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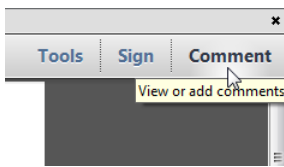
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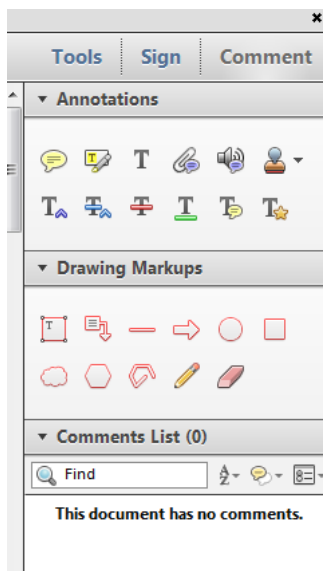
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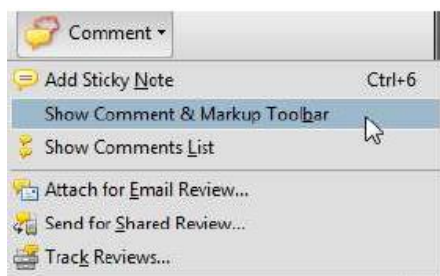


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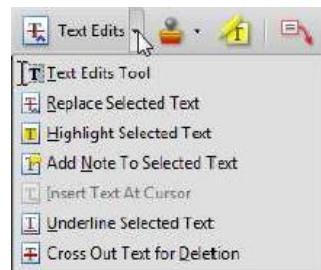
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RESEARCH ARTICLE

Tamarisk biocontrol alters bird community composition in the absence of cottonwood and willow vegetationSean M. Mahoney,^{1,2,*} Matthew J. Johnson,³ Jennifer A. Holmes,³ Tom L. Dudley,⁴ Michael Kuehn,^{4,5} and Tad C. Theimer¹¹ Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona, USA² Department of Biological Sciences, Thompson Rivers University, Kamloops, British Columbia, Canada³ Colorado Plateau Research Station, Northern Arizona University, Flagstaff, Arizona, USA⁴ Marine Science Institute, University of California, Santa Barbara, Santa Barbara, California, USA⁵ Bloom Research Inc., Santa Ana, California, USA*Corresponding author: sm2275@nau.edu

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ABSTRACT

Invasive plants threaten biodiversity worldwide, but control of non-native species may affect native species in complex ways. Non-native tamarisk (*Tamarix* spp.) is widespread in western U.S. riparian environments, and tamarisk beetles (*Diorhabda* spp.), a tamarisk-specific herbivore, were subsequently introduced as biocontrol. The primary effect of biocontrol is defoliation and branch dieback, with repeated defoliation killing the plant. We investigated the initial stages of site recovery after biocontrol and how tamarisk decline affected birds, their arthropod prey, and microclimate. We compared avian community diversity and composition, arthropod abundance, humidity, and temperature at sites along the Virgin River in Nevada and Arizona, USA characterized as either mixed native vegetation, tamarisk-dominated, or tamarisk-dominated where the majority of tamarisk died from biocontrol. We compared avian communities sampled after biocontrol to counts at the same locations before biocontrol. Prior to biocontrol, community compositions of all but one site grouped together using unbiased clustering algorithms. Following biocontrol, tamarisk-dominated sites grouped separately, and mixed sites grouped with the pre-biocontrol cluster. Comparison of pre- and post-biocontrol communities showed 7 common species declined by $\geq 30\%$ in dead tamarisk sites, while one species did so at mixed sites and 3 at tamarisk-dominated sites. Individual census points in dead tamarisk had significantly lower Simpson diversity than the same points censused before biocontrol, unless native vegetation was present, suggesting tamarisk death was the cause of dominant species abundance changes. Tamarisk-dominated sites were hotter and drier than sites with native vegetation and supported fewer non-tamarisk-obligate arthropods, consistent with the hypothesis that bird reductions were driven by changes in microclimate and prey abundance. How long these effects last will depend upon the rate of native vegetation recovery after biocontrol, therefore we recommend monitoring sites to determine the trajectory of vegetative recovery and considering the need and feasibility of active restoration in those sites with slow or no native regeneration.

Keywords: biological control, bird communities, defoliation, riparian, tamarisk, tamarisk beetles, Tamarix

LAY SUMMARY

- Invasive species disturb ecosystems and threaten biodiversity. Invasive species management, such as biological control, can cause additional disturbances, so quantifying how native species respond to invasive control is important to inform best management practices
- We quantified southwestern bird communities in sites that varied in the amount of the non-native plant tamarisk (*Tamarix* spp.), before and after biological control efforts
- Following biocontrol, we found significant differences in community composition and diversity, and several bird species declined by $\geq 30\%$
- Bird declines were ameliorated in the presence of native vegetation, consistent with the hypothesis that tamarisk biocontrol decreases prey availability and alters microclimate
- We recommend land managers monitor areas dominated by tamarisk after biocontrol, and if re-establishment of native vegetation is slow or lacking, consider the feasibility of active restoration

El control biológico del tamarisco altera la composición de la comunidad de aves en ausencia de vegetación de álamos y sauces

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RESUMEN

Las plantas invasoras amenazan la biodiversidad en todo el mundo, pero el control de las especies no nativas puede afectar a las especies nativas de formas complejas. El tamarisco (*Tamarix* spp.), una especie no nativa, está muy extendido en los ambientes ribereños del oeste de los EEUU, y el escarabajo del tamarisco (*Diorhabda* spp.), un herbívoro específico del tamarisco, fue introducido posteriormente como control biológico. El efecto principal del control biológico es la defoliación y el secado de las ramas, haciendo que la defoliación repetida mate la planta. Investigamos las etapas iniciales de la recuperación del sitio después del control biológico y cómo la disminución del tamarisco afectó a las aves, sus presas artrópodos y el microclima. Comparamos la diversidad y composición de la comunidad de aves, la abundancia de artrópodos, la humedad y la temperatura en sitios a lo largo del Río Virgin en Nevada y Arizona, EEUU, caracterizados como vegetación nativa mixta, dominada por tamariscos, o dominada por tamariscos donde la mayoría de los tamariscos murió a causa del control biológico. Comparamos las comunidades de aves muestreadas después del control biológico con conteos realizados en los mismos sitios antes del control biológico. Antes del control biológico, las composiciones de las comunidades de todos los sitios menos uno se agruparon juntas utilizando algoritmos de agrupamiento no sesgados. Después del control biológico, los sitios dominados por tamariscos se agruparon por separado y los sitios mixtos se agruparon con el grupo previo al control biológico. La comparación de las comunidades antes y después del control biológico mostró que siete especies comunes disminuyeron en $\geq 30\%$ en los sitios de tamariscos muertos, mientras que una especie lo hizo en sitios mixtos y tres en sitios dominados por tamariscos. Los puntos de censo individuales en tamariscos muertos tuvieron una diversidad de Simpson significativamente menor que los mismos puntos censados antes del control biológico, a menos que hubiera vegetación nativa presente, lo que sugiere que la muerte de los tamariscos fue la causa de los cambios en la abundancia de las especies dominantes. Los sitios dominados por tamariscos fueron más cálidos y secos que los sitios con vegetación nativa y albergaron menos artrópodos no obligados de los tamariscos, lo que concuerda con la hipótesis de que la reducción de las aves estuvo impulsada por cambios en el microclima y en la abundancia de presas. La duración de estos efectos dependerá de la tasa de recuperación de la vegetación nativa después del control biológico; por lo tanto, recomendamos monitorear los sitios para determinar la trayectoria de la recuperación vegetativa y considerar la necesidad y viabilidad de la restauración activa en aquellos sitios con regeneración nativa lenta o nula.

Palabras clave: comunidades de aves, control biológico, defoliación, escarabajo del tamarisco, ribereño, tamarisco, *Tamarix*

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INTRODUCTION

Non-native plant introductions may alter the structure, composition, and function of habitat, potentially changing the relative value of the habitat for the native faunal community (Vilà et al. 2011). Globally, non-native species are becoming increasingly widespread in introduced ranges, and may interact with native faunal communities in a variety of ways (reviewed in Rodríguez 2006, Hobbs et al. 2009, 2018), so management of non-native introductions has become an important goal in conservation biology. Classical biological control (hereafter, biocontrol) is a common cost-effective approach to manage naturalized non-native species. Introductions of biocontrol may also interact with native species in complex ways (Pearson and Callaway 2003); therefore, quantifying the responses of native species to non-native biocontrol is important to understand implications for the broader ecological community and to inform best management practices.

