# Plant-Pollinator Systems for Increasing Restoration Effectiveness for Desert Riparian Bird Habitats

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**Through a**
**INTERLOCAL AGREEMENT**
**FOR RIPARIAN PLANT-POLLINATOR ECOLOGY PHASE 1**
**between**
**CLARK COUNTY, NEVADA**
**DEPARTMENT OF AIR QUALITY AND ENVIRONMENTAL MANAGEMENT**
**DESERT CONSERVATION PROGRAM**
**and**
**BOARD of REGENTS, NSHE, obo UNIVERSITY OF NEVADA, LAS VEGAS**

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## EXECUTIVE SUMMARY

For the benefit of MSHCP covered riparian bird species, the Desert Conservation Program (DCP) manages a riparian reserve unit system with properties along the Virgin and Muddy Rivers. Restoration of degraded riparian habitats invaded by *Tamarix* (saltcedar or tamarisk) has been implemented in the past, and larger restoration projects are planned for the near future. Knowing and understanding the plant-pollinator systems within the riparian areas in Clark County could improve their function and restoration success. One component of riparian restoration is whether the plants can be self-sustaining, which is heavily influenced by pollinator presence/absence and behavior. Also, understanding where pollination is lacking could lead to improved restoration efforts and connectivity.

**Project objectives for this phase included:**

- Inventorying native patches planted in 2014 within the Mormon Mesa Subunit (Riparian Subunit 1), managed by Clark County, and inventory plants in adjacent *Tamarix*-invaded areas.
- Within native patches and adjacent *Tamarix*-invaded areas, assess the soil propagule or seed bank and seed rain to elucidate seed inputs provided by the native plant patches.

**Significant results**

- Native patches retained significant perennial cover (82% ± 14%; mean ± SEM) and included several planted species. Perennial cover was approximately evenly distributed among graminoids (grasses, sedges, and rushes), forb, and shrub-tree species, although there was considerable variability among native patches.
- While native annuals dominated native seed banks in native patches (62% ± 14), native perennials constituted about one-third to one-fifth (38% ± 14) of the native seeds detected in seed banks and over half of the native seed rain (61% ± 15) in native patches during the survey period.
- *Tamarix* areas were dominated by exotic perennial cover, particularly *Tamarix*. However, the understory consisted of mostly annual species (6-7% cover). These annual species, the native forb *Pluchea odorata* and the exotic grass *Polypogon monspeliensis*, contributed significantly to seed banks and seed bank inputs via seed rain in *Tamarix* plots. Few other perennial species were detected in the understory cover, seed banks, or seed rain in *Tamarix* areas. However, important pollinator and riparian species were detected in seed banks and seed rain, including *Baccharis*, *Pluchea sericea*, *Salix* species, and *Typha* species.
- During the one-growing-season monitoring, few planted native perennial plants contributed to native seed banks or seed bank input via seed rain in native patches. However, several of these species form important vegetative habitat structure and propagate through vegetative propagation via rhizomes, stolons, or spreading root systems, which may facilitate spread of native patches once *Tamarix* is removed.

**Conservation and Management Applications**

- Native patches restored by Clark County through planting native species in 2014 remained dominated by native trees, shrubs, grasses, and forbs in 2020. Many of the planted species were observed flowering in 2020 and likely represent important floral resources and structural habitat to pollinators and other fauna.
- Soil seed banks in native patches were dominated by native species, which is a positive finding suggestive of continued recruitment opportunities for native plants and the sustainability of the planted native patches.
- Seed rain into native patches was also dominated by native species, and the species composition differed to some extent from the vegetation and *in situ* soil seed banks. This diversity of native propagule seed sources could be important for "bet hedging" whereby there could be a full suite of mechanisms available for native species to persist in the patches through vegetative persistence, soil seed banks, and seed dispersal.
- The native patches restored by Clark County provide a sharp contrast with the surrounding matrix of primarily *Tamarix* monoculture, which had comparatively low plant diversity and few native species compared with the restored native patches.
- The project results suggest that the Clark County patch restoration effort was highly successful at persistently establishing native vegetation and associated floral resources at these sites while also supporting seed banks and seed rain dominated by native species. Based on the highly successful small-scale restoration effort achieved by Clark County, expanding native species restoration to provide diverse habitat structure for native wildlife is strongly supported by the project findings.
- Continued monitoring of vegetation, seed banks, and seed rain in and around the native patches may help inform the continued conservation and restoration of native vegetation at the sites and identify potential future threats to native species such as re-encroachment by *Tamarix* or seed dispersal by other non-native species. Continued monitoring could also provide insight as to the plant community maturation processes and the effects in restored riparian communities, as longer-term trends in these types of restored riparian communities are not well understood, and this project provides a unique opportunity to identify long-term community change in restored riparian ecosystems.

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## INTRODUCTION

### *Background*

Several species from the genus *Tamarix* L. (family Tamaricaceae; common names: saltcedar or tamarisk) were first introduced to the United States from Eurasia as ornamentals in the 1800s and used as erosion control agents throughout the early 1900s (Horton 1964; Stromberg & Chew 2002). By the middle of the twentieth century, *Tamarix* was noted to have invaded floodplains of the American Southwest, and the level of spread was connected to regulated temporary flooding events, common along the Colorado River (Robinson 1965; Schulz & Hislope 1972). The *Tamarix* genus consists of over fifty shrub and tree species. The most encountered species in the United States include *T. aphylla*, *T. parviflora*, morphologically similar *T. canariensis* and *T. gallica*, and morphologically similar *T. chinensis* and *T. ramosissima*. *Tamarix chinensis*, native to China, Mongolia, and Japan, and *T. ramosissima*, native to the region between eastern Turkey and Korea, are considered the two most common species occurring in the Southwest United States (Baum 1978; Friedman et al. 2005). Hybrids and new hybrids previously unidentified in *Tamarix*'s native range have been discovered in the United States, and *T. chinensis* and *T. ramosissima* represent the most common hybrids in invasions in the United States (Gaskin & Schaal 2002; 2003; Friedman et al. 2005).

