupancy models (MacKenzie et al. 2018).

We used model selection and model-averaged parameter estimation to assess giant reed effects when considered additively and in interaction with the three other vegetation cover types. We ranked models within species using Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002). Our main goal was to understand the influence of giant reed on habitat occupancy, and we wished to minimize the number of candidate models to simplify interpretation. We therefore only considered additive and interaction models that included giant reed with one other variable, in addition to single-covariate models for all cover types. This resulted in ten models: each cover type alone, and giant reed plus one other cover type, with and without their interaction. We included these models at both landscape extents (100 m and 500 m radius circles), and we included the top detection-only model for comparison (i.e., the intercept model for site-level covariates). This resulted in a total of 21 models per species (Table S2). We initially examined collinearity among variables and found that the highest Pearson correlation between any two variables that occurred together in a candidate model was 0.36 (Table S2). Correlations were well within a typical recommended threshold of 0.60 to avoid multicollinearity problems (Dormann et al. 2013).

We used model averaging to estimate model parameters and their 90% confidence intervals, and to predict occupancy probability at the site level for each species (Burnham et al. 2011; Dormann et al. 2018). Final estimates of coefficients on the scaled covariates were the weighted average, weighting by the model Akaike weights w_i (Burnham and Anderson 2001). We report model-averaged estimates only for the covariates that occurred in at least one model in the 90% confidence set, i.e., the minimum list of lowest-AIC$_c$ models whose weights summed to at least 0.90. We considered the most important covariates to be those whose model-averaged coefficients had both higher absolute values than other cover types (i.e., effect size), and confidence intervals that did not include zero. Our choice of a 90% confidence interval reflects a desire to be conservative in considering possibly important effects, while also recognizing effect size as a criterion for comparing effects. We performed model selection and model averaging routines with the *AICcmodavg* package version 2.3 in R version 4.3.0, using functions *modavg* for parameter estimates and *modavgPred* for occupancy prediction (Mazerolle 2023; R Core Team 2023). To visualize relationships between giant reed and other cover types in the model results, we plotted predicted occupancy probabilities at the site level, together with giant reed cover proportions and other cover type proportions that were important for particular species.

Results

Of 65 bird species and 49 butterfly species detected at least once during surveys, 16 and 11 species, respectively, met our criteria to include in analysis (Table S1). Species model selection tables are provided in Tables S3–S29. We focus results reporting on the model-averaged effects of vegetation cover types on species occupancy probabilities, examining 90% confidence intervals to judge significance.

Vegetation effects across taxa

Giant reed showed negative effects on site occupancy for more bird species than did any other vegetation type, but no butterfly species showed a direct negative giant reed effect (Fig. 3). In contrast, the vegetation types that are mainly displaced by giant reed in the system we studied— mesic tree-shrub and herbaceous—had mostly positive effects on species occupancies. But the largest number of effects for both birds and butterflies were from the xeric tree-shrub vegetation type, in terms of the number of species affected and the overall number of effects at either

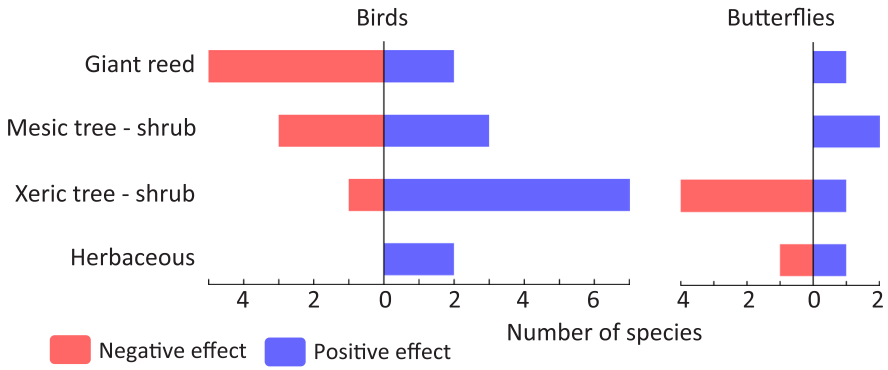

Fig. 3 Counts of bird and butterfly species showing vegetation cover effects on site occupancy. The x-axes show the number of species with main effects whose 90% confidence interval excluded zero (Figs. 5, 7). Giant reed had negative effects on more species than any other vegetation type, but only birds showed negative giant reed effects. Effects of the vegetation types that are mainly displaced by giant reed (mesic tree-shrub and herbaceous) were mostly positive

spatial scale. Those effects were largely positive for birds, and largely negative for butterflies (Fig. 3).

Model-averaged effect sizes of giant reed on individual species were within the range of effect sizes for other vegetation types, although the two strongest negative effects on birds were for giant reed on Lucy's warbler (*Leiothlypis luciae*) at both spatial scales (Fig. 4). Across vegetation types, positive effects had larger average effect size than negative effects (Fig. 4).

