Riparian bird density decline in response to biocontrol of Tamarix from riparian ecosystems along the Dolores River in SW Colorado, USA

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Riparian bird density decline in response to biocontrol of *Tamarix* from riparian ecosystems along the Dolores River in SW Colorado, USA

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Abstract Biocontrol of invasive tamarisk (*Tamarix* spp.) in the arid Southwest using the introduced tamarisk beetle (*Diorhabda elongata*) has been hypothesized to negatively affect some breeding bird species, but no studies to date have documented the effects of beetle-induced defoliation on riparian bird abundance. We assessed the effects of tamarisk defoliation by monitoring defoliation rates, changes in vegetation composition, and changes in density of six obligate riparian breeding bird species at two sites along the Dolores River in Colorado following the arrival of tamarisk beetles. We conducted bird point counts from 2010 to 2014 and modeled bird density as a function of native vegetation density and extent of defoliation using hierarchical distance sampling. Maximum annual defoliation decreased throughout the study period, peaking at 32–37% in 2009–2010 and dropping to 0.5–15% from 2011–2014. Stem density of both tamarisk and native plants declined throughout the study period until 2014. Density of all bird species declined throughout most of the study, with Song Sparrow disappearing from the study sites after 2011. Blue Grosbeak, Yellow-breasted Chat, and Yellow Warbler densities were negatively related to defoliation in the previous year, while Lazuli Bunting exhibited a positive relationship with defoliation. These findings corroborate earlier predictions of species expected to be sensitive to defoliation as a result of nest site selection. Tamarisk defoliation thus had short-term negative impacts on riparian bird species; active restoration may be needed to encourage the regrowth of native riparian vegetation, which in the longer-term may result in increased riparian bird density.

Keywords Defoliation · Density · Phenology · Point counts · Tamarisk beetles

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Introduction

Biocontrol of invasive plants using defoliating insects has been implemented successfully in many areas of the world. For example, introduction of the leaf-feeding beetle *Zygogramma bicolorata* and stemgalling moth *Epiblema strnuana* has reduced the density of both adults and seeds of the invasive forb *Parthenium hysterophorus* in Australia (Dhileepan 2001), resulting in greater grass production for livestock (Dhileepan 2007). Similarly, introduction of multiple defoliating insects to control *Mimosa pigra* in Australia has led to reductions in the seed bank of this invasive shrub (Routley and Wirf 2006). Biocontrol has successfully controlled 61% of targeted invasive plant species in South Africa, with no documented negative impacts to non-target species (Moran et al. 2005). While most proposed biocontrol agents undergo a rigorous screening procedure to ensure host specificity to reduce the risk of direct impacts on non-target species (e.g. Moran et al. 2005; Wilson et al. 2011), indirect non-target effects are more difficult to predict (Courchamp et al. 2011). Indirect impacts may result when the targeted invasive species serves as an ecological replacement for displaced native species, through alterations in food web structure, or when the targeted species responds in a compensatory manner to herbivory (Pearson and Callaway 2005). Few studies have investigated the indirect effects of defoliating biocontrol agents on vertebrate communities (but see Bateman et al. 2015).

Riparian corridors of the southwestern United States were historically dominated by cottonwood (*Populus fremontii*) and willow (*Salix gooddingii*; Webb et al. 2007), but much of this vegetation has been replaced by exotic tamarisk (*Tamarix* spp.) (Friedman et al. 2005; Shafroth et al. 2005). These changes have occurred especially in regions where livestock grazing takes place and the natural hydrology has been disrupted (Glenn and Nagler 2005; Hultine et al. 2010). Where present, tamarisk can occur as a significant component in a mosaic of riparian plant species, or as monotypic stands (Ohmart et al. 1988; Stromberg 1998; Shafroth et al. 2005). Tamarisk invasion further disrupts the ecosystem by increasing soil salinity (Ladenburger et al. 2006; Yin et al. 2009) and fire frequency (Busch 1995), altering local hydrological processes (Blackburn et al. 1982; Robinson 1965), and disrupting mycorrhizal associations (Meinhardt and Gehring 2012), thereby creating conditions that prevent the regeneration of native vegetation (Busch and Smith 1995).