*Tamarix* as a group are considered among the most widespread and influential invasions in North America, particularly in riparian habitats (see *Reviews* DiTomosa 1998; Smith et al. 1998; Stromberg 2001; Stromberg & Chew 2002; Zouhar 2003). Riparian zones along rivers of the desert Southwest are prime habitat for *Tamarix* (Everitt 1980; Brock 1994). *Tamarix* are prolific seed producers, have high salt and drought tolerance, are resistant to water stress, and have greater fire tolerance than many native mesic trees such as *Populus* species (cottonwood) and *Salix* species (willow). With mostly windborne seeds, these facultative phreatophytes spread quickly (Robinson 1965; DiTomasa 1998) and can displace native mesic plants (Fraiser & Johnson 1991; Cleverly et al. 1997; DiTomasa 1998; Fleishman et al. 2003). Under natural flow regimes, native trees can be competitive with *Tamarix* during germination and seedling establishment (Merritt & Pott 2010). However, many river and reservoir systems in the Southwest have regulated flows, which appear to benefit *Tamarix* (Everitt 1980; 1998; Shafroth et al. 2002; Stromberg & Chew 2002; Merritt & Pott 2010). Areas with sun exposure, minimal vegetation cover, along banks of flowing water (rivers, side channels, lakes), and along sandbars or areas disturbed by flooding, provide optimal habitat for rapid establishment. Seedlings require several weeks of wet, mostly exposed soils for survival (Horton et al. 1960; Kerpez & Smith 1987). Once established, *Tamarix* can form dense thickets or monocultures that displace or exclude natives and reduce opportunities for natives to establish (Fraiser & Johnson 1991; Cleverly et al. 1997; DiTomasa 1998). As a result of *Tamarix* colonization, native ecosystem functions, services, and wildlife utilization have been altered in some cases (Hunter et al. 1988; Zavaleta 2000; Shafroth et al. 2005). Impacts include changes to riparian habitat utilized by birds and invertebrates (Ellis et al. 2000; Shafroth et al. 2005; Wiesenborn et al. 2008), which are critical prey for many bird species (Hunter et al. 1988; Ellis 1995; Sherry & Holmes 1995; Walker 2006). In the Southwest, over 40% of bird species depend on river valleys and riparian vegetation for shelter or foraging (Carothers et al. 1974; Ohmart & Anderson 1982; Knofp et al. 1998), and riparian corridors are migratory routes and nesting sites for many terrestrial species whose movements coincide with flowering and seed production of native species (Ohmart et al. 1998). Although birds, including the endangered southwestern *Empidonax traillii extimus* (Willow flycatcher), utilize *Tamarix* stands (Sogge et al. 2008), *Tamarix* invasion alters bird demographics and utilization in these previously native riparian ecosystems (Hunter et al. 1998; Ellis 1995; Fleishman et al. 2003).

Because of characteristics of *Tamarix,* this group of species is a formidable barrier to native plant communities and restoration. Often aggressive and persistent tactics are required to deter a *Tamarix* invasion or re-invasion (Shafroth et al. 2005), including cutting and herbicide application, or large-scale removal using burning or mechanical equipment that rips into soil surfaces removing root crowns. Often, follow-up cutting and herbicide spot treatments are necessary to reduce the likelihood of re-invasion. Few examples present evidence of natural recovery of native riparian ecosystems after *Tamarix* removal (e.g., Dudley et al. 2000; Harms & Hiebert 2006). Often native plant propagule reintroduction is required to regain native riparian communities.

Large-scale plantings (transplanting, outplanting) are often difficult to institute due to landscape features, access to riparian sites, and the number of native individuals required to cover large areas. Without revegetation, however, many sites are vulnerable to re-invasion after *Tamarix* has been removed (Shafroth et al. 1998). Additionally, many *Tamarix*-invaded areas are utilized by resident and migratory birds for nesting and foraging. Removal of *Tamarix* without an immediate habitat replacement is a concern for some managers and scientists (Sogge et al. 2008; Stromberg et al. 2009; Hultine et al. 2010). Small, densely planted native patches installed before large-scale *Tamarix* removal within *Tamarix*-invaded sites may provide native habitat and sources for native propagules once *Tamarix* is removed (Hultine et al. 2009). Native patches can provide seed sources to build native seed banks, which often are depauperate on *Tamarix*-invaded sites (Vosse et al. 2008), or provide other propagule sources, such as rhizomatous or stoloniferous plants, that spread vegetatively into surrounding areas after *Tamarix* removal. High-density plantings may also deter or reduce *Tamarix* re-invasion through competitive exclusion (Sher et al. 2002).

*Goals and Objectives of the Project*

To test the hypothesis that native patches installed before large-scale *Tamarix* removal provide areas for native plants to thrive and reinvigorate native seed banks, we inventoried plants, seed banks, and seed rain within native patches installed within a dense stand of *Tamarix* at a site in Clark County, Nevada. Restoration of degraded riparian habitats has been implemented in the past, and larger restoration projects are planned for the near future. Knowing and understanding the plant-pollinator systems within the riparian areas in Clark County could improve their function and restoration success. Objectives for this phase of the project included: (1) inventorying native patches planted in 2014 within the Mormon Mesa Subunit (Riparian Subunit 1), managed by Clark County, and inventory plants in adjacent *Tamarix*-invaded areas, and (2) within native patches and adjacent *Tamarix*-invaded areas, assess the soil seed bank and seed rain to elucidate seed inputs provided by the native plant patches.

*Description of the Project*

We inventoried aboveground native patch vegetation within and around native patches along a distance-from-patch gradient, assessed soil seed banks from these same locations using seedling emergence and seed extraction, and assessed seed rain during one growing season at these locations to examine potential inputs into the seed bank. Parsing seed banks and seed rain from native patches provides information as to the likelihood of patch contribution to further native colonization.

## METHODS AND MATERIALS

This assessment occurred at the Mormon Mesa Subunit (Riparian Subunit 1), managed by Clark County, Nevada, 19.5 km (12 mi) south of Riverside, Nevada, along the eastern bank of the Virgin River, a tributary into Lake Mead reservoir and the Colorado River. The banks of the Virgin River have been invaded by *Tamarix*, either *T. chinensis*, *T. ramosissima*, or a hybrid, for an unknown period but for at least the last three decades. In 2014, Clark County removed *Tamarix* from five variable-sized small patches within this riparian subunit in strategic areas where groundwater was shallow and close to the surface during intermittent times of the year (Table 1). All five patches were planted with native plants, either as poles (~1.5 cm in diameter, <1 m), or seedlings grown in 2.5-L (#1 gallon) nursery pots. Species and the number of individuals planted varied by native patch (Table 2). Survival of the specific planted individuals is unknown.

Using coordinates provided by the Desert Conservation Program, Clark County, Nevada, of five planted native patches within the *Tamarix* stand, in 2020 we identified a central location within each native patch to install a 5.642-m radius survey plot (100 $m^2$ area) to assess vegetation (June 8, 2020), sample soils for seed bank analyses, and install seed rain traps (June 4, 2020). Additionally, we established four plots per native patch within the surrounding *Tamarix* stand in two directions 10 m and 20 m from the edge of the native patch (Table 3). Because of the high density of the *Tamarix*, these plots were placed adjacent to narrow access paths cut through the *Tamarix*. Paired *Tamarix* plots served at least two purposes. First, pairs provide a benchmark for comparison, especially for native seed banks and potential native seed rain conditions surrounding native patches. Second, measurements in the *Tamarix* plots can serve as a pre-treatment data of ecological conditions if *Tamarix* is removed in the future.