Birds

Giant reed had a negative effect on occupancy probability for five (31%) of 16 bird species, a positive effect on two species (13%), and nine species (56%) showed no direct effect (Figs. 5, 6). The two species with positive giant reed effects also had positive mesic tree-shrub effects, as did one additional species, while another three bird species had negative mesic tree-shrub effects. However, no bird species showed a significant interaction between giant reed and mesic tree-shrub cover where the main effects were also significant (Fig. 5).

Seven bird species showed positive xeric tree-shrub effects while only one species had a negative xeric tree-shrub effect. Two species showed interactions between giant reed and xeric tree-shrub cover. For *L. luciae*, a negative interaction suggested that its positive association with xeric tree-shrub cover weakened with increasing giant reed cover (Fig. 6). In contrast, Yellow-breasted chat (*I. virens*) showed positive

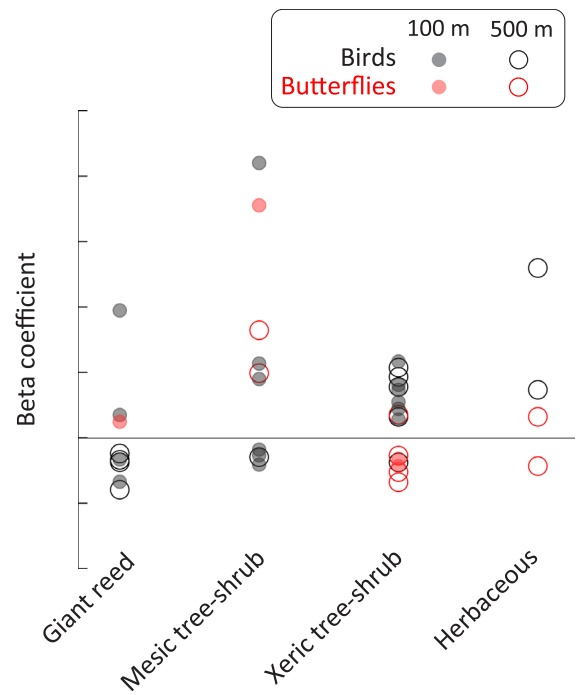

Fig. 4 Effect sizes of model-averaged vegetation cover effects on bird and butterfly site occupancy. Only main effects whose 90% confidence interval excluded zero are shown here (see Figs. 5, 7). Giant reed effect sizes were within the range of other vegetation classes, although the two strongest negative effects on birds were for giant reed (for *L. luciae* at both scales)

giant reed and xeric tree-shrub cover effects, with a positive interaction between them.

Two species, Mourning dove (*Z. macroura*) and White-winged dove (*Z. asiatica*), showed positive

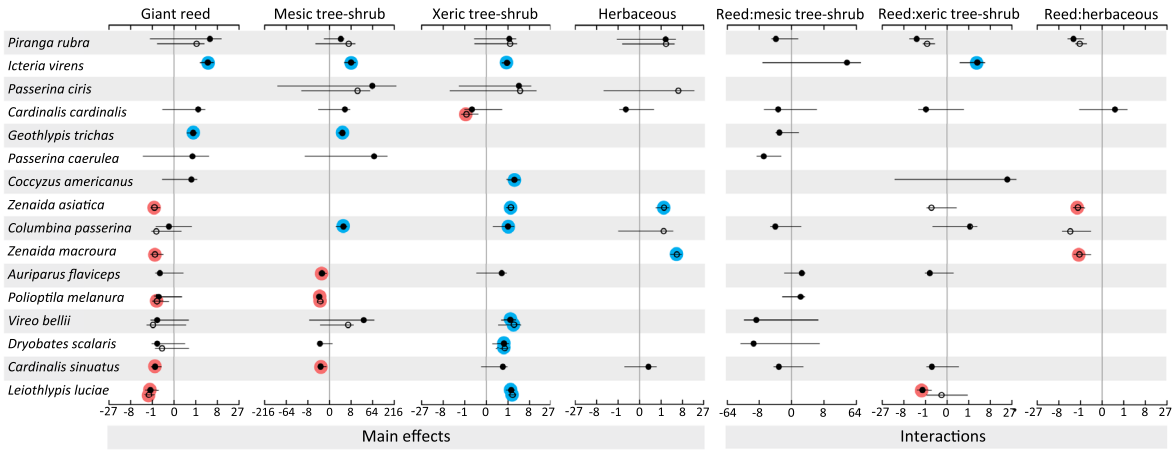

Fig. 5 Model-averaged effects of vegetation cover types on bird species occupancy (beta coefficients with 90% confidence intervals) at the local (100 m; solid dots) and floodplain (500 m; open dots) scales. Colors denote significant effects. Where estimates are missing, they did not appear in any model in the 90% confidence set. Species are ordered by giant reed effect size at the 100 m scale. Giant reed effects were mostly negative, mesic tree-shrub effects were mixed, xeric tree-shrub effects were mostly positive, and herbaceous effects were positive. Well-supported interactions were uncommon. X-axes use a cube-root scale to improve visualization of smaller effects and CIs