In the western United States, non-native tamarisk (*Tamarix* spp., also known as saltcedar), is now the third most dominant woody riparian plant (Friedman et al. 2005). To manage the continued spread of tamarisk, a biological control agent, the tamarisk beetle (*Diorhabda* spp.), an herbivorous tamarisk-obligate insect from southern

Europe and North Africa that consumes tamarisk foliage, was introduced into the United States in 2001 (Bean et al. 2013). Since the release, tamarisk beetles have defoliated thousands of hectares of tamarisk in the western U.S. (Sogge et al. 2008, Dudley and Bean 2012, Nagler et al. 2012). The tamarisk beetle was expected to colonize new areas slowly due to physiological diapause limitations (DeLoach et al. 2000, Lewis et al. 2003, USDA 2005), but in roughly ten generations tamarisk beetles adapted and established populations across a broader geographic area than anticipated (Bean et al. 2013).

Tamarisk spread and subsequent biocontrol is a conservation concern for native bird communities because although only 1% of the western USA landscape is riparian habitat, these areas support disproportionately more breeding birds than do surrounding upland habitats (Johnson et al. 1977, Stevens et al. 1977, Skagen et al. 1998, Cartron et al. 1999). The effect of tamarisk invasion on native riparian birds is complex depending on geographic region, climate, and stand composition, and it is confounded by variation in climate and stand composition. A variety of birds will use and breed in tamarisk (Hunter et al. 1988, Sogge et al. 2008, 2013), but several studies have documented lower avian abundance and richness in tamarisk relative to native Fremont cottonwood (*Populus fremontii*)

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	and willow (<i>Salix</i> spp.) stands, and in areas where high summer temperatures may preclude nesting in tamarisk because it lacks the multi-layered canopy cover of native stands (Anderson and Ohmart 1977, Ellis 1995, Brand et al. 2008). Others have argued that total vegetation volume and structural diversity drives richness and diversity independent of the identity of the dominant tree (Fleishman et al. 2003, Cable et al. 2015, Raynor et al. 2017). A confounding factor in studies evaluating the role of tamarisk as habitat for native birds may be variation across study sites in the abundance of tamarisk relative to native vegetation, as use by native birds may depend upon the presence and relative abundance of native trees within a stand (Holmes et al. 2005, Sogge et al. 2008, van Riper et al. 2008; and reviewed in Shafroth et al. 2005).	
3.5		herbivory. During both sampling periods, sites were characterized as either mixed native vegetation (50–75% of canopy comprised of native vegetation), or tamarisk-dominated vegetation (70–90% canopy was tamarisk), allowing a comparison of sites differing in the amount of tamarisk, while in the later sample tamarisk-dominated sites could be separated into those in which tamarisk were defoliated but not dead as a result of beetle herbivory compared to sites in which most tamarisk were dead or dying.
3.10		We analyzed avian community responses to vegetation change at the landscape scale by comparing communities across sites and at a smaller local scale more representative of individual territory size by comparing individual census points that differed in the presence or absence of a native plant component. At the larger spatial scale of sites, we predicted bird communities would be more diverse in sites with a mix of native and tamarisk vegetation than in sites dominated by tamarisk prior to biocontrol. After biocontrol, we predicted avian community diversity would be lower in tamarisk-dominated sites that experienced dieback and death due to defoliation by the tamarisk beetle. At smaller spatial scales, we predicted that diversity at census points with some native vegetation would be higher than at points that lacked a native component. Finally, although we lacked pre-biocontrol data, we predicted that after biocontrol, arthropod abundance would be lower, temperature higher and humidity lower in tamarisk-dominated sites that experienced dieback and death due to loss of foliage.
3.15	Much less is known about avian responses to biocontrol of tamarisk. Biocontrol could affect birds positively in the short term by increasing prey abundances for bird species that include tamarisk beetles and their larvae in the diet, and in the long term if biocontrol is successful in allowing native riparian vegetation to replace tamarisk (Paxton et al. 2011). The potential for tamarisk beetles to serve as prey for birds is supported by studies from tamarisk-dominated riparian areas of northern Nevada that documented higher indices of bird use and greater avian diversity in tamarisk stands in which tamarisk beetles and their larvae were present compared to stands lacking beetles (Longland and Dudley 2008, Bean et al. 2013). In contrast, fecal diet analyses of native insectivorous birds in southern Nevada (Virgin River) and Colorado (Dolores River) found tamarisk beetles were not selected (Mahoney et al. 2017, van Riper et al. 2018). Alternatively, defoliation caused by the beetle could decrease abundance of other insect prey. For example, tamarisk leafhoppers (<i>Opsius stactogalus</i>), a tamarisk-obligate insect also found in diets of several native birds (Yard et al. 2004, Wiesenborn and Heydon 2007, Durst et al. 2008, Mahoney et al. 2017, van Riper et al. 2018), declined significantly when tamarisk defoliation reached 60% (Eckberg and Rice 2016). Defoliation by the beetle could also reduce nesting cover while increasing temperature and reducing humidity due to increased solar radiation. Only one study we are aware of reported avian productivity in sites defoliated by tamarisk beetles and it found decreased nest success by Southwestern Willow Flycatchers (<i>Empidonax trailii extimus</i>) in defoliated habitats, with nest predation and failure to hatch as the major causes (McLeod 2018). Failure to hatch was rare at these sites in other years, and at other sites during the same year, but was consistent with eggs being addled due to higher nest temperatures (McLeod 2018).	3.55 3.60 3.65 3.70 3.75 3.80
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3.30		METHODS
3.35		Study Area
3.40		Bird communities were assessed using point counts at 8 sites along the Virgin River in Arizona and Nevada, USA in 2009 and 2010 (prior to when beetles first arrived at the sites) and again in 2013 and 2014 after tamarisk beetles had been present for several years (Bateman et al. 2013) (Figure 1, Table 1). Sites varied in the proportion of tamarisk (“tamarisk” as used here refers to <i>Tamarix ramosissima</i> and related species and hybrids; Gaskin and Schaal 2002, Bateman et al. 2013) and native vegetation (mainly Fremont cottonwood, Goodding’s willow [<i>Salix gooddingii</i>], and coyote willow [<i>Salix exigua</i>]). In 2013, 2 observers independently estimated percentage of tamarisk and native riparian vegetation cover from a high point overlooking each site and the 2 estimates were averaged to obtain an index of vegetation type (Mahoney et al. 2017). Sites with riparian vegetation cover comprising predominantly native cottonwood and willow vegetation (50–75% native) were categorized as “mixed native sites” (Beaver Dam, AZ [25% tamarisk cover], Mesquite, NV [40% tamarisk cover], Bunkerville, NV [50% tamarisk cover]); sites with >75% tamarisk cover were categorized as “predominately defoliated tamarisk” sites (“tamarisk*” in figures and tables; Desert Springs, AZ [75% tamarisk cover], Big Bend, AZ [80%
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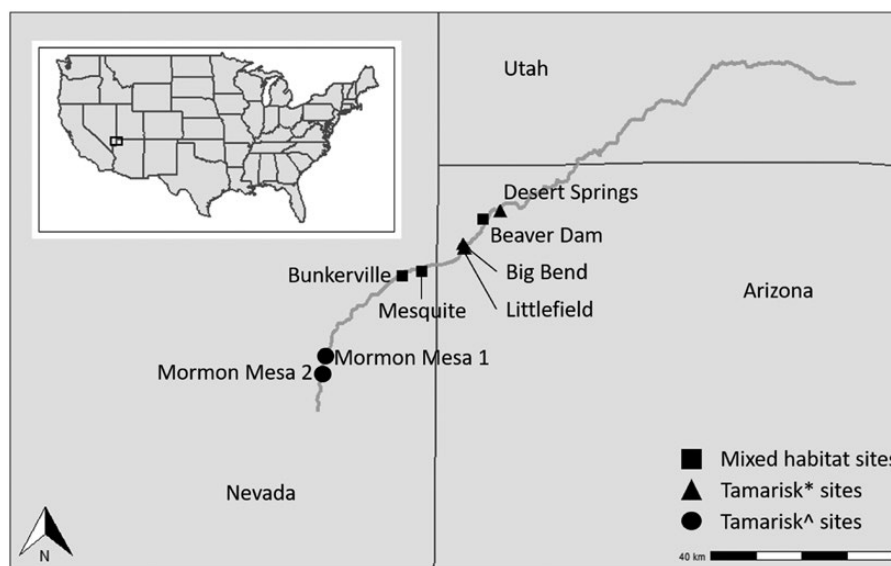