Tamarisk removal is a high priority for many environmental agencies due to the economic costs of tamarisk invasion (Zavaleta 2000). Traditional control methods, such as herbicide and mechanical removal, are costly and often have non-target impacts (Hultine et al. 2010), although they are still being implemented at many sites (Tamarisk Coalition 2009). In 2001, the Asian tamarisk leaf beetle (*Diorhabda elongata*) was released as a biocontrol agent at seven sites throughout the Southwest (DeLoach et al. 2003). Beetle populations were established in Colorado, Wyoming, Nevada, and Utah, quickly spreading throughout the region and leading to widespread tamarisk defoliation (Dennison et al. 2009; Meng et al. 2012; Jamison et al. 2015). Repeated herbivory and defoliation can result in up to 40% tamarisk mortality near release sites within 5 years (Hultine et al. 2010), although beetle-induced tamarisk mortality may be lower in areas far from release sites that have lower beetle density (Dudley et al. 2001). In addition, reduced defoliation rates have been observed over time due to a presumed increase in herbivory defense mechanisms by tamarisk plants (Dudley and DeLoach 2004). The replacement of defoliated or dead tamarisk with native riparian vegetation is not guaranteed and in some cases may be hindered by increased grazing access, soil salinity, or altered geochemistry (Bay and Sher 2008; Shafroth et al. 2008; Stromberg et al. 2009). If tamarisk serves as an ecological replacement of native vegetation for riparian bird species, then biocontrol has the potential to negatively affect these species via indirect methods if native vegetation does not regrow quickly (Pearson and Callaway 2005).

Numerous studies have investigated the impact of tamarisk invasion on bird communities, with mixed results; some studies reveal a negative impact on species richness or a strong preference for native vegetation by breeding or migrating birds (Anderson and Ohmart 1977; Rice et al. 1983; Yong and Finch 1997; Yong et al. 1998; Kelly and Finch 1999; DeLoach et al. 2000; Kelly et al. 2000), while other studies demonstrate widespread use of tamarisk or functional equivalency between tamarisk and native vegetation for birds (Hunter et al. 1988; Brown and Trosset 1989; Ellis 1995; Fleishman et al. 2003; Cerasale and Guglielmo 2010; Sogge et al. 2013). This discrepancy has been attributed to geographical or altitudinal dependency of the response, variation in tamarisk structure, and species- or guild-specific variation in responses (Hunter et al. 1988; 2006, 2008). Additionally, mixtures of tamarisk and native vegetation may support higher bird species richness (van Riper et al. 2008) and increased insect abundance (Drost et al. 2003; McGrath and van Riper 2005) than pure native vegetation or tamarisk monocultures, providing adequate habitat for species of conservation concern (Sogge et al. 2008) and superior stopover habitat for some migrant landbirds (Paxton et al. 2008; Walker 2008; Cerasale and Guglielmo 2010). Thus, biocontrol of tamarisk using a defoliating insect may have short-term negative impacts on riparian bird communities that use this invasive shrub for foraging or breeding.

Defoliation has the potential to negatively impact riparian birds in the short-term by decreasing insect abundance and nest success due to increased solar radiation or loss of nest camouflage (Paxton et al. 2011; Peterson et al. 2015). The extent of any negative effect will depend on such factors as selection of tamarisk for breeding, within-season overlap between nesting activities and defoliation periods, and any mitigating factors such as tamarisk beetles providing additional food resources. Tamarisk beetles were originally hypothesized to provide additional food for insectivorous birds (Longland and Dudley 2008; Paxton et al. 2011); however, a recent studies suggests they may not be preferred by most bird species (Puckett and van Riper 2014; Mahoney et al. 2017), and it is unknown if this additional food would counteract the potential loss in nest survival as a result of defoliation-related exposure.

The purpose of our study was to track the responses of both vegetation and riparian birds at two sites experiencing annual tamarisk defoliation, by monitoring site-level responses of bird species density to defoliation and changing vegetation community structure. To our knowledge, this is the first study to document the responses of riparian birds to tamarisk biocontrol. Our goals were: (1) to determine if defoliation in this system continues year after year or declines over time; (2) to determine if native vegetation density increases in response to tamarisk defoliation and mortality; and (3) to test the hypothesized effects of annual tamarisk defoliation on riparian bird density. We model the effects of native vegetation in the current year and defoliation in the previous year on bird density; given that defoliation occurs in the latter part of the breeding season, we expect any immediate effects on bird density (due to within-season emigration) to be negligible and/or undetectable given our methods, while declines in productivity or survival of riparian breeding birds might result in decreased bird density the following year.