herbaceous cover effects. These effects both interacted negatively with giant reed, suggesting that the positive herbaceous cover associations weakened with increasing giant reed cover (Fig. 6). Common ground-dove (*C. passerina*) also showed a negative giant reed-herbaceous cover interaction, but CIs for the main effects included zero. Likewise, Summer tanager (*Piranga rubra*) showed negative interactions between giant reed and both xeric tree-shrub and herbaceous cover, but CIs for all main effects contained zero.

Butterflies

No butterfly species showed a negative giant reed effect, and only one species, Sleepy orange (*Abaeis nicippe*), showed a positive giant reed effect (Figs. 7, 8). Two species, Queen (*Danaus gilippus*) and American snout (*Libytheana carinenta*), showed positive mesic tree-shrub effects, and no species had a negative mesic tree-shrub effect. In contrast, only Checkered white (*Pontia protodice*) showed a positive xeric tree-shrub effect, while four species had negative xeric tree-shrub effects, including *A. nicippe*. Contrary to expectations only one species showed a positive herbaceous cover effect (Western pygmy-blue, *Brephidium exilis*), while Variegated fritillary (*Euptoieta claudia*) showed a negative herbaceous effect. No butterfly species showed interacting effects where the main effects were also significant (Fig. 7).

Spatial scale

Vegetation cover

The proportional cover of each of the four vegetation types was correlated between scales but tended to be higher at the local (100 m) scale than at the floodplain (500 m) scale (Fig. 9). However, this difference was stronger for giant reed than for any other vegetation type based on linear regression slopes (Fig. 9). This suggests that giant reed was more locally concentrated and less widespread across the floodplain than other vegetation. At its highest levels, giant reed cover could reach nearly 40 percent at the local scale, versus nearly 15 percent at the floodplain scale. Pearson correlation between the two spatial scales was also lower for giant reed than for the other vegetation types (Fig. 9). Xeric tree-shrub cover showed the highest mean and maximum values of any vegetation type at both scales, with values at the floodplain scale frequently above 40 percent (Fig. 9).