FIGURE 1. Invasive tamarisk and its introduced biocontrol are widespread throughout the Virgin River in Arizona and Nevada. Inset shows study area within the United States. Biocontrol at “Tamarisk*” sites defoliated but did not kill the plant, whereas biocontrol resulted in plant death at “Tamarisk^” sites. Mixed habitat indicates areas with tamarisk and native vegetation.

tamarisk cover], Littlefield, AZ [80% tamarisk cover]); and sites with >75% tamarisk, but with the majority of the tamarisk at the site dead from repeated defoliation events, was categorized as “predominately dead tamarisk” sites (“tamarisk^” in figures and tables; Mormon Mesa 1, NV [90% dead tamarisk] and Mormon Mesa 2, NV [90% dead tamarisk]). During surveys in 2009 and 2010, no tamarisk experienced defoliation, but tamarisk at all sites in 2013 and 2014 during our surveys were being actively defoliated or had already been killed by beetles (Mosher and Bateman 2016). In our study we define “defoliation” as the response of tamarisk actively experiencing herbivory, including browning of foliage and die-back of some of the canopy (Hultine et al. 2015). We define “dead tamarisk” as those trees that had no foliage following biocontrol, with the caveat that some tamarisk may have resprouted in subsequent years but showed no evidence of doing so during the course of our study (Hultine et al. 2015). Our estimates of the status of tamarisk (“defoliated” or “dead”) at our tamarisk-dominated sites were consistent with assessments by other researchers working independently at these same sites at the same time (Bateman et al. 2013, Hultine et al. 2015, Nagler et al. 2018). Native arrowweed (*Pluchea sericea*) was documented as increasing in abundance after tamarisk biocontrol along the Virgin River (González et al. 2020), but because no point count locations (see below) were in areas dominated by arrowweed, we did not quantify its abundance.

Bird Species Diversity, Richness, and Community Composition

To assess the native bird community at each site, we conducted point-count surveys at 6 point locations within each site prior to the arrival of beetles in 2009 and 2010, and

after beetle arrival in 2013 and 2014 following methods in Reynolds et al. (1980). Each point count location was separated by ~250 m. We visited each point 2 times during the breeding season (once in late May/June and once in July) each year. During each point count, we recorded all birds seen or heard during an 8-min period. We recorded the distance to the bird using laser range finders. To avoid over sampling, we only recorded individuals once during the survey period. All surveys were conducted on clear days with low wind (≤ 3 on Beaufort scale or ≤ 20 km hr⁻¹) between sunrise and 1100 hours. Because all sites included some tamarisk and some native vegetation, and because tamarisk beetles were present at all sites, individual sampling points within any of the sites could potentially be located in areas of dead or defoliating tamarisk and/or have native vegetation present. Therefore, once per year in 2013–2014, the vegetation surrounding each point was categorized as 1 mix of green tamarisk and native vegetation, 2 mix of defoliating tamarisk and some native vegetation, 3 mix of dead tamarisk and some native vegetation 4 green tamarisk, 5 defoliating tamarisk, 6 dead tamarisk, or 7 edge, in which any of the preceding categories was adjacent to open water, wetland, or upland.

Arthropod Surveys and Microclimate Estimates

During June and July 2013 and 2014, we repeatedly monitored ($n = 3-4$ visits per point) the presence of tamarisk beetles and other arthropods by sweeping vegetation using canvas nets 5 times every 5 m along a 20-m transect (25 sweeps total per transect) at a subset of point count locations, chosen arbitrarily (*sensu* Mahoney et al. 2017, Smith et al. 2017). Vegetation that was swept along

TABLE 1. Study site locations (site abbreviations), habitat type, number of point count stations (*n*) and approximate percentage of native and tamarisk vegetation at each site. Tamarisk* refers to sites where biological control did not result in the death of tamarisk. Tamarisk^ refers to sites where biological control resulted in the death of tamarisk. Bird community composition cluster assignment pre- and post-biocontrol is also indicated

Site	State	Habitat	Area	<i>n</i>	Latitude	Longitude	Native vegetation (%)	Tamarisk vegetation (%)	Pre-biocontrol cluster	Post-biocontrol cluster
Beaver Dam (BD)	AZ	Mixed	25.4	6	36.89	-113.93	75	25	1	1
Mesquite (MQ1)	NV	Mixed	29.5	6	36.79	-114.08	60	40	1	1
Bunkerville (MQ2)	NV	Mixed	31.6	6	36.78	-114.13	50	50	1	1
Desert Springs (DS)	AZ	Tamarisk*	33.8	6	36.90	-113.89	25	75	2	2
Big Bend (BB)	AZ	Tamarisk*	47.8	6	36.84	-113.98	20	80	1	2
Littlefield (LI)	AZ	Tamarisk*	44.2	6	36.83	-113.98	20	80	1	2
Mormon Mesa 1 (MM1)	NV	Tamarisk^	52.2	6	36.62	-114.32	10	90	1	2
Mormon Mesa 2 (MM2)	NV	Tamarisk^	70.2	6	36.59	-114.33	10	90	1	2

transects included: Fremont cottonwood, coyote willow, Goodding's willow, quailbush (*Atriplex lentiformis*), mesquite (*Prosopis* spp.), arrowweed, seepwillow (*Baccharis salicifolia*), cattail (*Typha* spp.), and tamarisk. We recorded the total numbers of 3 tamarisk-obligate insects (tamarisk leafhoppers, tamarisk weevils (*Coniatus splendidulus*), and tamarisk beetles), as well as the number and type of any other arthropods (mainly spiders (Araneae), ladybird beetles (Coccinellidae) and ants (Formicidae)) collected in each sweep.

To assess how site temperature and relative humidity were affected by tamarisk defoliation, in 2013 and 2014 we arbitrarily (*sensu* Smith et al. 2017) placed 2–4 microclimate dataloggers (HOBO model Pro v2) at a subset (*n* = 5) of native sites (Beaver Dam), mixed sites (Mesquite), defoliated tamarisk sites (Big Bend, Desert Springs), and dead tamarisk sites (Mormon Mesa 1). Microclimate dataloggers were placed 1.5-m high in an individual tamarisk, close to the trunk on 1 June and were retrieved on 31 July and recorded temperature and relative humidity every 30 min from 0600 to 1800 hours. We did not control for the cardinal direction of the logger on the trunk.

Data Analysis

Bird species diversity, richness, and community composition. We assessed species diversity by first combining species detections across all 4 visits (1 June and 1 July visit in each of 2 years) at each sampling point in 2009–2010 and again in 2013–2014 to generate a list of all species detected at each point either pre- or post-biocontrol. With 6 sampling points at each site, this generated 18 points in mixed native vegetation from 3 sites (Beaver Dam, Mesquite and Bunkerville), 18 in tamarisk-dominated vegetation from 3 sites (Big Bend, Desert Springs, Littlefield), and 12 in dead tamarisk-dominated vegetation at 2 sites (Mormon Mesa 1 and 2). We then compared estimated species diversity indices in mixed native, tamarisk and dead tamarisk vegetation types using the asymptotic approach for sampling-unit-based incidence data in the program iNEXT (Chao et al. 2016). iNEXT uses an asymptotic approach to infer asymptotic diversity based on statistical estimation of the true Hill number at various orders of *q* (Chao et al. 2014, Chao and Jost 2012). We assessed diversity at 3 orders of *q*; *q* = 0 generates an estimate of richness without accounting for relative abundance of species, *q* = 1 generates an estimate of diversity that incorporates relative frequency of each species and reflects the effective number of common species (analogous to Shannon diversity), and *q* = 2 generates an estimate that incorporates relative dominance of each species and reflects the effective number of dominant or very abundant species (analogous to Simpson's diversity) (Chao et al. 2014). This approach was conservative in that it was based only on whether a species was present at any one point in any one of the 4 visits and

did not incorporate the number of individuals of a species detected at a point or whether a species was detected in more than 1 count.