Methods

Study area

We conducted our study at two sites [Middle Dolores (MIDO), 38.04390°N, 108.89185°W; Lower Dolores (LODO), 38.30705°N, 108.89305°W] along the Dolores River, a tributary of the Colorado River that flows through southwest Colorado and southeast Utah (Fig. 1). Each study area encompassed a 4-km stretch of the Dolores River where beetle defoliation of tamarisk was present. At both sites, riparian vegetation was predominantly tamarisk and willow, mixed with sumac (*Rhus trilobata*) and desert olive (*Forestiera neomexicana*) especially at MIDO. Upland vegetation surrounding the riparian corridor was pinyon (*Pinus edulis*) –juniper (*Juniperus* spp.) woodland with a scrub component of big sage (*Artemisia tridentata*) and greasewood (*Sarcobatus* spp.). Trees were largely absent from both sites, except for a few individual boxelder (*Acer negundo*) and Gambel oak (*Quercus gambelii*) trees at MIDO and a single cottonwood at LODO. At both sites, stands of mature cottonwood were present within 2 km of the study areas.

Bird point counts

Bird point count stations were established within the riparian corridor at each site (23 at LODO, 20 at MIDO), spaced a minimum of 200 m apart running parallel to the river. Observers visited each station at least three times per year from 2010 to 2014, between 31 May and 31 July each year when avian breeding activities take place and late spring passage migrants have already moved through. We considered the population open due to births and deaths. Each point count comprised a 1-min “settling period” after the observer reached the station, followed by a 5-min count period during which the observer recorded all birds seen or heard within 100 m, recording species identity and distance from observer. While distance estimation to singing birds is notoriously difficult (Alldredge et al. 2007), the open habitat of our study sites allowed observers to use hand-held laser range finders to measure exact distances for visual detections

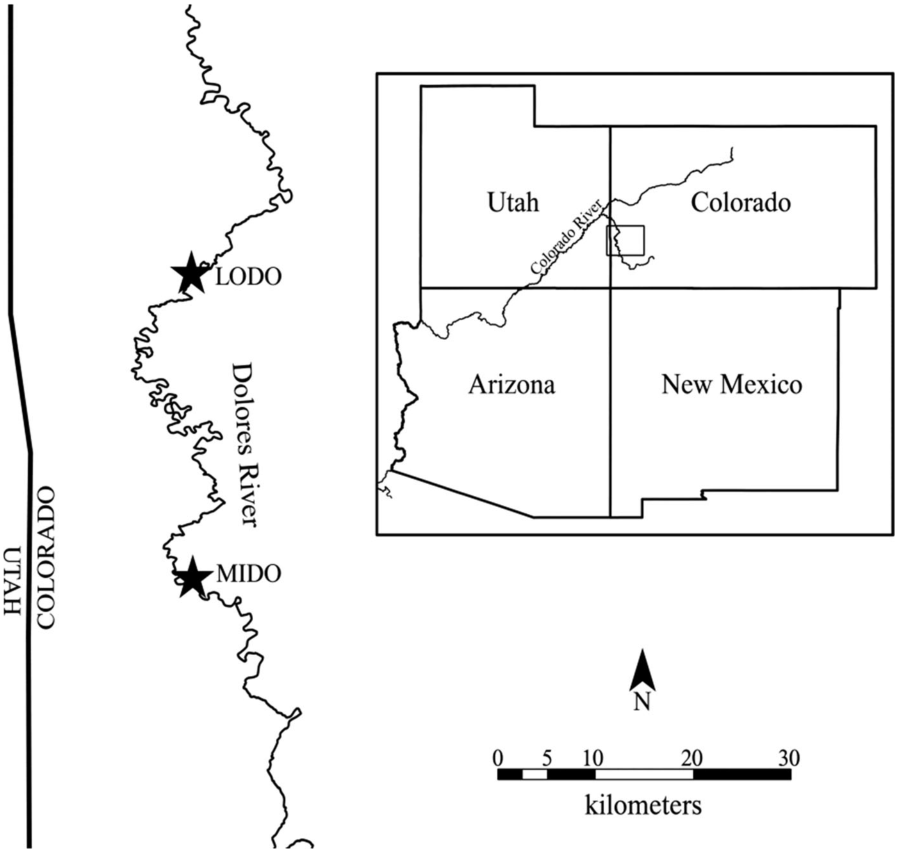

Fig. 1 Map of study areas where tamarisk (*Tamarix* spp.) defoliation, vegetation density, and riparian bird species density were recorded along the Dolores River from 2009 to 2014

and to ascertain the border of the 100-m radius cutoff. Counts were conducted between a half hour before sunrise to 1000 h, when bird vocal activity was highest, and when wind was less than 5 on the Beaufort Scale (where dust, leaves, and loose paper are lifted and small tree branches move).