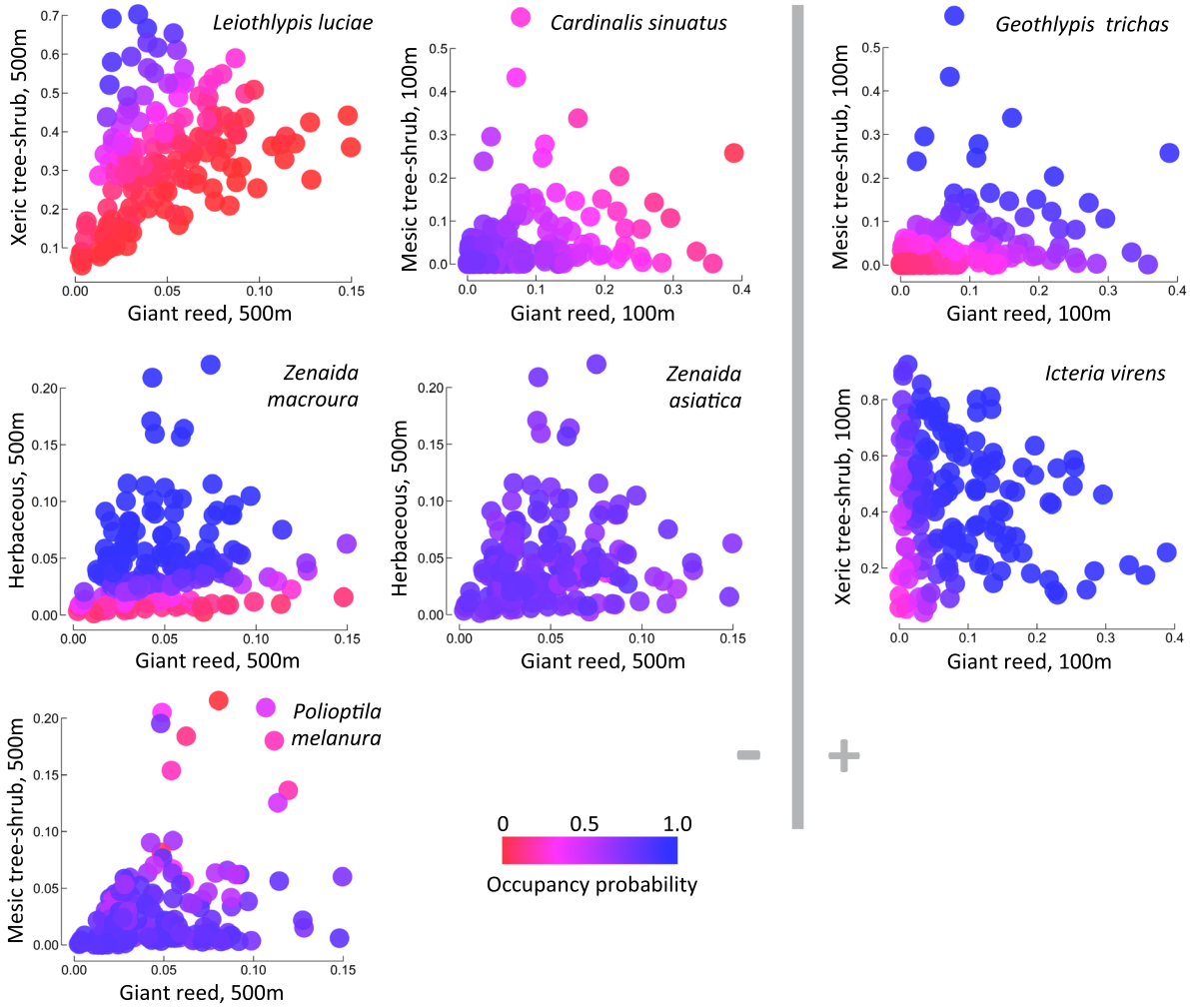

Fig. 6 Effect of giant reed cover proportion on the probability of site occupancy by bird species, across 167 sites. Species shown are those for which the 90% confidence interval for a giant reed effect did not contain zero (Fig. 5). Five species with negative giant reed effects are on the left, and two with positive giant reed effects are on the right. The variable on the y-axis is that with the largest model-averaged effect aside from giant reed (Fig. 5)

Occupancy effects

Across vegetation types, most effects on site occupancy occurred at the local scale for birds, and at the broader floodplain scale for butterflies (Table 2). But giant reed impacts, which primarily affected birds, occurred with equal frequency at both scales. This is notable given the sharp decline in giant reed cover proportion at the floodplain scale.

Vegetation effects were exclusively at the local or the floodplain scale for six and three bird species, respectively. Mesic tree-shrub effects on birds were at the local scale with only one exception, whereas the mainly positive xeric tree-shrub effects on birds occurred at both scales, and herbaceous effects were only at the floodplain scale (Fig. 5). For butterflies, vegetation effects were exclusively at the local or the floodplain scale for one and five species, respectively, and effects overall were twice as frequent at the floodplain scale (Table 2). Positive and negative effects occurred at both scales for various butterfly species, with no clear pattern across vegetation types (Fig. 7).

Whenever a significant vegetation effect occurred at both spatial scales for a given bird or butterfly species, the effect was always in the same direction. That is, there were no opposing effects between scales.

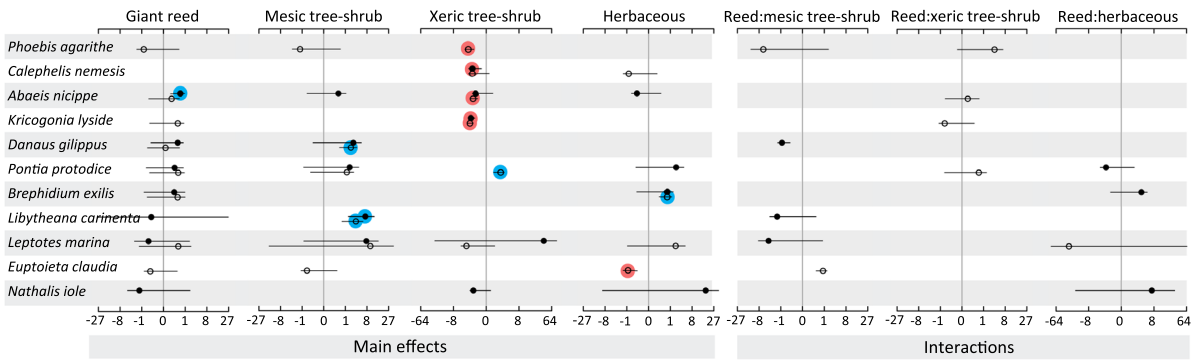

Fig. 7 Model-averaged effects of vegetation cover types on butterfly species occupancy (beta coefficients with 90% confidence intervals) at the local (100 m; solid dots) and floodplain (500 m; open dots) scales. Colors denote significant effects. Where estimates are missing, they did not appear in any model in the 90% confidence set. Species are ordered by giant reed effect size at the 100 m scale. There was little support for giant reed effects. Mesic tree-shrub effects were positive, xeric tree-shrub effects were mainly negative, and herbaceous effects were few and mixed. Well-supported interactions were rare. X-axes use a cube-root scale to improve visualization of smaller effects and CIs

This was consistent for near-significant effects as well (Figs. 5, 7).