All annual and perennial native and exotic plant cover was estimated in each of the 25 plots using cover classes following (Peet et al. 1998). A full list of species identified at sites is in Supplement Table S1. Per native plot, eight random seed bank subsamples were obtained from the top 0-5 cm soil (8 cm diameter; 250 $cm^3$ per subsample) and pooled, resulting in a 2000 $cm^3$ seed bank sample per native plot. Per set of two 10-m and 20-m distance *Tamarix* plots per native patch, we obtained eight seed bank subsamples, or four subsamples each per 10-m and 20-

m *Tamarix* plot, and pooled samples by respective native patch and distance from native patch. At seed bank sampling, soils were slightly-to-moderately wet. Following, at all 25 plots, we installed seed rain traps. In each native plot, we randomly installed six plastic seed rain traps (98 mm in diameter, total trap area 434 $cm^2$) embedded into the ground at surface level (Fig. 1). In each of the 10-m and 20-m *Tamarix* plots (10 plots each), we randomly installed three seed rain traps, for a total of six seed rain traps per set of 10-m and 20-m *Tamarix* plots per native patch.

*Seed bank assessments*

The fifteen seed bank samples were assessed using both a seedling emergence assay and seed extraction followed by germination tests, where feasible. For seedling emergence, half of each homogenized sample (1000 $cm^3$) was soaked in 1.5 L of polished water for 30 min, stirring occasionally to break up clay clods and create a slurry. Field soils were heavy with clay and required dispersing before adding to nursery trays. The slurry was poured onto a 2-cm deep bed of washed, sterilized medium-coarse sand in a 27.8 cm wide × 54.5 cm long × 6.2 cm deep nursery tray. Sand used as a substrate was sterilized to remove contaminants. Trays were covered with clear 4-cm tall plastic humidity domes and placed into a GL-36VL Intellus Environmental Controller (Percival Scientific, Perry, Iowa, USA) on a diurnal setting (12-hour periods; 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$), with dark/light temperatures set to 15°C/25°C. Trays were watered with polished water and rotated in the chamber every two-three weeks. Emerged seedlings were surveyed once a month for seven months. As seedlings were identified and counted, they were removed. A 1-L 500-ppm gibberellic acid solution was added to each flat during the fifth month of monitoring to stimulate additional emergence. Total cumulative emergence per sample over the monitoring period was calculated.

For seed extraction, we used flotation to remove seeds from the remaining portion of samples (1000 $cm^3$). Samples were processed simultaneously as the seedling emergence assay. The remaining portion of each seed bank sample was soaked in 1.5 L of polished water for 30 minutes, stirring occasionally to break up clay clods. Additional polished water was added after the soaking period, the mixture stirred, and poured sequentially through No. 18 (1 mm) and No. 270 (53 µm) sieves. This process was repeated until all finer material was removed from samples and the water ran clear. All material > 53 µm was reserved and dried at 30°C for 12-18 hours in a drying oven. Once material was dry, material was sieved through a series of sieves, No. 18 (1 mm), No. 35 (500 um), No. 60 (250 um), and No. 270 (53 um), to separate material to make processing and removing seeds and flower parts easier. Using a stereoscope, all flower parts and seeds were removed from debris, and flower parts were dissected to extract seed, if present. Seeds were separated into different taxa and counted on a per taxa per sample basis. Extracted samples were stored at 4°C in the dark until further processing. Where enough seeds were obtained either from each plot and plot type over time or at a whole-site level (all samples pooled), we conducted seed germination tests (radicle emergence). Seeds were placed on wetted filter paper in a 100-mm diameter Petri dish, sealed with parafilm, and placed into the Environmental Controller on a diurnal setting (12-hour periods; 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$), with dark/light temperatures set to 8°C/15°C. Seed germination was monitored for eight weeks starting in October 2020, or until all seeds germinated or no germination was observed for several weeks. To dishes with no germination, we added a 1-2 mL of a 500-ppm gibberellic solution to stimulate germination.

### *Seed traps*

Seed traps were visited every two weeks after installation from June 8 to August 13, 2020, then once a month from September - December 2020. At each visit we observed different groups of species actively flowering and seeding. All debris in traps was collected and pooled the same as soil seed bank samples, resulting in fifteen samples per sampling period. In the laboratory, wet samples (i.e., due to flooding at field site) were dried in a drying oven for 2-4 hours before processing. Similar to seed extraction, dry trap samples were passed through a series of sieves to make seed extraction easier. Using a stereoscope, all flower parts and seeds were removed from debris, and flower parts were dissected to extract seed. Seeds were separated into separate taxa and counted on a per taxa per sample basis. Cumulative seed counts per native plot and the two sets of *Tamarix* plots per native patch were calculated. Extracted samples were stored at 4°C in the dark until further processing. Where enough seeds were obtained either within each sample or at a whole-site level (all samples pooled), we conducted seed germination tests like described above starting at the end of October 2020. Seed germination was monitored for eight weeks, or until all seeds germinated or no germination was observed for several weeks. To dishes with no germination, we added a 1-2 mL of a 500-ppm gibberellic solution to stimulate germination.

### *Analyses*

Native patch plot and *Tamarix* plot vegetation, seed bank, and seed rain variables were compared using generalized linear models in PROC GLIMMIX (SAS v 9.4, 2013, Cary, NC, USA). Where Box Cox transformations did not improve normality, distributions were assessed and applied in models (continuous data, lognormal; count data, Poisson or negative binomial). Post hoc tests with Tukey adjustments were applied to further elucidate significant effects ($p<0.05$). Statistics results are reported in Supplement Table S2. For analyses and presentation of results, seed bank and seed rain results are scaled to a 1-$m^2$ area for comparison purposes.

## RESULTS AND EVIDENCE OF THE RESULTS

### *Objectives Completed*

We completed vegetation surveys June 8, 2020, and sampled soil seed banks and installed seed rain traps simultaneously on June 4, 2020. We monitored seed rain from June 4 through December 4, 2020. We assessed seed banks using a seedling emergence assay and seed extraction using rinsing and flotation. Seedling emergence ran from June 6, 2020 through December 4, 2020. When possible, we conducted germination testing on seeds extracted from seed banks and seed rain. We analyzed vegetation, cumulative seed bank, and cumulative seed rain data.

### *Vegetation*

While total plant cover was moderately significantly higher in native patch plots compared to *Tamarix* plots, native and exotic plant cover significantly differed between plot types

(Supplement, Table S2; Fig. 2). Native plant cover was higher in native plots, while exotic plant cover was significantly higher in *Tamarix* plots, and *Tamarix* plots did not differ from each other. In all plot types, perennial plants contributed most to total cover compared to annual plants (Appendix, Table A1), and differences in native and exotic plant cover followed the same pattern as total cover (Fig. 2). Planted species contributed to a large proportion of cover within native plots (66-100%), while *Tamarix* dominated the cover in *Tamarix* plots (51.1% ± 2.2%; mean ± SEM). Native perennial species that contributed most to cover in plots in native patches included in order of contribution *Salix gooddingii* (Goodding's willow), *Anemopsis californica* (Yerba mansa), *Eleocharis palustris* (Common spikerush), *Salix exigua* (Sandbar willow), *Juncus mexicanus* (Mexican rush), and *Typha latifolia* (Broad-leaf cattail). All except the latter species was planted within native patches. In all native plots, we detected *Tamarix* at varying cover levels (1.5-17.5%), and we observed individuals flowering during the study period. An exotic perennial species *Lepidium latifolium* (Broad-leaf pepperwort) was also detected within native plots but cover tended to be <1%.