We used a similar approach to examine avian responses at smaller spatial scales by testing whether the community of birds detected at points dominated by dead tamarisk in 2013–2014 was different from the community detected at those points before biocontrol in 2009–2010. In this case, detections at individual points characterized as “dead tamarisk” in 2013–2014 were used ($n = 12$ across 3 sites) and compared to the same points sampled in 2009–2010 using the same species diversity estimates at 3 orders of q calculated in iNEXT as above. To control for changes over time independent of tamarisk death, we did the same analysis comparing points characterized in 2013–2014 as “mixed native” (13 points over 3 sites). Finally, to determine whether the presence of native vegetation influenced the community of birds detected at points with dead tamarisk, we compared points characterized as “dead tamarisk with some native vegetation” (11 points over 5 sites) in 2013–2014 using the same approach.

We then assessed whether bird community composition among habitats occupied different community space following biocontrol using an unbiased and unsupervised classification approach that is independent of habitat classification. First, we tested the null hypothesis that there are no groupings of bird communities (and therefore the data fit best within one group cluster) using the *factoextra* package (Kassambara and Mundt 2017) for R (R Core Development Team 2018). This analysis assesses the quality of group clusters (i.e. how well the data fit within clusters) by calculating the silhouette width for $n = 1–6$ clusters (i.e. all combinations from a single cluster up to 6 clusters, representing each habitat before and after biocontrol). The silhouette width is a relative measure of confidence for group membership within a cluster and values range from -1 to $+1$ with values closer to 1 represent better clustering (Rousseeuw 1987). Next, we determined the appropriate number of group clusters using package *ClValid* (Brock et al. 2008) for R which evaluates clustering models and the numbers of clustering groups independent of habitat or site classification and subsequently identifies the appropriate clustering algorithm. In our analyses, we evaluated hierarchical, K -means, and partitioning around medoids (PAM) clustering models with $n = 2–6$ clustering groups. *ClValid* assesses group clustering based on three indices: connectivity, Dunn, and silhouette width. The connectivity index assigns group membership of data points based on the spatial proximity to other samples (i.e. points closer in space are assigned to the same group). Connectivity ranges from 0 to infinity and smaller values represent well-clustered data (Handl et al. 2005). The Dunn and silhouette indices are measures of the “compactness” and

“spread” of clusters. The Dunn metric is the ratio between the smallest distance between data points from different clusters and the largest intracluster distance (Dunn 1974). Dunn indices range from 0 and infinity and higher values represent better clustering. Silhouette values estimate the degree of confidence in membership within a particular cluster (Rousseeuw 1987). The silhouette indices are estimated by calculating the mean distance of points within a cluster and the mean distance between clusters and range from -1 to $+1$ and values close to 1 represent better clustering. Therefore, we chose the number of groups and the clustering method in our analyses based on models with optimized connectivity, Dunn, and silhouette values (Brock et al. 2008). In our study, there was no disagreement among indices. Our clustering analysis was optimized at $n > 1$ clusters, indicating some grouping in bird communities (Silhouette value = 0.29, Supplementary Material Table 1) and all clustering indices identified $n = 2$ clusters and hierarchical clustering as the best algorithm (Supplementary Material Table 1). We then calculated a Euclidean distance matrix among all combinations of community compositions in each habitat type before and after biocontrol using the *vegan* package (Oksanen et al. 2013) for R and plotted the results. Finally, we tested for community differences between cluster assignment, biocontrol period, and their interaction using a permutational multivariate analysis of variance (PERMANOVA) test with Euclidean distances using the *vegan* package (Oksanen et al. 2013) for R.

Bird densities. We modeled overall and species-specific bird densities (birds ha^{-1} for each species) using the *Distance* package for program R (R Core Development Team 2018), which accounts for differences in detectability between bird species, habitats, and observers. Species-specific densities were calculated for all birds with at least 25 detections (DeSante 1986). We selected detection functions for each bird species using Akaike’s Information Criterion (AIC) and evaluated models using Kolmogorov–Smirnov goodness-of-fit tests (Buckland et al. 2001). For each candidate model, we fit either half-normal or hazard-rate detection curves and included the covariates site, habitat type, or observer, and additive models including site and observer or habitat type and observer. Because we included covariates, we did not use uniform detection curves (Buckland et al. 2001). Truncation distance for each species was determined by visual inspection of detection function plots (Buckland et al. 2001). We then calculated densities (birds ha^{-1}) based on the top model within each site.

Arthropod surveys and microclimate estimates. We assessed differences in the arthropod community by averaging the total number of adult tamarisk beetles, adult tamarisk leafhoppers, adult tamarisk weevils, and all other

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7.5	arthropods (“other”) collected during each sweep net survey transect and then plotted the mean abundances for group versus habitat type. We then used mixed effects models to test for differences in arthropod abundance between site and habitat types using the <i>lme4</i> and <i>lmerTest</i> packages in R (R Core Development Team 2018). In our models, arthropod abundance was the response variable, site and habitat type were the fixed effects, and point ID (location of the sample) was included as a random intercept term.	7.55
7.10	We assessed normality and homoscedasticity by visual inspection of QQ and residual plots. We then assessed pairwise differences among habitats using the <i>lsmeans</i> package in R. We corrected for multiple hypothesis testing using a Bonferroni correction (corrected $\alpha = 0.015$).	7.60
7.15	To assess the relationships between temperature, relative humidity, and tamarisk biocontrol, we determined the maximum temperature and relative humidity for each day from 1 June to 31 July in 2013 and 2014 (Bateman et al. 2013). We then assessed differences among habitats and sites in maximum temperature and relative humidity using the <i>lme4</i> and <i>lmerTest</i> packages in R (R Core Development Team 2018). In our models, maximum daily temperature or relative humidity was the response variable ($n = 1$ value/day/site for $n = 61$ days), habitat and site were fixed effects, and datalogger ID number was included as a random intercept term. We assessed normality and homoscedasticity by visual inspection of QQ and residual plots. We then assessed pairwise differences between habitats using the <i>lsmeans</i> package in R. We corrected for multiple hypothesis testing using a Bonferroni correction (corrected $\alpha = 0.025$).	7.65
7.20		7.70
7.25		7.75
7.30		7.80
RESULTS		
7.35	Bird Species Diversity, Richness, Community Composition, and Densities	
7.40	Site-level comparisons of species diversity estimates among habitats characterized as “mixed-native”, “tamarisk-dominated”, and “tamarisk-dominated dead” showed that 95% confidence interval (CI) of estimates of effective richness ($q = 0$) and Shannon diversity ($q = 1$) overlapped across all sites and times (Figure 2). However, sites characterized as dead in 2013–2014 had lower effective numbers of dominant species ($q = 2$, Simpson’s diversity) both before and after biocontrol (Figure 2).	7.85
7.45	When the number of sampling points at which each species was detected in each of the 3 vegetation types was compared for communities prior to biocontrol and after biocontrol, only 1 common species (common = detected in >50% of points, $n = 10$ common species) declined by >30% in the mixed-native sites (Lesser Goldfinch [<i>Spinus psaltria</i>]), 3 common species declined by >30% in tamarisk-dominated sites (Brown-headed Cowbird [<i>Molothrus ater</i>], Song Sparrow [<i>Melospiza melodia</i>], and House Finch [<i>Haemorhous mexicanus</i>]), and 7 common species declined in dead tamarisk-dominated sites by >30% (Brown-headed Cowbird, Song Sparrow, Mourning Dove [<i>Zenaidura macroura</i>], Yellow Warbler [<i>Setophaga petechia</i>], Red-Winged Blackbird [<i>Agelaius phoeniceus</i>], Common Yellowthroat [<i>Geothlypis trichas</i>], and the endangered subspecies Least Bell’s Vireo [<i>Vireo bellii pusillus</i>]; Figure 3).	7.90
7.50	When the community of birds detected at the 12 sampling points characterized as “dead tamarisk” in 2013 were compared using data collected at the same points both pre- and post-biocontrol, 95% CI overlapped for diversity estimates based on $q = 0$ (richness) and $q = 1$ (Shannon diversity) but not for $q = 2$ (Simpson diversity) indicating that the effective number of dominant species was lower at these points after biocontrol (Figure 4). In contrast, similar comparisons of points characterized as “mixed native” and “dead tamarisk with native component” showed no difference in these parameters between pre- and post-biocontrol communities (Figure 4).	7.95
7.54	Based on our clustering analyses, all sites grouped together prior to biocontrol, with the exception of one defoliated tamarisk site (Figure 5). Following biocontrol, mixed habitat sites grouped with the pre-biocontrol cluster and defoliated tamarisk and dead tamarisk sites grouped separately (Figure 5). Bird species composition differed among clusters (pseudo- $F_{1,12} = 5.68, P < 0.0001$), but not between biocontrol periods (pseudo- $F_{1,12} = 1.25, P = 0.24$). However, there was an interaction between biocontrol period and cluster (pseudo- $F_{1,12} = 0.13, P = 0.009$), indicating community composition in defoliated and dead tamarisk sites differed before and after biocontrol, whereas mixed sites remained similar (Figure 5).	7.100
	Among species that were detected most often (Supplementary Material Table 2) we found several lines of evidence of species declines in tamarisk habitat following biocontrol, based on non-overlapping 95% CIs. Black-chinned Hummingbirds (<i>Archilochus alexandri</i>), Least Bell’s Vireos, Common Yellowthroats, and Yellow Warblers declined in dead tamarisk sites (Supplementary Material Table 3). House Finches, Lesser Goldfinches, Lucy’s Warblers (<i>Vermivora luciae</i>), Mourning Doves, Song Sparrows, and Yellow-breasted Chats (<i>Icteria virens</i>) declined in defoliated sites following biocontrol (Supplementary Material Table 3).	7.105
	Some species showed increases in dead tamarisk sites following biocontrol, including Blue-gray Gnatcatchers (<i>Polioptila caerulea</i>), Black-tailed Gnatcatchers (<i>Polioptila melanura</i>), and Verdins (<i>Auriparus flaviceps</i> , Supplementary Material Table 3). In defoliated sites, Black-chinned hummingbirds and Great-tailed Grackles (<i>Quiscalus mexicanus</i>) increased following biocontrol (Supplementary Material Table 3).	7.106