Discussion

In this study we asked how bird and butterfly site occupancies are impacted by invasive giant reed, and by other major components of desert riparian vegetation, at two spatial scales. Several key findings emerged that indicate varying responses between birds and butterflies, as well as distinctive responses to giant reed in comparison to other vegetation types. First, giant reed impacted 31% of bird species negatively, while it showed no direct negative effects on butterflies. Second, birds and butterflies showed mostly positive associations with the mesic riparian vegetation types that are displaced by giant reed. Third, responses to xeric tree-shrub vegetation were common, but they were mostly positive for birds and negative for butterflies. Finally, vegetation associations occurred at both spatial scales for both taxa, but local effects were more frequent for birds while floodplain-scale effects dominated for butterflies. We focus the first part of our discussion on the implications of these wildlife-vegetation associations for efforts to control giant reed and restore riparian habitats. We then ask why avian and butterfly responses to giant reed differed. The ecological mechanisms driving the observed responses were not the object of this study, but we link our findings to available literature to highlight important avenues of continued research.

Giant reed in the context of riparian vegetation mosaics

Giant reed and other invasive plants such as *Tamarix* spp. (Brand et al. 2008; Waer et al. 2018) normally occur as a component of broader riparian vegetation mosaics. Habitat quality for highly mobile animals is influenced by multiple components of these mosaics, so that the impact of invasives may be shaped in part by this broader context (Richardson et al. 2007). Moreover, anticipating the consequences of invasive plant control requires understanding how habitat quality is affected by both invasives and the vegetation that benefits from restoration (Zavaleta et al. 2001).

Mesic tree-shrub and herbaceous vegetation have benefited the most among dominant vegetation types during recovery after giant reed control treatments in BIBE (Briggs et al. 2021; Coffey et al. 2023). These cover types had mostly positive effects on bird and butterfly occupancy—eight of the 27 species we studied (30%) showed positive associations with one of these two cover types. This together with the mostly negative effects of giant reed suggest that giant reed removal and subsequent passive revegetation are likely to benefit bird and butterfly habitats in this system. This comes with a caveat that we identified