We detected a few planted species in *Tamarix* plots, including the two *Salix* species (willow) and *A. californica*. Individuals detected were primarily in plots 10 m from native patches and contributed little to cover (Appendix, Table A1). We also detected non-planted native species in *Tamarix* plots, including *Baccharis salicina* (Emory's baccharis), *Typha latifolia* (Broad-leaf cattail, Bulrush), and *Pluchea sericea* (Arrow-weed). Individuals contributed little to cover. Total annual species contributed significantly more to the understory in *Tamarix* plots compared to native plots. In fact, besides *L. latifolium* and the occasional native perennial plant, annual plants dominated the understory of *Tamarix* plots. While native and exotic annual plant cover did not significantly differ between plot types, both native and exotic annuals tended to be higher in *Tamarix* plots than native plots and increased in cover the farther away from native patches. The native forb *Pluchea odorata* (Sweetscant) and the exotic annual grass *Polypogon monspeliensis* (Annual rabbitsfoot grass) contributed the most of annual cover. Although other annuals were detected (Table A1), these other species contributed little to cover (0.1%) and did not occur frequently among plots.

Because of differences between plot types, most native plots had more diverse understory-overstory layer composition compared to *Tamarix* plots (Table A1; Fig. 2). Native plant life history groups, except plants classified as forbs, had significantly lower cover the farther away from native plots (Table S2). Native forb species were detected within several *Tamarix* plots 10 m from native patch edges, and these plots contained similar cover as native plots. For exotic species, *Tamarix* contributed a dominant proportion of the cover in all plots. Exotic grass and forb cover did not differ among plot types, although a higher proportion of grasses contributed to exotic cover compared to forbs in native plots.

### *Seed banks*

Seed extraction detected more species and more individuals than seedling emergence (Tables A2, A3), although germination tests of extracted seed reflected trends observed in the seedling emergence assay (Table A4). With extraction, we detected 12 species compared to the four species detected using the seedling emergence method. From composited samples, we extracted 3,394 positively identified seeds (226 ± 89 per sample; mean ± SEM) compared to 1,283 seedlings (86 ± 18 seedlings per sample). Of these, 39.6% and 98.8% of total seeds, respectively, were annual species. Two species were a large proportion of individuals in both methods, *P. odorata* and *P. monspeliensis*, both annual species with readily germinable seeds (Tables A4). While these annual species comprised 90.0-100.0% (98.3% ± 0.88%) of total seedlings within composited samples, using extraction, detection of these same species was much more variable among samples, ranging 1.6%-98.0% (59.7% ± 7.4%). Germination testing of *P. odorata* and *P. monspeliensis* extracted seeds resulted in 67.7% ± 6.6% germination, or per species 56.4% ± 6.6% for *P. odorata* and 90.2% ± 4.3% for *P. monspeliensis*. Perennial species were rarely detected in the emergence assay. While <1% of seedlings (15 seedlings among five plots) detected were perennial plants, in extraction perennial seeds were detected in all samples and averaged 40% ± 7.4% per sample. Although germination testing was conducted on several perennial species and germination was not observed, this does not indicate that no seeds are viable necessarily.

Species detected in seed banks differed between native patch plots and *Tamarix* plots, although total seeds detected and total native and total exotic seeds detected did not significantly differ among plot types (Table S2; Fig.3). Additionally, total annual and perennial seeds detected did not differ among plot types (Fig. 3). The only two annual species detected, *P. odorata* and *P. monspeliensis,* contributed to a large proportion of seed banks in all plot types (Table A2, A3). While the number of seeds of the exotic annual *P. monspeliensis* only moderately significantly differ between plot types with a higher number of seeds detected in native plots, the number of seeds contributed by *P. odorata* significantly differ between plot types, with significantly fewer seeds of this species detected in seed banks from native plots. Although the number of *P. odorata* seeds detected differed between plot types, seedling emergence (Fig. 4) and extracted seed germination testing (Table A4) results suggest that seed viability was actually similar across plot types. Seedling emergence of *P. monspeliensis* generally followed the same trends observed in extraction, with higher emergence among native plot seed banks than *Tamarix* seed banks (Fig. 4). Although perennial seed banks did not differ among plot types, more seeds from native species were detected in native patch plot seed banks compared to *Tamarix* plot seed banks, and an increasing number of exotic perennial seeds, mostly *Tamarix* seeds, was detected along the distance-from-native-patch gradient away from native patches (Fig. 3).

Similar to vegetation, seed banks from native plots had more compositional diversity compared to *Tamarix* plots (Fig. 3). All plant life history groups detected in aboveground vegetation surveys, including planted species, were detected in the seed banks (Table A1, A2). Counts of native sedge/rush and native shrub/tree seeds significantly differed among plot types (Table S2; Fig. 3). In native plot seed banks, we detected significantly more seeds from sedges/rushes than *Tamarix* plots, while native forb seeds were similar between native plots and plots 10 m from native patches. Exotic components of seed banks did not differ among plot types, although similar to vegetation, *Tamarix* contributed to a dominant proportion of the exotic seed bank.

### *Seed rain*

Seed rain shared similar characteristics and trends with seed banks, although native species groups differed between seed banks and seed rain. Similar to seed banks, annual seed capture was highly variable 5.7%-95.2% among plots and tended to dominate seed rain, with 72%

(60.0% ± 8.2%; mean ± SEM) of total seeds from annual species (Table A5). Common annuals included the same two species that were also dominant in aboveground vegetation surveys and seed banks, the native forb *P. odorata* and exotic grass *P. monspeliensis*. Germination testing of *P. odorata* revealed much lower germination rates in seeds obtained from seed rain (10.2% ± 3.9%) compared to germination of extracted seed. Germination of *P. monspeliensis* was more similar between seed rain (90.8% ± 4.3%) and seed banks. While another native annual *Laennecia coulteri* (Coutler's horseweed) contributed to a small proportion of seed rain in 11 plots, this species was only detected in aboveground vegetation in a single plot during the survey period and not at all in the seed bank. We detected ten native and two exotic perennial species contributing to seed rain during the study period, and species detected between seed rain and seed banks differed (Tables A2, A3, A5). While contributions to seed rain by native perennials was variable among plots, *Tamarix* contributed to most of the exotic perennial seed rain during the study period.