Vegetation and defoliation

To monitor changes in vegetation density and composition over time, we measured vegetation once per season (during a late June or early July visit) within 10 11.3-m radius circular plots at each site placed at 100-m intervals approximately 25 m from the river bank. In a modification of the protocol described in James and Shugart (1970), observers walked through the diameter of the circle, perpendicular to the river, while holding a 2-m pole parallel to the ground at breast height. Observers counted all woody stems less than 7.5 cm diameter that touched the pole, identifying each to species; these counts were subsequently used to estimate stem density of each shrub species at each site. We tested for a significant trend in tamarisk density and native vegetation density at each site with a linear model of vegetation density as a function of year.

Starting in 2009, observers assessed the extent of tamarisk defoliation during each site visit using visual phenology assessments sensu van Riper (1980) and McGrath et al. (2009). Observers sampled 100 individual tamarisk trees along an established transect at each site, and for each individual tree, the observer visualized a full canopy and estimated the percent composed of green and brown (beetle damaged) foliage, with 100% green representing a fully leafed-out canopy of all green leaves. Observations from 100 individual trees were averaged for each visit to obtain estimates of current conditions (average % green leaf and % brown leaf). This visual estimation method produces similar results to more rigorous measures using a digital camera (McGrath et al. 2009). For analysis, brown leaf was used as a measure of defoliation, and average defoliation per site per year was multiplied by the proportion of tamarisk estimated from the vegetation density measurements.

Data analysis

We estimated density of the six obligate or dependent riparian passerines (Rich 2002) detected in more than 1 year during the study: Common Yellowthroat (*Geothlypis trichas*), Yellow Warbler (*Setophaga petechia*), Yellow-breasted Chat (*Icteria virens*), Song Sparrow (*Melospiza melodia*), Lazuli Bunting (*Passerina amoena*), and Blue Grosbeak (*Passerina caerulea*). We estimated bird density in a Bayesian framework using an open hierarchical distance sampling model sensu Kéry and Royle (2016, p. 518; Appendix S1). We modeled bird abundance as a function of time (linear trend), mean defoliation at each site in the previous year, and density of native vegetation at each site and year, with all parameters modeled with a species-specific random slope. We derived average density of each species per site per year by dividing the estimated abundances by the area surveyed (number of point counts multiplied by a 100-m radius) and number of visits per site per year. To model detection probability, we used the half-normal detection function with random effect of species and fixed effect of year to account for observer differences among years. We used wide uniform priors for all coefficients in the models (Appendix S1). Parameters were estimated using Markov Chain Monte Carlo with Gibbs sampling as implemented in the program JAGS 4.2.0 (Plummer 2016), called from program R 3.3.2 (R Core Team 2015) using package jagsUI (Kellner 2015). We ran three parallel chains for 100,000 iterations, with the first 50,000 iterations discarded as burn-in. We assessed convergence by inspecting the trace plots and using the Gelman-Rubin diagnostic ($\hat{R} < 1.1$; Brooks and Gelman 1998).

Results

Vegetation and defoliation

At the start of the study, MIDO had denser vegetation cover than LODO (232 vs. 159 stems/ha, respectively) and less tamarisk cover (9 vs. 31%; Table 1). Total native stem density at MIDO declined from 212 stems/ha in 2010 to 94 stems/ha in 2014, and native stem density at LODO declined from 109 to 57 stems/ha from 2010 to 2014, resulting in a significant decrease in native vegetation density over time (trend coefficient = − 0.81, 0.13 SE, $p < 0.001$). Willow experienced the greatest decline of all native vegetation species, declining by 46% at MIDO and 85% at LODO by 2014. In contrast, upland native vegetation species experienced lesser declines followed by an increase in density in 2014 (Table 1). Stem density of tamarisk also declined at both sites over time (− 0.65, 0.13 SE, $p = 0.001$), therefore we could not test for a positive response in native vegetation to loss of tamarisk. Tamarisk disappeared from MIDO by 2012, though seven tamarisk sapling stems were recorded in 2014.