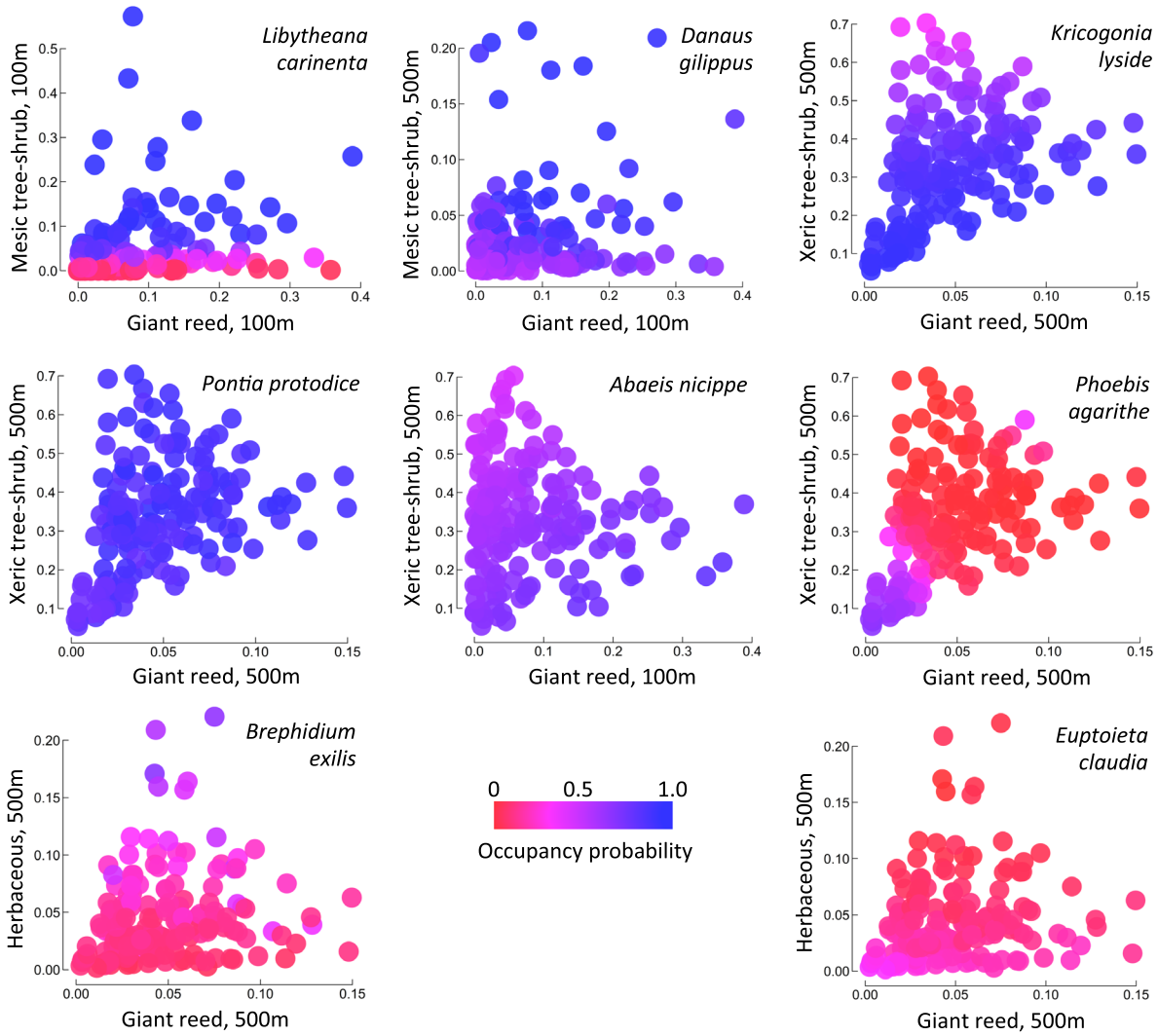

Fig. 8 Effect of vegetation cover proportions on the probability of site occupancy by butterfly species, across 167 sites. Giant reed is shown on the x-axis for comparison, but only one butterfly species (*A. nicippe*) had a model-averaged giant reed effect whose confidence interval did not contain zero. The variable on the y-axis is that with the largest model-averaged effect (Fig. 7)

positive giant reed associations for three species (*A. nicippe*, *I. virens*, and *G. trichas*). However, *I. virens* and *G. trichas* also showed positive associations with mesic tree-shrub vegetation, so it is unclear if those species would be negatively impacted by giant reed removal. Both *A. nicippe* and *I. virens* were identified in a previous study as indicator species not only for unmanaged habitat with an important giant reed component, but also for older giant reed removal sites with mostly native recovering mesic vegetation (Coffey et al. 2023). Thus, potentially negative consequences of giant reed removal may be compensated by subsequent native vegetation recovery even for these species.

Bird species with positive herbaceous cover associations were *Z. macroura* and *Z. asiatica*, both ground-foraging species. Both also showed negative interactions with giant reed, consistent with the expectation that the quality of herbaceous habitat was degraded for these species where it was more intermixed with giant reed stands. Only one butterfly species, *B. exilis*, showed a positive relationship with