Also, like seed banks, seed rain did not significantly differ among plot types, and total native and exotic species' seed rain did not differ among plot type (Table S1; Fig 5). Unlike seed banks, however, native annual seed rain, which tended to be a larger proportion of annual contributions to seed rain and was mostly composed of *P. odorata,* did not differ among plot types, but exotic annual seed rain, composed of *P. monspeliensis*, did significantly differ among plot types, with more seeds detected in native plots compared to *Tamarix* plots. Also, unlike seed banks, total perennial seed rain, and specifically native perennial seed rain, significantly differed between plot types, with both significantly higher (three-five times) in native plots compared to *Tamarix* plots, and seed rain between *Tamarix* plot types did not differ. Exotic perennial seed rain contributed mostly by *Tamarix* did not differ among plot type.

As with the aboveground vegetation and seed banks, seed rain from native plots had greater compositional diversity compared to seed rain from *Tamarix* plots. All plant life history groups detected in aboveground vegetation and seed banks were represented in seed rain samples, although not all taxa. Proportions of native plant groups differed among seed rain, seed banks, and aboveground vegetation. A larger proportion of seed rain compared to the seed bank during this survey period consisted of seeds from native forbs, although contribution of forbs to seed rain did not significantly differ among plot types. Among plot types, seed rain from native shrub/tree, cattail, and sedge/rush plant groups were significantly higher among native plots. *Tamarix* plots had significantly lower seed rain from these native plant groups, but seed rain from native forbs did not significantly differ among plot types. Exotic plant contributions to seed rain did not vary among plot types. *Tamarix* contributed a majority proportion of seeds to exotic species seed rain among plots.

## TABLES AND FIGURES

*List of Tables*



### Supplementary Tables



### Appendix Tables

from-patch gradient plots, four subsamples were obtained from each of the 10 m and 20 m plots and composited on a native patch paired-distance gradient. (Excel workbook)

**Table A4.** Germination rates for extracted seed. Germination tests were limitedly conducted on taxa seed where enough seeds were available per plot, per the plot types, or pooled among all plots. Tests included 20-100 seeds. (Excel workbook)

**Table A5**. Cumulative seed rain captured in five native patch plots and ten sets of plots along a distance-from-native-patch gradient over one growing season from June 8 through December 4, 2020. The distance-from-native-patch gradient included sampling 10 m and 20 m from the native patch edge into the surrounding *Tamarix* stand in two directions and compositing the samples by native patch and distance from native patch. Cumulative trap effort per native patch or per set of distance-from-native-patch-gradient plots was 434.3 $cm^2$. (Excel workbook)

**Table A6.** Germination rates for seed obtained from seed rain sampling. Germination tests were limitedly conducted on taxa where enough seeds were available per plot, per the plot types, or pooled among all plots. Tests included 20-100 seeds. (Excel workbook)

**Table 1.** Centroids of native plant patches which received planting treatments after clearing *Tamarix* in 2014. Coordinates are in projection NAD 1983, Zone 11.

| Native patch | *Tamarix* Cleared ($ft^2$) | *Tamarix* Cleared ($m^2$) | Easting | Northing |
|---|---|---|---|---|
| AB | 886 | 82.3 | 739138 | 4055611 |
| B | 1,506 | 139.9 | 739189 | 4055630 |
| E | 10,921 | 1014.6 | 739249 | 4055590 |
| D | 2,093 | 194.4 | 739224 | 4055571 |
| F | 3,298 | 306.4 | 739284 | 4055538 |

**Table 2**. Species planted in *Tamarix*-cleared patches in 2014 at the Mormon Mesa Subunit (Riparian Subunit 1), managed by Clark County, Nevada. Species were planted either as poles (~1.5 cm in diameter, <1 m), or seedlings grown in 2.5-L (#1 gallon) nursery pots.

| Native patch | Goodding's Willow (*Salix gooddingii*) | | Sandbar willow (*Salix exigua*) | | Cottonwood (*Populus fremontii*) | Velvet ash (*Fraxinus velutina*) | Mule-fat (*Baccharis salicifolia*) | Yerba mansa (*Anemopsis californica*) | Common spikeruch (*Eleocharis palustris*) | Mexican rush (*Juncus mexicanus*) |
|---|---|---|---|---|---|---|---|---|---|---|
| | January 2014 | | | | | | | | | |
| Planting type -> | pole | | pole | | pole | | | | | |
| AB | - | | 60 | | 32 | | | | | |
| B | 36 | | 60 | | 19 | | | | | |
| D | 80 | | 110 | | 48 | | | | | |
| E | 44 | | 65 | | 32 | | | | | |
| F | 48 | | 65 | | 32 | | | | | |
| | February 2014 | | | | | | | | | |
| Planting type -> | #1 gal | pole | #1 gal | pole | #1 gal | #1 gal | #1 gal | #1 gal | #1 gal | #1 gal |
| AB | 1 | 2 | 4 | 62 | 33 | 1 | 2 | 2 | 3 | 3 |
| B | 2 | 39 | 8 | 62 | 21 | 2 | 3 | 2 | 3 | 3 |
| D | 20 | 98 | 65 | 120 | 61 | 3 | 25 | 3 | 3 | 3 |
| E | 3 | 49 | 18 | 67 | 35 | 2 | 5 | 3 | 3 | 3 |
| F | 8 | 52 | 19 | 75 | 36 | 2 | 8 | 3 | 3 | 3 |

**Table 3.** Plot locations within native plant patches and 10 m and 20 m away in two directions from the edge of native patches. Plot identification matches native patch identification by Clark County, Nevada. Coordinates are in projection NAD 1983, Zone 11.

| Plot ID | Distance from native patch | Easting | Northing |
|---|---|---|---|
| AB | 0 m | 739138 | 4055611 |
| AB | 10 m | 739159 | 4055613 |
| AB | 10 m | 739122 | 4055610 |
| AB | 20 m | 739167 | 4055615 |
| AB | 20 m | 739113 | 4055604 |
| B | 0 m | 739189 | 4055630 |
| B | 10 m | 739177 | 4055615 |
| B | 10 m | 739171 | 4055619 |
| B | 20 m | 739172 | 4055607 |
| B | 20 m | 739163 | 4055613 |
| D | 0 m | 739224 | 4055571 |
| D | 10 m | 739249 | 4055557 |
| D | 10 m | 739198 | 4055573 |
| D | 20 m | 739255 | 4055551 |
| D | 20 m | 739195 | 4055574 |
| E | 0 m | 739249 | 4055590 |
| E | 10 m | 739254 | 4055607 |
| E | 10 m | 739259 | 4055596 |
| E | 20 m | 739263 | 4055604 |
| E | 20 m | 739265 | 4055603 |
| F | 0 m | 739284 | 4055538 |
| F | 10 m | 739292 | 4055557 |
| F | 10 m | 739269 | 4055545 |
| F | 20 m | 739300 | 4055561 |
| F | 20 m | 739262 | 4055548 |

*Figures*

**Figure 1.** Examples of seed traps with top edge of traps at ground level.

**Figure 2.** Percent or proportions of native and exotic annual and perennial cover in plots within native patches and within plots along a distance-from-native-patch gradient 10 m and 20 m into the surrounding *Tamarix* stand. Plots were 0.01 ha (r = 5.642 m). Lower case letters indicate significant differences among plot types within plant variables, if detected. Letters above error bars represent differences between the main captioned variables. For the first variable listed in the legend, significant effects among plot types are displayed to the left of bars. For the second variable mentioned in the legend, significant effects among plot types are displayed within bars. Error bars display +1 SE of the plant variable identified in the graph caption. For graph D, percent of plant life history group differences among plots types include shrub/tree, cattail, and sedge/rush = a, b, b and forb = a, ab, b. For graph E, significant differences among plot types include tree = a, b, b.