Peak tamarisk defoliation occurred in 2009–2010, when LODO lost 32–36% of tamarisk canopy (10% of total canopy cover) and MIDO lost 36–37% of tamarisk canopy (3% of total canopy cover). Extent of defoliation declined in subsequent years at both sites, with tamarisk canopy cover losses of 1–9%in all subsequent years (Fig. 2). Averaged among years, defoliation began after 23 June, reaching peak values between 18 July and 10 August (Fig. 3).

Bird density

Blue Grosbeak and Yellow-breasted Chat were the most frequently recorded species throughout the study, followed by Yellow Warbler, Common Yellowthroat, and Lazuli Bunting (Table 2). Lazuli Bunting was only observed once each during years 2012 and 2013, followed by a jump to 42 observations in 2014 (Table 2). Song Sparrow was encountered infrequently (11 observations) and not recorded at all in years 2011, 2013, and 2014 (Table 2). Willow Flycatcher was recorded only three times, all in 2013, and thus was not included in the density estimates (Fig. 4). All species except Lazuli Bunting showed significant declining trends in density (Table 3, Fig. 4). Blue Grosbeak, Yellow-breasted Chat, and Yellow Warbler densities were negatively related to defoliation in the previous year, while Lazuli Bunting exhibited a positive relationship with defoliation (Table 3). All species except Song Sparrow were negatively correlated with native shrub stem density (Table 3).

Table 1 Mean (± SE) stem densities (# per hectare) per year of nine woody plant species at two sites [Middle Dolores (MIDO) and Lower Dolores (LODO)] along the Dolores River in southwestern Colorado

Site/year	Willow *Salix gooddingii*	Tamarisk *Tamarix* spp.	Desert Olive *Forestiera neomexicana*	Rabbitbrush *Ericameria* spp.	Sumac *Rhus trilobata*	Greasewood *Sarcobatus* spp.	Big Sage *Artemisia tridentata*	Salt Bush *Atriplex* spp.	Baccharis *Baccharis* spp.
MIDO									
2010	105.9 (17.5)	19.9 (15.1)	27.8 (8.7)	18 (4.4)	20.3 (7.9)	3 (1.5)	16.5 (7.8)	0.9 (0.9)	0
2011	84.6 (7.9)	7.5 (5.4)	17.6 (6.9)	17.5 (5.2)	18.5 (7.5)	3.7 (3.0)	14.9 (5.1)	0	4.8 (3.3)
2012	62.3 (29.7)	0	14.6 (6.8)	5.1 (3.0)	16.8 (6.1)	4.7 (4.0)	7.7 (3.3)	0	1 (0.8)
2013	67.3 (27.5)	0	10.2 (5.1)	5.9 (2.8)	9.0 (3.9)	0.2 (0.2)	1.8 (0.8)	0	0
2014	56.8 (28.3)	0.7 (0.6)	15.5 (7.5)	8.1 (3.1)	17.8 (4.5)	2.3 (2.3)	7.6 (5.3)	0.3 (0.2)	0
LODO									
2010	54.8 (26.9)	50.8 (28.8)	6.2 (2.7)	6.5 (3.0)	1.0 (1.0)	30.3 (12.2)	8.2 (2.5)	0	0
2011	57.3 (12.8)	36.1 (11.0)	2.0 (1.0)	7.4 (3.3)	1.4 (1.4)	4.4 (2.6)	7.7 (2.5)	0	2.4 (1.8)
2012	25.9 (12.4)	32.7 (6.2)	2.1 (1.7)	7.5 (3.2)	0	10.4 (4.0)	8.3 (3.8)	0.5 (0.4)	0
2013	15.6 (13.1)	15.5 (7.8)	1.1 (0.8)	2.4 (2.2)	0	5.6 (2.7)	1.8 (0.9)	0	0
2014	8.2 (8.2)	6.9 (2.7)	4.7 (3.1)	15.8 (10.5)	0	8.9 (3.0)	10.2 (4.2)	0	0