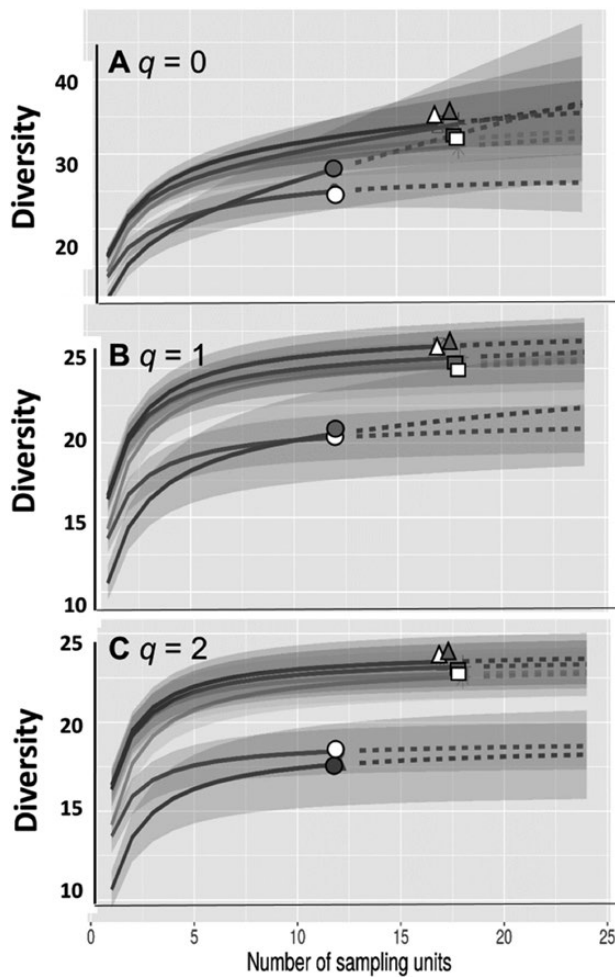


FIGURE 2. Site-level diversity estimates and 95% CI at 3 orders of q comparing sites characterized as mixed-native in 2009–2010 (open triangles) and 2013–2014 (shaded triangles), tamarisk-dominated in 2009–2010 (open squares) and 2013–2014 (shaded squares), and sites dominated by tamarisk that were largely dead by 2013 in 2009–2010 (open circles) and 2013–2014 (shaded circles). Overall, sites dominated by tamarisk that were largely dead by 2013 had lower effective numbers of dominant species ($q = 2$, Simpson’s diversity) both before and after biocontrol. All sites were along the Virgin River in Arizona and Nevada, USA.

Arthropod Surveys and Microclimate Estimates

Based on mixed effects models, we found no differences in abundances of adult tamarisk beetles ($F_{2,22.6} = 0.92, P = 0.41$) or tamarisk weevils ($F_{2,22.7} = 1.77, P = 0.19$) among habitat types, with leafhoppers ($F_{2,22.4} = 2.93, P = 0.07$) marginally significantly lower in dead tamarisk sites (Supplementary Material Table 4). Non-tamarisk-obligate arthropods, categorized in our study as “other,” were more abundant in native mixed sites than in defoliated or dead tamarisk sites (Supplementary Material Table 4, $F_{2,19} = 5.87, P = 0.01$).

We monitored microclimate conditions following biocontrol and from our mixed effects models, daily maximum temperatures increased from 1 June to 31 July

($F_{60,840} = 111.22, P < 0.0001$), but did not vary among sites ($F_{2,10} = 0.51, P = 0.61$) or among habitat type ($F_{2,10} = 1.77, P = 0.22$; Figure 6). Relative humidity also increased from 1 June to 31 July ($F_{60,1740} = 41.46, P < 0.0001$) and varied among habitat types ($F_{2,25} = 6.81, P = 0.004$; Figure 6), but not among study sites ($F_{2,25} = 1.17, P = 0.33$; Supplementary Material Supplementary Material Table 5). Humidity in mixed sites was higher than in both defoliated tamarisk and dead tamarisk sites (all post-hoc comparisons $P < 0.007$; Figure 6).

DISCUSSION

Prior to tamarisk biocontrol, bird communities along the Virgin River were similar regardless of the dominant vegetation at our study sites. Following biocontrol, however, bird communities in tamarisk habitat that suffered dieback due to biocontrol were different, primarily because of reduced abundance of common species. Our results indicate that when some species, like Yellow Warblers, remain in biocontrol-affected tamarisk stands, they are associated with the presence of remnant native cottonwoods and willows. We hypothesize that other species, like Lucy’s Warblers and Verdins, may remain because they are able to exploit resources in the surrounding native matrix. Overall, our findings suggest that tamarisk stands during the initial recovery from biocontrol dieback could support a moderately diverse assemblage of birds that could act as sources for repopulating these areas if appropriate riparian vegetation establishes after biocontrol. In tamarisk-dominated areas lacking remnant native vegetation that have lost riparian-dependent birds like Yellow Warblers, however, recolonization by those species would need to be through immigration from other stands with a native vegetation component.

Tamarisk-dominated stands that have experienced extensive dieback as the result of biocontrol can appear to the human eye as unproductive dead zones. Thus, it was surprising that we found no difference between pre- and post-biocontrol in our dead tamarisk sites in the bird community measures that reflect species richness and Shannon diversity. Although community compositions were significantly different in those dead tamarisk sites pre- and post-biocontrol, primarily due to greater decreases in a broader array of dominant species, the majority of bird species were still present, albeit in fewer locations for some species. In terms of species q -diversity estimates (Shannon’s and Simpson’s diversity calculated from iNEXT), the sites that were characterized as predominantly dead tamarisk in 2013–2014 differed from the other sites in the number of common species both prior to and after biocontrol. Had we lacked pre-biocontrol data, the comparison of sites using only post-biocontrol data would have shown a pattern consistent with the hypothesis that these sites differed because