**Figure 3.** Estimates of seeds per 1 $m^2$ (0-5 cm deep) or proportions of native and exotic annual and perennial seeds detected in seed banks using a seed extraction method from plots within native patches and within plots along a distance-from-native-patch gradient 10 m and 20 m into the surrounding *Tamarix* stand. Samples (1000 $cm^3$) were obtained before flowering and seeding of native riparian plants. Lower case letters indicate significant differences among plot types within plant variables, if detected. For the first variable listed in the legend, significant effects among plot types are displayed to the left of the bars. Error bars display +1 SE of the plant variable identified in the graph caption. For graph D, plant life history group differences among plots types include sedge/rush = a, b, b and forb = a, ab, b.

**Figure 4.** Estimates of seeds per 1 $m^2$ (0-5 cm deep) of native and exotic annual seeds detected in seed banks using a seedling emergence method from samples plots within native patches and within plots along a distance-from-native-patch gradient 10 m and 20 m into the surrounding *Tamarix* stand. Samples (1000 $cm^3$) were obtained before flowering and seeding of native riparian plants. Error bars display +1 SE of the plant variable identified in the graph caption.

**Figure 5.** Cumulative or proportional amount of native and exotic annual and perennial seed (1 $m^2$) detected between June 8 and December 4, 2020 from plots within native patches and within plots along a distance-from-native-patch gradient 10 m and 20 m into the surrounding *Tamarix* stand. Lower case letters indicate significant differences among plot types within plant variables, if detected. Letters above error bars represent differences between the main captioned variables. For the first variable listed in the legend, significant effects among plot types are displayed to the left of the bars. For the second variable listed in the legend, significant effects among plot types are displayed to the right of the bars. Error bars display +1 SE of the plant variable identified in the graph caption. For graph D, plant life history group differences among plot types include shrub/tree = a, b, ab; cattail = a, b, c; and sedge/rush = a, b, b.

**Figure 1.**

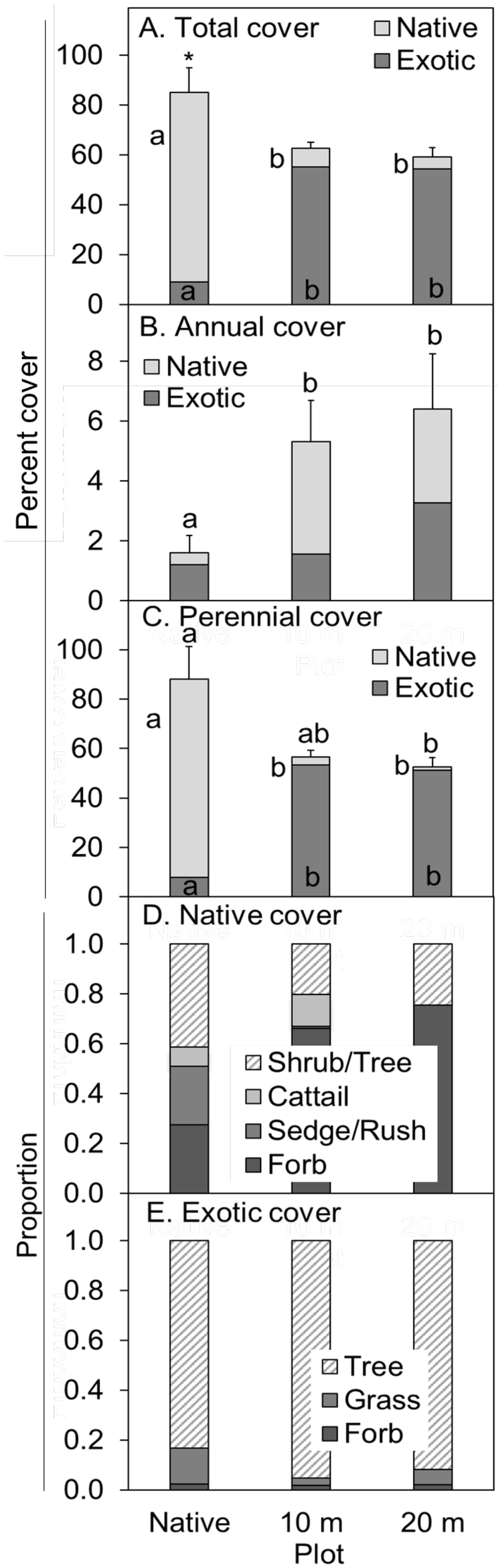

A. Total cover
Native
Exotic
100
80
60
40
20
0
*
a
b
b
a
b
b
B. Annual cover
Native
Exotic
8
6
4
2
0
a
b
b
Percent cover
C. Perennial cover
Native
Exotic
100
80
60
40
20
0
a
a
ab
b
b
b
a
b
b
D. Native cover
1.0
0.8
0.6
0.4
0.2
0.0
Shrub/Tree
Cattail
Sedge/Rush
Forb
Proportion
E. Exotic cover
1.0
0.8
0.6
0.4
0.2
0.0
Tree
Grass
Forb
Native
10 m
20 m
Plot