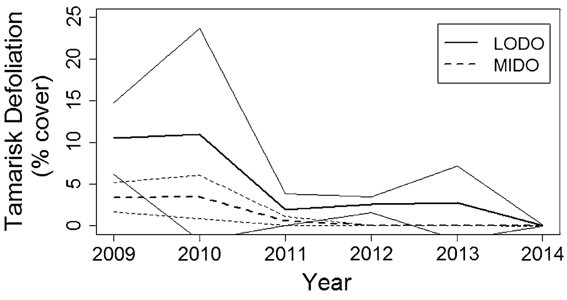

Fig. 2 Mean annual percent canopy cover (with 95% CI) affected by tamarisk defoliation, a function of average defoliation of 100 individual tamarisk trees multiplied by the relative density of tamarisk stems, estimated separately for two sites [Middle Dolores (MIDO) and Lower Dolores (LODO)] along the Dolores River in southwestern Colorado

Discussion

Given the geographic variation observed in bird responses to tamarisk invasion and restoration efforts, with a heavy focus in the literature on studies along the Lower Colorado River (reviewed in Walker 2006), this study provides a complementary perspective from a little-studied region where tamarisk occurs. Like many other studies (Shafroth et al. 2005; Walker 2006; Stromberg et al. 2007; Bay 2013), we found that native riparian vegetation does not regenerate quickly in response to defoliation, and thus active replanting and/or hydrology manipulation will be necessary if the goal is to restore sites to their original state. Furthermore, we provide the first evidence of indirect negative effects of defoliation on the riparian bird community, despite the fact that our study area contained a significant component of native vegetation; defoliation would likely have more severe impacts on birds at sites with less cover of native vegetation. Indirect negative impacts of biocontrol on riparian breeding birds would be of great concern when dealing with small populations of endangered species or subspecies such as the Southwestern Willow Flycatcher (*E. traillii extimus*). This highlights the difficulty in predicting the consequences of biocontrol and the need for follow-up monitoring (Courchamp et al. 2011).

Defoliation rates declined over time throughout the study, with almost no defoliation recorded in 2014. Reduced defoliation rates were observed at some sites after the first few years following beetle release in Utah (Meng et al. 2012), in Colorado (Jamison et al. 2015), and the Virgin River in Nevada (Nagler et al. 2012). It has been hypothesized that tamarisk can adapt to heavy insect herbivore pressure, leading to reduced defoliation and mortality (Dudley and DeLoach 2004). Extent of defoliation and mortality also varies widely among sites, with some variation resulting from tamarisk stand structure and soil salinity (Hultine et al. 2015). Beetles along the Dolores River enter diapause in late summer, after

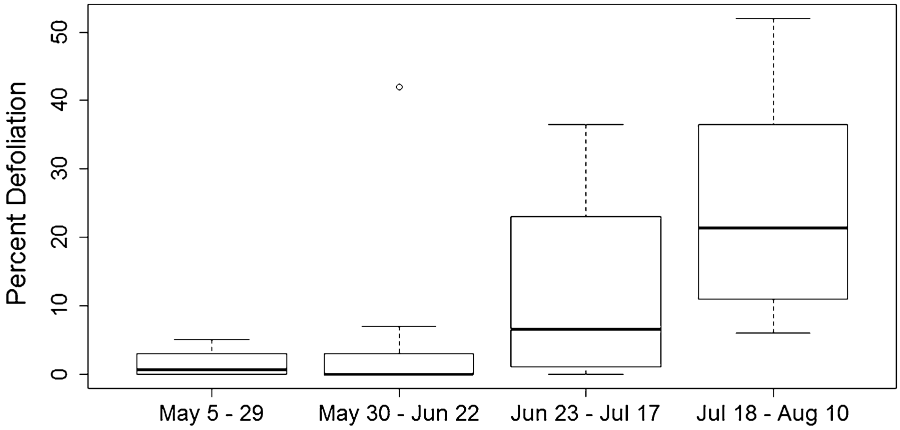

Fig. 3 Seasonal phenology of beetle defoliation (measured as percent brown leaf) of tamarisk (*Tamarix* spp.), averaged among years (2009–2014) and sites along the Dolores River in southwestern Colorado. Boxes represent 25–75% interquartile ranges (IQR), lines represent medians, and whiskers represent data range excluding outliers (> 1.5 times IQR), open dots indicate outliers

Table 2 Raw counts, summed across point counts and visits, of seven obligate riparian bird species observed during 5 years at two study areas along the Dolores River in southwestern Colorado