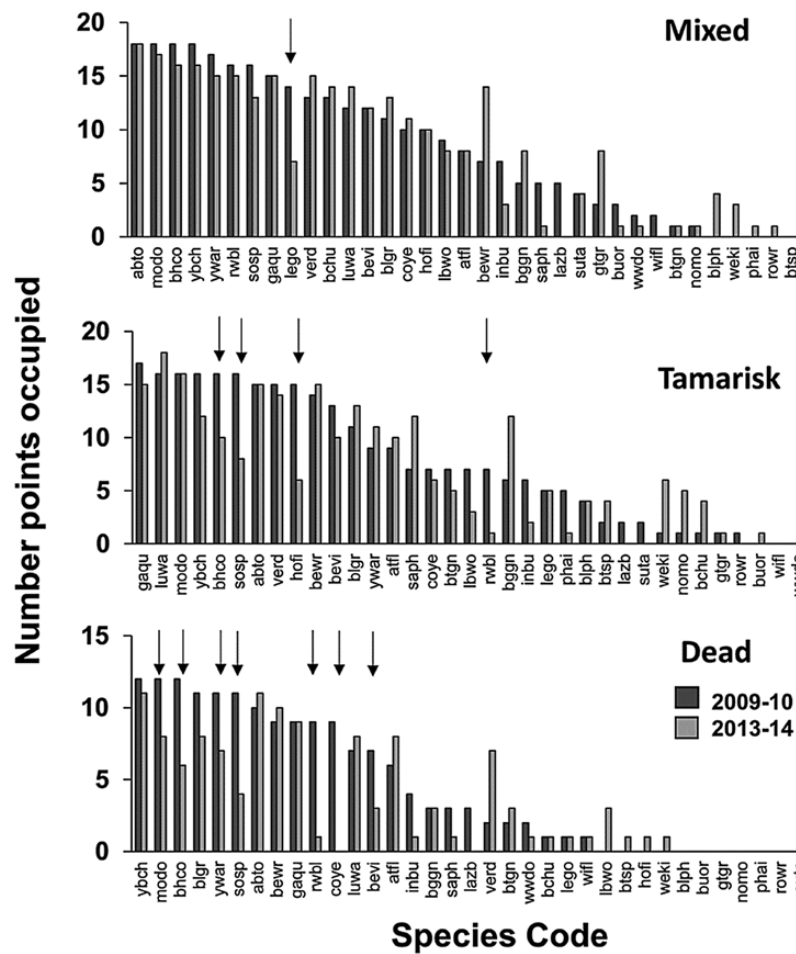


FIGURE 3. More native bird species declined in areas dominated by tamarisk that suffered dieback due to biocontrol. Bars represent the number of census points at which each bird species was detected at sites characterized as mixed-native, tamarisk-dominated, and tamarisk-dominated but largely dead by 2013, prior to biocontrol in 2009–2010 (dark shaded bars) and after biocontrol in 2013–2014 at 8 sites along the Virgin River in Arizona, Nevada, USA. Arrows indicate species in which number of census points at which they were detected declined by at least 30% from 2009–2010 to 2013–2014.

they were largely comprised of dead tamarisk. Instead, those sites already had lower numbers of dominant species prior to biocontrol. Those general community estimates of diversity, however, failed to reflect the compositional changes associated with biocontrol and tamarisk death. Based on unbiased clustering algorithms, pre-biocontrol community composition of most sites grouped together, but community composition in mixed and tamarisk-dominated sites differed following biocontrol, supporting the hypothesis that biocontrol altered bird community composition. Some species, like Yellow Warblers, Least Bell’s Vireos, Song Sparrows, and Common Yellowthroats, declined markedly in tamarisk-dominated sites that suffered dieback due to defoliation by tamarisk beetles.

Changes in species abundances were generally consistent with hypotheses proposed by Paxton et al. (2011), in which they predicted 14 species to be sensitive to tamarisk biocontrol due to alterations in prey availability, increased

nest predation and/or abandonment, or the combined effect of both factors (their Table 1). We found support for this hypothesis in seven species (50%) which showed declines in dead tamarisk sites: densities of Black-chinned Hummingbirds, Least Bell’s Vireo, Common Yellowthroats, Lucy’s Warblers, Mourning Dove, Song Sparrow, and Yellow Warbler decreased. Brown-headed Cowbirds also decreased, possibly in response to reduced host availability. Several species hypothesized by Paxton et al. (2011) to be sensitive to tamarisk biocontrol, including Bewick’s Wren (*Thryomanes bewickii*) and Yellow-breasted Chat, showed neutral responses to biocontrol. Our results were generally consistent with a similar study (Darrah and van Riper 2018) that also found a negative relationship between Yellow Warbler densities and tamarisk biocontrol, but contrasted in that Song Sparrows decreased in abundance in our study but did not in their study. Interestingly, Verdin abundances increased following biocontrol, possibly

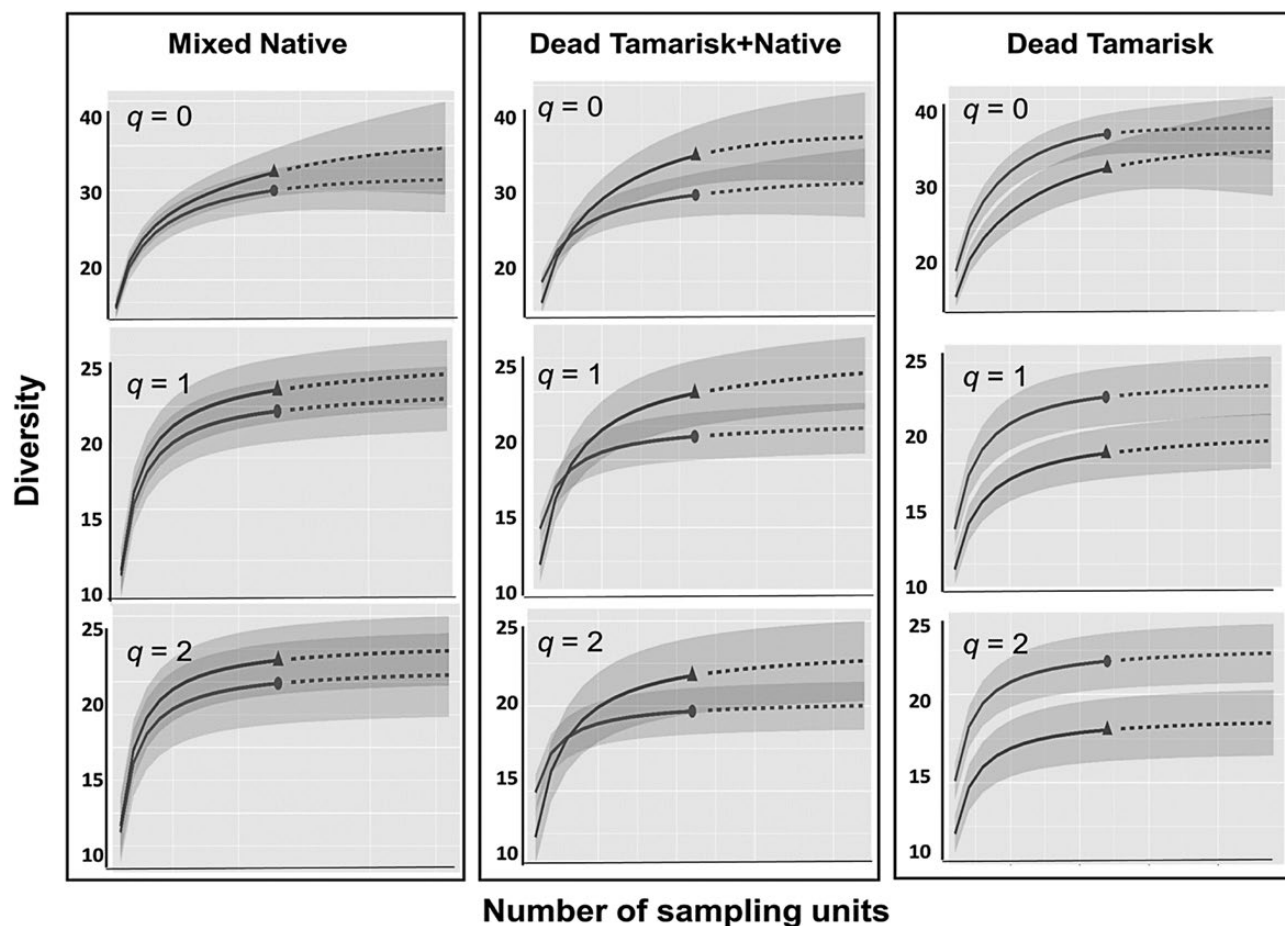


FIGURE 4. Survey-point level diversity estimates and 95% CI at 3 orders of q comparing avian communities based on the same points censused pre-biocontrol (oval) and post-biocontrol (triangle) at census points characterized as “mixed native” ($n = 13$), “dead tamarisk with some native component” ($n = 11$) and “dead tamarisk” ($n = 12$). Census points were a subset of those monitored at 8 sites along the Virgin River in Arizona and Nevada, USA, in 2009–2010 pre-biocontrol and in 2013–2014 post-biocontrol. Overall, avian diversity at survey points that included live native vegetation did not differ before or after biocontrol, while diversity was significantly lower at survey points dominated by tamarisk experiencing dieback and death with no live native component.

because they build enclosed nests (Austin 1970, 1976) that may shield them from microclimate alterations associated with tamarisk biocontrol. Darrah and van Riper (2018) found Yellow-breasted Chat densities decreased with tamarisk biocontrol, whereas we found no significant decline. Yellow-breasted Chat densities declined following mechanical removal of tamarisk (Raynor et al. 2017), suggesting that responses to tamarisk removal by species like Yellow-breasted Chat may be more sensitive to habitat structure than whether vegetation is alive or dead.