**Figure 2.**

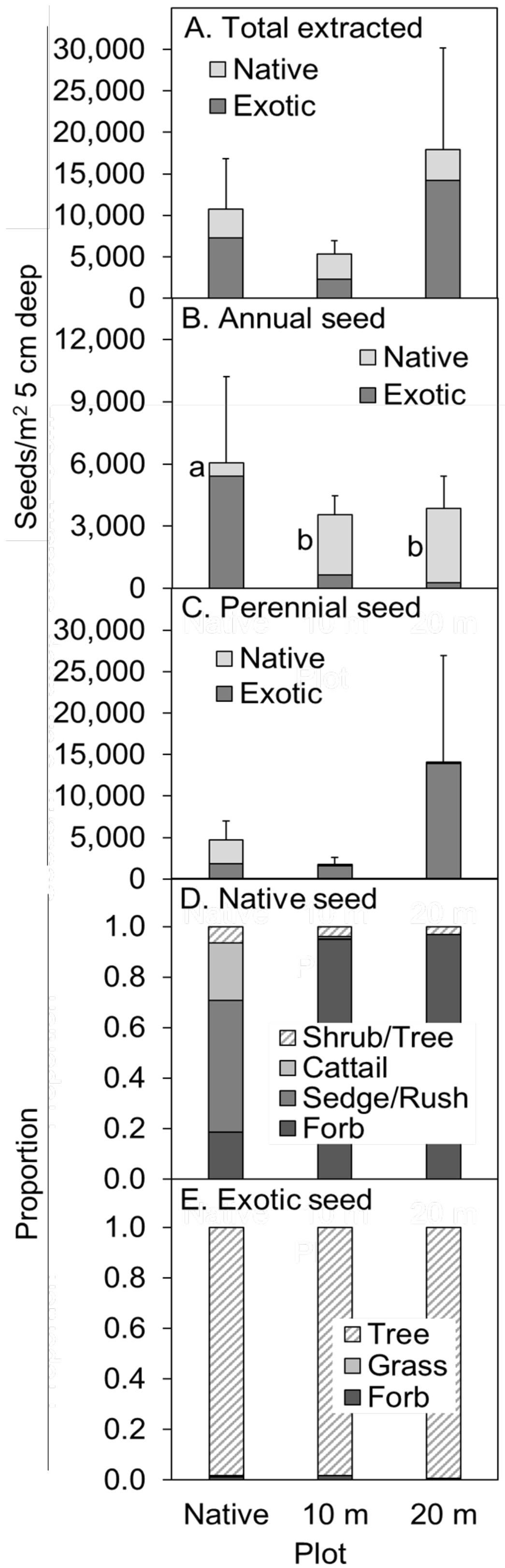
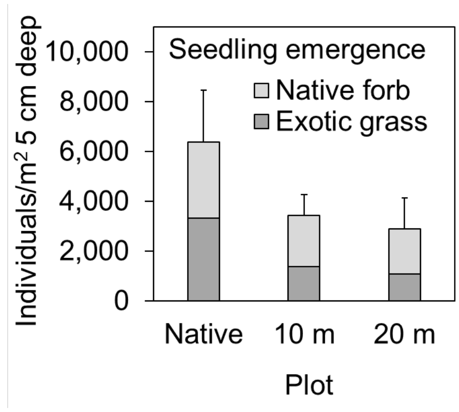
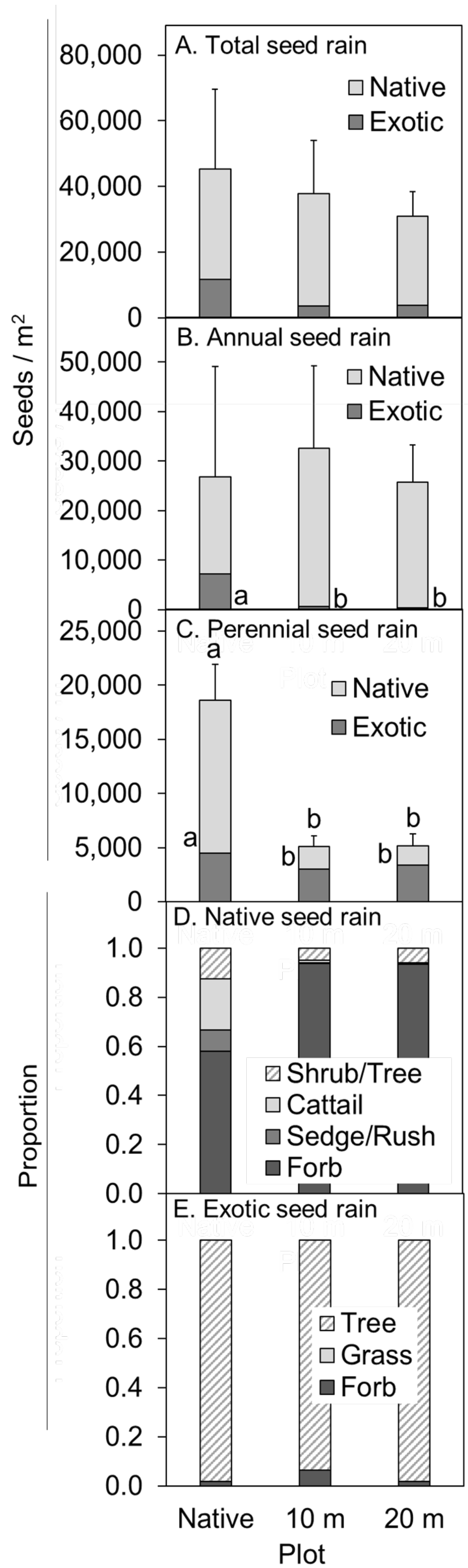

A. Total extracted
Native
Exotic
30,000
25,000
20,000
15,000
10,000
5,000
0
B. Annual seed
Native
Exotic
12,000
9,000
6,000
3,000
0
a
b
b
C. Perennial seed
Native
Exotic
30,000
25,000
20,000
15,000
10,000
5,000
0
Seeds/m² 5 cm deep
D. Native seed
Shrub/Tree
Cattail
Sedge/Rush
Forb
1.0
0.8
0.6
0.4
0.2
0.0
E. Exotic seed
Tree
Grass
Forb
1.0
0.8
0.6
0.4
0.2
0.0
Proportion
Native
10 m
20 m
Plot

**Figure 3.**



Seedling emergence
Native forb
Exotic grass
Individuals/m2 5 cm deep
10,000
8,000
6,000
4,000
2,000
0
Native
10 m
20 m
Plot


**Figure 4.**



A. Total seed rain
Native
Exotic
80,000
60,000
40,000
20,000
0
B. Annual seed rain
50,000
40,000
30,000
20,000
10,000
a
b
b
C. Perennial seed rain
25,000
20,000
15,000
10,000
5,000
D. Native seed rain
Shrub/Tree
Cattail
Sedge/Rush
Forb
1.0
0.8
0.6
0.4
0.2
0.0
E. Exotic seed rain
Tree
Grass
Forb
Seeds / m²
Proportion
Native
10 m
20 m
Plot


**Figure 5.**

## EVALUATION AND DISCUSSION OF THE RESULTS

Results of vegetation surveys and assessments of seed banks and seed rain suggest that: (1) small-patch *Tamarix* removal and native planting successfully established native plants within *Tamarix* stands, (2) planted natives continue to persist in native patches and support additional native recruitment, (3) native species contribute to native seed banks through seed rain, and (4) although surrounding *Tamarix* stands have limited native perennial seed banks in soils, removal may promote establishing native perennial seed banks and continued expansion of native patches. Native patches contained more species and greater structural and functional diversity compared to *Tamarix* stands. While seed banks and seed rain in native patches contained native patch species, native species limitedly contributed to cover and seed banks in *Tamarix* plots. However, the expansion of natives into cleared *Tamarix* areas since planting, recruitment of non-planted native species in native patches, and contributions by natives to a propagule bank via seeds or other methods (e.g., rhizomes, stolons, colonial sprouting via spreading roots), suggest that continued clearing of *Tamarix* around native patches may continue to promote native patch expansion through multiple mechanisms.