Species	Raw counts					Corrected counts				
	2010	2011	2012	2013	2014	2010	2011	2012	2013	2014
BLGR	31	50	106	42	34	8.2	8.3	7.1	4.7	5.7
COYE	15	25	26	27	22	2.5	1.7	2.9	4.5	5.8
LAZB	11	6	1	1	42	0.7	0.7	0.2	0.3	7.0
SOSP	9	0	2	0	0	1.0	0.0	0.5	0.0	0.0
WIFL	0	0	0	3	0	0.0	0.0	0.0	0.3	0.0
YBCH	102	167	213	127	95	17.0	43.9	35.5	8.5	10.6
YEWA	13	37	65	40	45	3.4	6.2	4.3	4.4	7.5

Corrected counts represent raw counts divided by the number of site visits per year

which tamarisk can produce new green leaves before fall senescence (Jamison et al. 2015), perhaps representing a slightly mismatched phenology between the beetles and tamarisk that prevents full resource exploitation by the beetles and dampens their impact on tamarisk relative to other locations. Tamarisk beetles are also known to make episodic movements and can undertake long-distance dispersal following local depletion of resources (Bean et al. 2013; Jamison et al. 2015). While we cannot elucidate the causes of the reduced defoliation rates in the last 2 years at our study sites, it is important to note that this coincided with the return of some species including Lazuli Bunting and the first detections of Willow Flycatcher. A review of ongoing studies at other locations experiencing tamarisk biocontrol may eventually reveal patterns that will allow us to better predict which sites are likely to experience recovery of tamarisk foliage and which sites will continue to experience high levels of defoliation and mortality.

As tamarisk density declined due to defoliation-induced mortality, it was not replaced by native riparian vegetation; overall vegetation density decreased throughout the study period until 2014, when density of upland shrubs began to increase in the riparian corridor. The decline in native vegetation might be due to a combination of ongoing drought in the Southwest (Cayan et al. 2010), exacerbated by trampling by livestock observed at the study sites, and could have contributed to the observed decline in bird species density. Revegetation of native woody riparian vegetation might not be expected within the time frame of this study (Ostoja et al. 2014), but the lack of willow or cottonwood saplings detected suggests that additional restoration management will be necessary at these sites to encourage regeneration of native plant

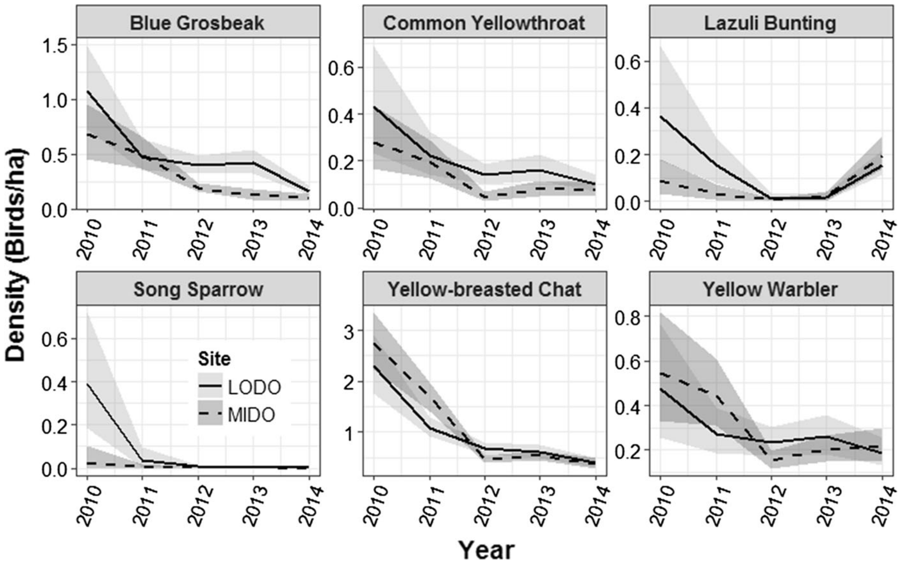

Fig. 4 Mean density of six obligate riparian bird species during the breeding seasons of 2010–2014 at two sites [Middle Dolores (MIDO) and Lower Dolores (LODO)] along the Dolores River in southwestern Colorado. Error bars represent 95% Bayesian Credible Intervals

species. In particular, restoration of natural hydrology conducive to sprouting and survival of native seedlings is often essential to successful revegetation of sites (Bay 2013; Shafroth et al. 2013).