One hypothesis to explain the changes in the avian community we documented is that tamarisk biocontrol alters the microclimate such that it is too hot or dry for successful nesting (e.g., McLeod 2018, Mueller et al. 2019). Although we did not have pre-biocontrol microclimate estimates, following biocontrol, mean maximum temperatures did not differ among habitats, but temperatures at all sites reached or exceeded temperatures estimated to be lethal for both

embryos in the egg and adults (approximately $>41^{\circ}\text{C}$ and 47°C , respectively; Lundy 1969, Grant 1982, McKechnie and Wolf 2010). Tamarisk sites had significantly lower humidity, however, and eggs may be particularly sensitive to changes in humidity due to its effect on egg water loss (Deeming 2011). Coupled with high temperatures, eggs and adults in tamarisk habitats may lose water more rapidly than in mixed vegetation sites with higher humidity. One caveat of our temperature measurements was that they reflected ambient temperature rather than operative temperature (ambient + solar radiation + convection) (Elmore et al. 2017). Given the loss of foliage and increased solar radiation associated with biocontrol, operative temperatures may have been higher in dead tamarisk sites than reflected in our ambient temperature measurements. We know of no studies examining nest microclimate in tamarisk-dominated sites that experienced dieback after biocontrol, but studies of Willow Flycatchers at our dead tamarisk sites documented increased rates of nest abandonment

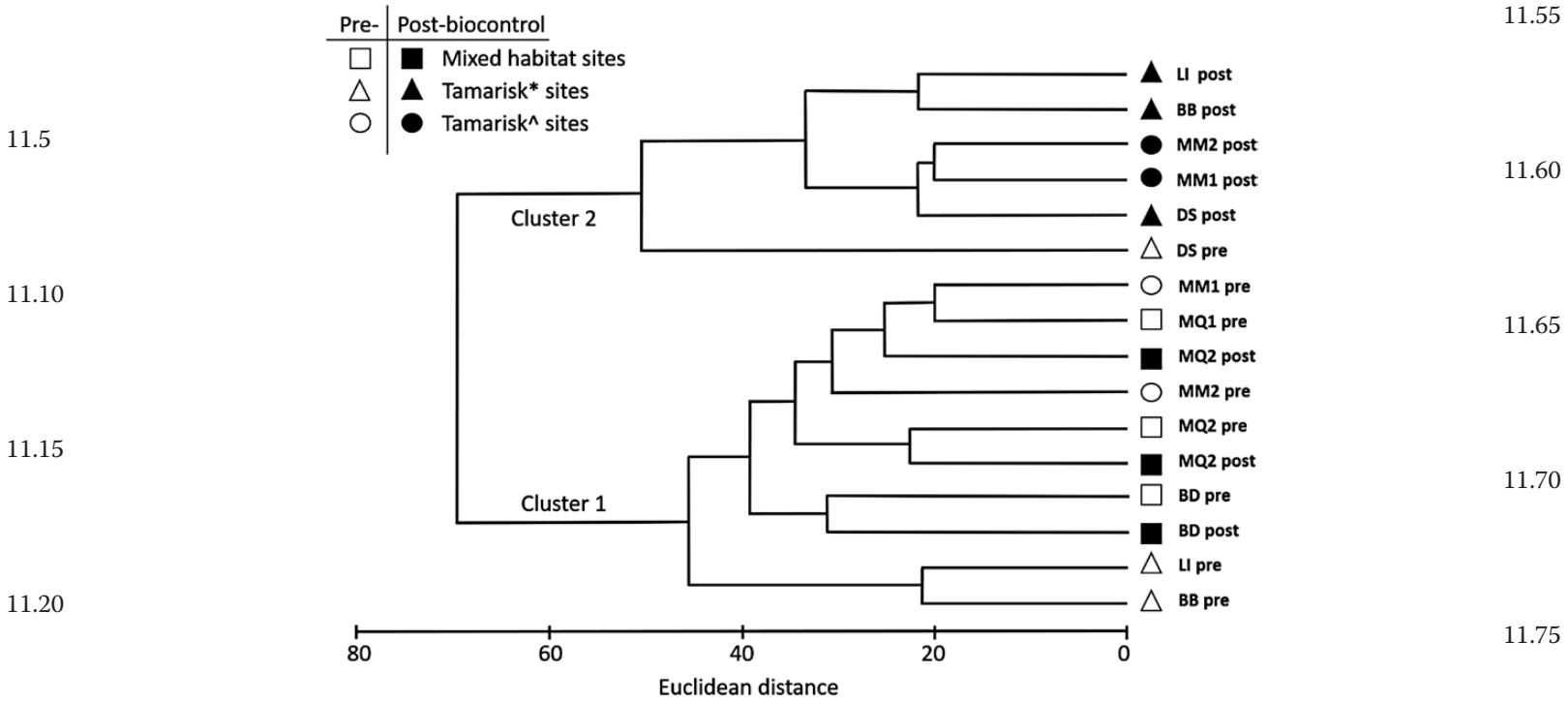


FIGURE 5. Tamarisk biocontrol significantly altered bird community composition in sites dominated by tamarisk. Dendrogram represents bird community composition relationships among mixed, defoliated tamarisk (tamarisk*), and tamarisk sites killed by biocontrol (tamarisk^). Tips are labeled with site names. Prior to biocontrol, all but one site (DS) grouped together in Cluster 1, regardless of habitat type. Following biocontrol, tamarisk-dominated sites grouped in Cluster 2 and mixed vegetation sites grouped with Cluster 1, indicating biocontrol altered bird community composition in tamarisk-dominated sites.