Limited and small patch-size removal of *Tamarix* with native revegetation resulted in successfully introducing native species and structural and compositional diversity in aboveground vegetation, seed banks, and seed rain. Native patches had greater richness and cover of species from diverse plant life history and functional groups, including trees and shrubs, herbaceous and graminoid species, and plants with diverse root morphologies. Although native patch composition among planted patches at planting and during this assessment differed, in all five native patches, re-invasion by *Tamarix* was limited and non-planted native species naturally colonized available microsites within patches. Recruitment through a diversity of propagules, seeds, rhizomes, stolons, or spreading roots, contributed to native patches filling in the available area over time, limiting available microsites for *Tamarix* to reestablish. Previous work on a limited number of species has demonstrated *Tamarix* can be competitive; however, *Tamarix* tends to invade areas with exposed soils with limited plant establishment. Under conditions in which native trees and larger shrubs, such as *Populus* and *Salix*, occur at higher densities and in which higher growth rates of natives are supported, natives appear to compete with *Tamarix* (Horton et al. 1960; Sher et al. 2000, 2002, 2003). If these pioneer species are able to establish a dominant overstory, *Tamarix* re-invasion may be limited or slowed (Stromberg et al. 1993; Sher et al. 2000; Stromberg & Chew 2002). Cover of understory plants by herbaceous or graminoids species may also limit *Tamarix* establishment by reducing available microsites.

Seed or propagule banks are often biodiversity reservoirs, sources of material that enable native species to persist during invasions or unfavorable conditions, and sources of material for regeneration during favorable conditions or during ecosystem recovery after a disturbance (Templeton & Levin 1979; Venable & Brown 1979; Adondakis & Venable 2004; Vandvik et al. 2016). Here, *Tamarix* dominated the seed banks in *Tamarix* plots and, as with aboveground vegetation in *Tamarix* plots, native species were depauperate, both features previously observed in some *Tamarix* infestations (Vosse et al. 2008). Tamarix is a prolific seed producer and produces seeds for longer periods during the growing season than many native species (Horton et al. 1960; Warren & Turner 1975; Fenner et al. 1984). However, although seeds are readily germinable, seeds are viable for short periods (Glen & Negler 2005). Our germination results suggest that *Tamarix* seed in the seed bank and in seed rain were non-viable. A proportion of seeds may in fact be viable, and the metric of radicle emergence over a short observation period or the sample size available was insufficient for testing viability accurately. However, we did not detect Tamarix in seedling assays either. At field sites, few to no *Tamarix* seedlings were detected in any plots during plot surveys and none observed over the study period, suggesting that if seeds were viable, high plant cover in all plots may have excluded *Tamarix* seedlings during the study period. In *Tamarix* plots, the exclusion of *Tamarix* seedlings may have been in part due to the high cover of annual species in the understory throughout the growing season. Often annuals form larger and more persistent seed banks (Templeton & Levin 1979). *Tamarix* plot seed banks had few perennial species. The limited contributions by native perennials to seed banks in *Tamarix* plots, which included *Pluchea sericea* (Arrow-weed), an important nectar source for butterflies (Nelson & Anderson 1994), suggest that most native plant seeds were unable to penetrate into *Tamarix* stands, possibly due to the structure of the mature *Tamarix* stand. The limited cover and lack of detection of non-seed propagule species in *Tamarix* plots also support the hypothesis that dense *Tamarix* stands are exclusionary to most other riparian perennial species, while the success of native patch establishment also suggests removal of *Tamarix* will promote native seed banks and native propagule sources.

## CONCLUSION

The native patches restored by Clark County at the Mormon Mesa riparian subunit provide a sharp contrast with the surrounding matrix of primarily *Tamarix* monoculture, which had comparatively low plant diversity and few native species compared with the restored native patches. Restoration of native riparian vegetation has been demonstrated to improve habitat and increase richness of bird, pollinator, and other invertebrate species (Trathnigg & Phillips 2015). In the absence of herbaceous plants or in areas that lack plant community diversity, some pollinator groups may be absent (Fleishman et al. 1999, 2003; Wiesenborn et al. 2008; Trathnigg & Phillips 2015). While vegetative structure provided by *Tamarix* and native riparian plant communities both benefit birds in Southwest deserts (Fleishman et al. 2003), plant composition, particularly of flowering herbaceous plants, has been shown to significantly benefit other faunal groups including butterflies and other important pollinators (Fleishman et al. 1999, 2003; Trathnigg & Phillips 2015). The marked improvements of native species dominance in propagule banks and seed rain in planted patches could be important for "bet hedging" whereby a full suite of mechanisms is available for native species to persist in the patches through vegetative propagation, soil seed banks, and seed dispersal. Although not all native perennials planted contributed to seed banks, several species contributing to cover in native patches are rhizomatous, stoloniferous, or species which colonize with spreading roots, including *A. californica*, *B. maritimus*, *E. palustris*, *J. mexicanus*, and *Salix* species, which does not preclude these species from expanding through vegetative reproductive means into areas cleared of *Tamarix* around native patches. Additionally, these same species provide *in situ* propagule resources for restoration of surrounding areas once *Tamarix* is cleared by providing on-site material for direct transplanting. Restoration of target plants and plant communities relying on seed banks is unlikely to be feasible over short periods of time where seed banks are lacking (Bossuyt & Honnay 2008), and restoration may require planting soon after *Tamarix* removal of target species to deter *Tamarix* re-invasion.

Continued monitoring of vegetation, seed banks, and seed rain in and around the native patches or further treated patches may help inform the continued conservation and restoration of native vegetation at the field site and identify potential future threats to native species, such as re-encroachment by *Tamarix* or seed dispersal by other non-native species. Continued monitoring could also provide insight as to the plant community maturation processes and the effects in restored riparian communities, as longer-term trends in these types of restored riparian communities are not well understood, and this project provides a unique opportunity to identify long-term community change in restored riparian ecosystems. Monitoring of patches if surrounding *Tamarix* is removed would also provide an opportunity to assess which species contribute to patch expansion and by what means, either via seed production or vegetative propagation. Additionally, assessing pollinator resources and monitoring bird utilization of native patches may provide a better understanding of specific uses of native patches and help identify which species or species combinations best foster restoration of habitat at field sites and promote target wildlife communities.

## RECOMMENDATIONS

- Continue monitoring of vegetation, seed banks, and seed rain in and around the native patches.
- If *Tamarix* is removed from around existing native patches, monitor native patches for expansion and identify which plant species contribute to patch expansion and methods used, such as through seeding or vegetative reproduction.
- Monitor utilization by fauna of specific native species to identify plant species or plant species associations within planted native patches that foster target fauna communities.
- Utilize patch propagules to test transplanting *in situ* to identify which species are easiest to utilize for onsite restoration and propagation.

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