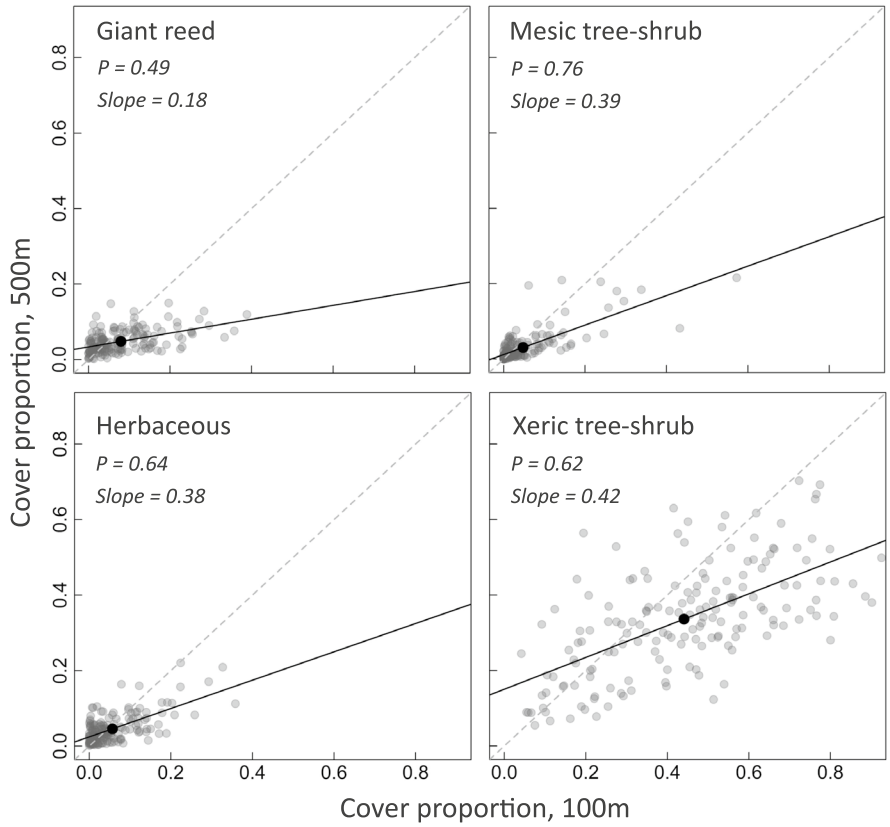

Fig. 9 Cover proportions of major riparian vegetation types at two spatial scales, at 167 survey sites (gray dots). The reduction in cover proportion from the 100 m scale to the 500 m scale was stronger for giant reed than any other cover type. Dotted lines are the one-line, where values are equal between scales. Solid lines and slope values are based on linear regression; the larger black dots are mean values. *P* = Pearson correlation coefficient

Table 2 Spatial scale of vegetation cover effects whose 90% confidence interval excluded zero (Figs. 5, 7). The numbers of species with main effects are shown, with rounded percentages based on the 16 bird and 11 butterfly species included in analyses

Scale of effect	Birds	Butterflies	Both taxa
All vegetation types			
100 m only	6 (38%)	1 (9%)	7 (26%)
500 m only	3 (19%)	5 (45%)	8 (30%)
Both	4 (25%)	3 (27%)	7 (26%)
Neither	3 (19%)	2 (18%)	5 (19%)
Giant reed only			
100 m only	3 (19%)	1 (9%)	4 (15%)
500 m only	3 (19%)	0 (0%)	3 (11%)
Both	1 (6%)	0 (0%)	1 (4%)
Neither	9 (56%)	10 (91%)	19 (70%)

Most effects on species occupancy occurred at the local (100 m) scale for birds, and at the broader floodplain (500 m) scale for butterflies

herbaceous cover—fewer than expected given the role of herbaceous vegetation in providing nectar sources and larval host plants (Hanula and Horn 2011; Kral-O'Brien et al. 2019; Mac Nally et al. 2004). The remote sensing-based herbaceous cover class we used did not distinguish forb and grass species, and in particular the invasive grass *C. dactylon* forms localized matts in mesic riparian habitat in BIBE (Coffey et al. 2023). It is possible that the inclusion of grass cover made it difficult to detect effects of forb cover, which is a more important resource for the butterfly species we examined.

The xeric tree-shrub cover we quantified was dominated by closed-canopy mesquite (*Prosopis* spp.) gallery forest stands—known regionally as mesquite bosques—with a secondary component of sparse xeric shrub cover. The differing responses to xeric tree-shrub vegetation between birds and butterflies are likely related to the role of these gallery

forest stands. Mesquite bosques provide diverse avian nesting and foraging opportunities and harbor a large number of riparian-associated bird species and other vertebrate wildlife in desert riparian systems in the US (Brand et al. 2008; Johnson et al. 2020a, 2018). But the closed structure of these dense stands is not favored by most butterfly species, likely due to low light penetration to the ground layer and limited nectar resources (Hannon et al. 2009).

Mesquite bosques occupy a higher floodplain position than more mesic vegetation (Johnson et al. 2020a) and they are not strongly displaced by giant reed. Nonetheless, our findings for Lucy's warbler (*L. luciae*) suggest the potential for giant reed to degrade gallery forest habitats for some species, when these vegetation types co-occur within the riparian mosaic. *L. luciae* breeds and forages primarily in mesquite bosque habitat in the US desert southwest (Johnson et al. 2020b), and it was restricted to this habitat at our study sites. However, the negative interaction we found between giant reed and xeric tree-shrub cover for *L. luciae* suggests that it avoids this habitat where it is intermixed with giant reed stands.

Giant reed control may therefore show different wildlife benefits depending on site location relative to riparian gallery forests including mesquite bosques. Given that butterflies showed floodplain-scale negative associations with xeric tree-shrub cover including mesquite bosques, restoration sites further from gallery forest in more open, near-stream channel reaches may maximize benefits for butterflies. At the same time, bird species such as *L. luciae* that occupy gallery forest but have negative giant reed associations could benefit from giant reed removal near gallery forest. The siting of restoration efforts may therefore involve tradeoffs among different wildlife benefits depending on landscape context. Such tradeoff considerations likely extend to additional benefits of invasive plant control that is strategically sited to improve stream channel dynamics and sediment movement, reduce wildfire risks, and improve recreational use opportunities (Litt and Pearson 2013; Shelby and Whittaker 2020; Wieting et al. 2023).