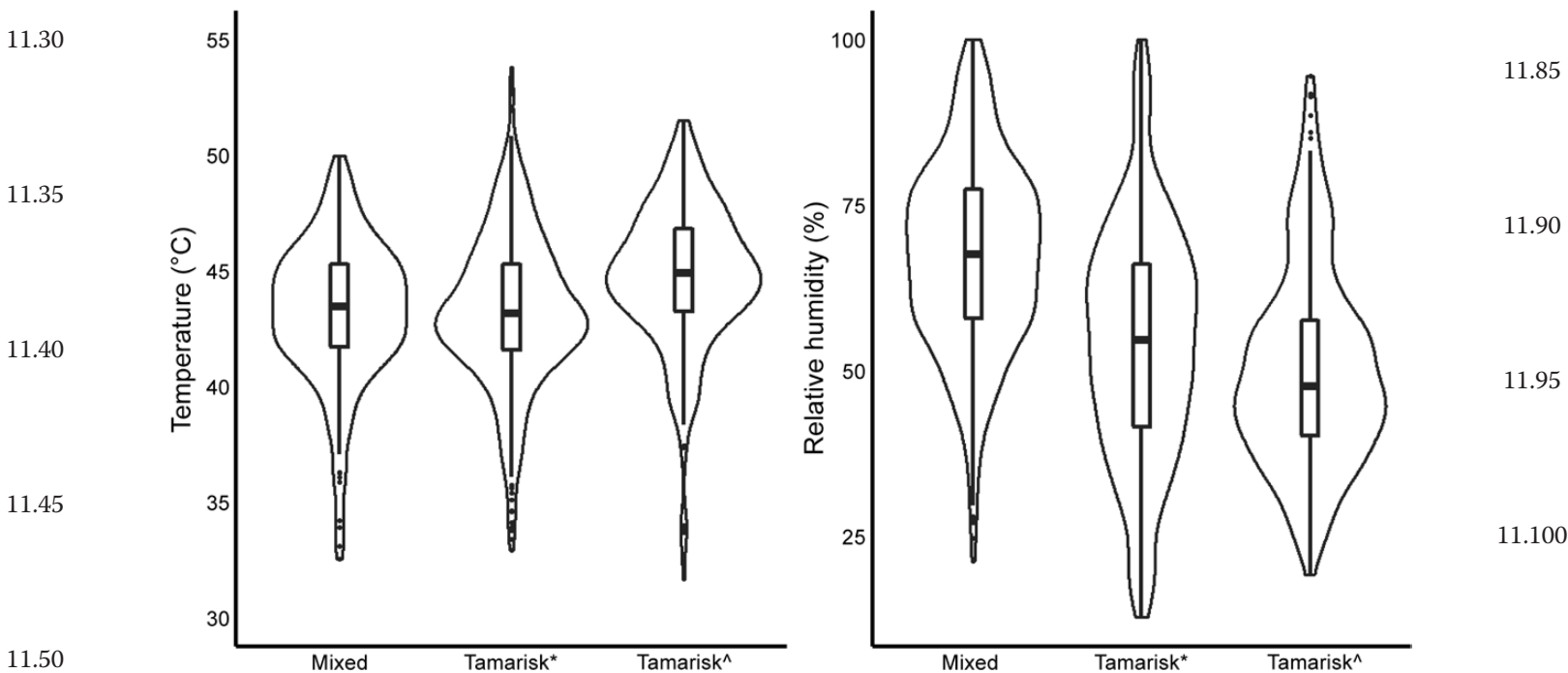


FIGURE 6. Tamarisk-dominated sites that experienced biocontrol were hotter (°C, left panel) and drier (% , right panel) than sites with a native vegetation component. Violin plots show distribution of maximum daily temperature and mean maximum daily relative humidity in predominately native, mixed tamarisk-native, predominately defoliated tamarisk (tamarisk*), and dead tamarisk (tamarisk^). Mean maximum temperatures did not differ among habitats ($F_{2,10} = 1.77, P = 0.22$), but mean relative humidity was higher in mixed and lower in defoliated and dead tamarisk sites ($F_{2,25} = 6.81, P = 0.004$).

and the presence of addled eggs with subsequent lower return rates and overall population decline (McLeod 2018).

An alternate hypothesis to explain changes in avian communities after biocontrol is that loss of tamarisk foliage may reduce the availability and abundance of insect prey for insectivorous birds (e.g., Pelech and Hannon 1995). Although we did not assess arthropod abundance prior to biocontrol, following biocontrol we found no significant difference in the amount of tamarisk beetles or tamarisk weevils across sites while dead tamarisk sites supported marginally lower abundances of tamarisk leafhoppers. Studies along Las Vegas Wash, Nevada, were similar, documenting that tamarisk leafhoppers declined significantly when defoliation reached 60%, while weevils did not (Eckberg and Rice 2016). All 3 tamarisk-obligate insect species have been documented in native bird diets. The tamarisk leafhopper has been found to be widely consumed by native birds (Yard et al. 2004, Wiesenborn and Heydon 2007, Durst et al. 2008, Mahoney et al. 2017, van Riper et al. 2018) and the tamarisk weevil was found to be preferred prey for populations of Yellow and Lucy's Warbler along the Virgin River (Mahoney et al. 2017). Non-tamarisk-obligate arthropods, which would include primarily native species, were significantly more abundant in mixed sites compared to both tamarisk and dead tamarisk sites. Overall, our arthropod comparisons supported the importance of native vegetation in maintaining non-tamarisk arthropods, but failed to show a major decline in abundance of tamarisk-obligate insects in the early stages of biocontrol.

Of the 10 insectivorous bird species for which we had enough detections to generate species-specific densities, 3 riparian associates—Least Bell's Vireos, Common Yellowthroats, and Yellow Warblers—showed declines following extensive tamarisk defoliation and dieback. Densities of other insectivorous birds may have been maintained by their ability to exploit insect resources in the upland habitat surrounding our riparian sites. For example, our tamarisk-defoliated and dead tamarisk sites were largely set within a matrix of mesquite or upland desert, and several species that commonly occur in these upland habitats, Lucy's Warblers, Verdins, and Ash-throated Flycatchers (*Myiarchus cinerascens*), were found in similar densities before and after biocontrol in dead tamarisk sites. Studies of the diet of these species in tamarisk-dominated riparian areas of the Colorado River in Grand Canyon found arthropods in their diet more closely reflected the arthropod community of surrounding uplands than that of the tamarisk stands they were captured in (Yard et al. 2004), consistent with the hypothesis that these birds could be maintained in dead tamarisk stands by foraging elsewhere. For other bird species, remnant willows or cottonwoods within the tamarisk-dominated sites may have been critical in allowing them to persist (van Riper et al. 2008). Consistent with this, bird diversity at survey points surrounded by dead tamarisk that

also had a willow or cottonwood component were similar before and after biocontrol, whereas points surrounded by dead tamarisk without native riparian vegetation showed significantly lower diversity. Likewise, several species were not recorded in tamarisk-dominated areas following defoliation and dieback, including Mourning Doves, Brown-headed Cowbirds, Song Sparrows, Red-winged Blackbirds, Common Yellowthroats, Least Bell's Vireos, and Yellow Warblers, while these species continued to occupy areas with mixed native vegetation and tamarisk.

Our study documented changes in bird communities after tamarisk defoliation and dieback that represents the initial stage of recovery following biocontrol using the tamarisk beetle. How long these community-level changes will remain and what further changes may occur will depend on the longer-term trajectory of plant regeneration after tamarisk dieback. Seedling establishment by cottonwoods and willows is episodic, relying on scouring floods to create suitable germination sites, but if those conditions are met, native riparian vegetation can grow rapidly enough to provide habitat for riparian birds relatively quickly. Along the retreating edge of a reservoir in Arizona, for example, native willows and cottonwoods established and grew to a stage that was colonized by Willow Flycatchers in roughly 3 years (Theimer et al. 2018). Although regeneration of native cottonwoods and willows may occur at these rates in some sites after tamarisk removal, in others it may be slowed or prevented by altered soil characteristics, seed sources, and reduced water availability from human-altered hydrological processes (Stromberg 1998, Stromberg et al. 2009). An analysis of over 200 sites across 4 western states at which tamarisk was removed mechanically, chemically or through biocontrol documented that removal enhanced native recovery by <2% over 5 years (González et al. 2017). This suggests that at some sites the kinds of changes we documented in avian communities may persist for 5 to 10 years or longer. In other sites, regeneration after defoliation and death may be dominated by other native or non-native plant species. In some of the Virgin River sites we studied, for example, the native shrub arrowweed has increased in abundance and overall cover following tamarisk biocontrol (González et al. 2020). Arrowweed is structurally simple compared to willow, cottonwood, and tamarisk, and monotypic stands along the Colorado River attract only a few resident bird species like Mourning Doves, Gambel's Quail, and Abert's Towhees (Rosenberg et al. 1991). Thus, areas that become dominated by native species like arrowweed or non-native plant species lacking in structural diversity and insect resources are likely to support bird communities with lower richness and abundance (Knutson et al. 2003).

Overall, our results demonstrate that the short-term effects of tamarisk biocontrol on avian communities can be

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substantial in sites already dominated by tamarisk, in that dieback will have greater relative impact to overall habitat suitability than in ecosystems where significant native riparian vegetation remains. How long these effects remain will vary depending upon the rate of native plant recovery, and therefore we recommend monitoring sites to determine the trajectory of native recovery over time. If native tree recovery in these sites is rapid, avian communities may recover rapidly as well. However, in areas where native tree recovery is slow or forestalled by invasion by other non-native plant species, land managers will need to consider the feasibility of active restoration, which can be cost-prohibitive (Taylor and McDaniel 1998), particularly where the altered hydrologic regimes of southwest rivers may limit the ability of native cottonwoods and willows to germinate (Stromberg 1998, Stromberg et al. 2009). Therefore, restoration efforts should assess the likelihood of success based on an evaluation of several factors including water availability necessary for native vegetation establishment (Stromberg 1998), the abundance and distribution of extant native vegetation, the potential impacts of flooding and fire, and financial resources available (Shafroth et al. 2013, Orr et al. 2014). More broadly, our study highlights the ability of many bird species to remain in areas greatly modified by invasion and subsequent biocontrol, and the importance of even relatively small remnants of native vegetation in allowing species sensitive to those changes to persist.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithological Applications* online.

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Ethics statement: All work was approved by institutional IACUC, BLM, and USFWS.

Conflict of interest statement: The authors declare no competing interests.

Author contributions: All authors conceived of project; S.M.M., M.J.J., and M.K. conducted fieldwork, S.M.M. and T.C.T. analyzed data; S.M.M. and T.C.T. wrote initial manuscript draft; All authors wrote revised paper.

Data deposits: Analyses reported in this article can be reproduced using the data provided by Mahoney et al. (2022).

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