The densities of three of six riparian bird species were negatively affected by tamarisk defoliation, density of one species was positively correlated, and densities of two species were apparently unaffected by defoliation along the Dolores River in Colorado. Five of these relationships are consistent with the predictions by Paxton et al. (2011; Table 1) based on species-specific nesting habitat preferences, with Yellow Warbler, Yellow-breasted Chat, and Blue Grosbeak predicted to be sensitive to defoliation, and Common Yellowthroat and Lazuli Bunting not predicted to be sensitive to defoliation. The one exception was Song Sparrow, which did not have a significant relationship between density and defoliation in our study but it was predicted to be sensitive to it (Paxton et al. 2011). However, the relatively few observations of Song Sparrow (n = 11) made modeling the effects of defoliation difficult, as evidenced by the wide Bayesian Credible Intervals around the Song Sparrow defoliation coefficient estimate in Table 2. It is possible that Song Sparrow experienced local extinction due to defoliation events preceding the study; on the other hand, more than half of its breeding activity takes place before the onset of defoliation in mid-June (Arcese et al. 2002), thus its disappearance may not be due to reduced productivity resulting from defoliation, rather it may indicate either a preference for defoliated habitats or a change in food abundance related to defoliation.

While we did not model Willow Flycatcher density due to the small number of observations (n = 3), this species began to appear in the study area after 2012, corresponding to years of decreased tamarisk defoliation. This species may be particularly sensitive to defoliation because it readily nests in tamarisk shrubs (Sogge et al. 2008), productivity is strongly correlated with foliage density (Paxton et al. 2007; Peterson et al. 2015), and it initiates nesting relatively late in the season, with 80% of the nesting season potentially occurring after defoliation begins (Paxton et al. 2011). It is unknown whether this species was present at the study area before defoliation.

Management implications

Biocontrol of tamarisk using a defoliating beetle has the potential to do more harm than good to the riparian ecosystem if other conservation measures are not taken. The lack of willow or cottonwood regrowth detected during the study suggested that the sites are

Table 3 Effects of mean tamarisk defoliation in the previous year, linear time trend, and stem density of native shrubs on the average density of six obligate riparian bird species during the breeding seasons of 2010–2014 at two sites along the Dolores River in southwestern Colorado

Parameter	Mean	SD	2.5% BCI	97.5% BCI
Defoliation effect				
BLGR	− 2.31	0.57	− 3.43	− 1.19*
COYE	− 0.73	0.80	− 2.33	0.82
LAZB	7.00	1.67	3.85	10.48*
SOSP	3.43	2.83	− 1.98	9.24
YBCH	− 2.02	0.38	− 2.76	− 1.27*
YEWA	− 2.15	0.71	− 3.56	− 0.78*
Linear time trend				
BLGR	− 1.07	0.14	− 1.37	− 0.80*
COYE	− 0.57	0.17	− 0.92	− 0.23*
LAZB	1.28	0.31	0.71	1.92*
SOSP	− 2.13	0.98	− 4.32	− 0.47*
YBCH	− 0.68	0.09	− 0.86	− 0.50*
YEWA	− 0.49	0.14	− 0.76	− 0.23*
Native shrub effect				
BLGR	− 1.24	0.19	− 1.62	− 0.87*
COYE	− 0.64	0.25	− 1.12	− 0.16*
LAZB	1.91	0.49	0.99	2.92*
SOSP	− 1.03	1.17	− 3.59	1.04
YBCH	− 0.56	0.13	− 0.81	− 0.32*
YEWA	− 0.61	0.20	− 1.00	− 0.23*

*Indicates parameter significance

not on a trajectory toward restoration of native riparian forest. Given this, we suggest that active management such as replanting or hydrological manipulation in conjunction with biocontrol might be necessary to encourage regrowth of willow and cottonwood and thus increase density of riparian breeding birds. Invasive plant eradication efforts in other regions of the world have similarly demonstrated that biocontrol is more effective when combined with other management actions (e.g. Paynter and Flanagan 2004; Lym 2005). This study also highlights the potential danger of using defoliating insects for biocontrol when the targeted invasive has high value for wildlife in an altered ecosystem. An alternative strategy may be to use biocontrol that targets the reproduction of the invasive plant; for example, the use of gall-forming and seed-feeding insects has successfully halted the spread of invasive Australian acacia in South Africa while preserving existing stands that have commercial value (Moran et al. 2005).

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Authors contributions CVR conceived and designed the research, supervised and assisted with data collection, and edited the paper; AJD assisted with data collection, performed the analyses and wrote the paper.

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