Perhaps our most surprising finding regarding spatial scale was the difference between birds and butterflies, with most butterfly habitat associations occurring at the floodplain scale. Butterflies appeared to maintain site occupancies in association with the broader landscape mosaic of mostly native vegetation, even when giant reed was locally present (but note that we did not examine butterfly abundance changes). This highlights that butterflies in desert riparian systems may select habitat at larger spatial scales than their immediate foraging environment; large-scale habitat selection by butterflies has also been found in grassland and wetland study systems (Cozzi et al. 2008; Kral-O'Brien et al. 2019; Kral et al. 2018). We suggest that a mitigating influence against giant reed impacts on butterflies is likely exerted by the mosaic of other vegetation at the floodplain scale, at least in situations where giant reed is a minor component of total cover at that scale.

In contrast, our results suggest that giant reed has an outsized effect on avian habitat occupancies relative to its abundance. All riparian vegetation types including giant reed had higher cover proportions at the local scale than at the floodplain scale, consistent with the limits imposed by floodplain morphology and diminishing soil moisture at higher floodplain positions. It is therefore not surprising that riparian-associated birds responded to local vegetation cover. However, while proportional giant reed cover declined from the local to broad scale at nearly twice the rate as the other vegetation types, giant reed impacts on birds remained broadly consistent between scales. This suggests that bird occupancies were sensitive to giant reed cover even when it was a small fraction of total vegetation at the floodplain scale.

These different findings for birds and butterflies further suggest the importance of considering invasives removal in a landscape context (Zavaleta et al. 2001). Given that giant reed may never be fully removed from invaded systems, maximizing the benefits of control efforts for wildlife may involve assessing the mitigating influence of other floodplain vegetation, accepting that isolated giant reed stands in otherwise well-vegetated reaches may be tolerable, and targeting restoration where it can consolidate native vegetation mosaics along large reaches.

Why do birds and butterflies respond differently to giant reed?

Explaining direct impacts of giant reed on particular species will depend on studying ecological mechanisms related to avian nest site availability, butterfly larval host plant abundances, and foraging resource availabilities for both taxa (Hannon et al. 2009; Litt and Pearson 2013). However, indirect evidence suggests that giant reed stands have low value as

immediate habitat for either birds or butterflies as a group. Avian habitat quality depends crucially on the structure and composition of vegetation and on arthropod prey availability, whereas native riparian plants and a wide variety of ground-dwelling and aerial arthropods show reduced abundance and diversity in giant reed stands (Cushman and Gaffney 2010; Herrera and Dudley 2003; Maceda-Veiga et al. 2016; Osbrink et al. 2017, 2018). It also appears unlikely that butterflies in either their larval or adult stages use invasive giant reed. Giant reed produces a suite of chemical defense compounds and physical defenses (silica phytoliths) that limit herbivory by arthropods; few herbivores of giant reed have been found in the United States; and giant reed is not a source of nectar (Kato-Noguchi and Kato 2025; Tracy and DeLoach 1998). Finally, although we situated surveys randomly to sample all vegetation and only some transect sections passed through giant reed (Fig. 2), we detected essentially no adult butterflies immediately within dense giant reed stands during field sampling. (Potentially lower butterfly detectability in giant reed stands did not appear to influence our findings, since this would create bias towards negative effects, whereas we found no such effects. Birds were also unlikely to show this bias, since detections were primarily by sound).

It is therefore unclear whether differences in the direct use of giant reed stands can explain the different responses we found between birds and butterflies. Our findings concerning spatial scale point instead to another possibility. Across all vegetation types, birds showed mostly local-scale associations, whereas butterflies showed mostly floodplain-scale associations. Given the unusually strong decline in importance of giant reed cover from the local to the floodplain scale, it may be expected that taxa with stronger sensitivity to local-scale conditions show stronger giant reed impacts. This would also be consistent with a potentially mitigating influence of broadscale mesic riparian vegetation for butterflies but not birds. The possibility that the basic scales of habitat selection influence which taxa are most susceptible to localized invasive plant cover is compelling (Kral et al. 2018). Speculatively, this could be related to strong territoriality and fixed home ranges in riparian breeding birds versus low territoriality and high mobility in the butterfly species we studied (Cozzi et al. 2008; Scott 1992). But this remains beyond the scope of the current study.

Conclusions

Our findings highlight taxon-specific and multi-scale wildlife habitat associations in relation to an invasive plant that strongly reshapes overall riparian habitat structure and composition. Giant reed impacts on riparian birds were mostly negative. Despite a lack of direct negative giant reed impacts on butterflies, findings confirm the value of mesic woody and herbaceous riparian vegetation as restoration targets for butterflies and birds, and contribute to a growing understanding of context-dependent effects of invasive plants on wildlife. Ecosystem management approaches that strategize invasive plant control in the context of whole vegetation mosaics can be advanced by considering the variety of influences exerted on wildlife habitat by invasive plants and the other vegetation with which they occur.

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Data availability All datasets used in the analyses reported in this manuscript are publicly archived at the open data publishing platform Zenodo: https://doi.org/10.5281/zenodo.17725851.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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