THESIS

LONG-TERM MONITORING FOLLOWING *TAMARIX* SPP. BIOLOGICAL CONTROL SUGGESTS VARIABLE SUCCESS

Submitted by

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ABSTRACT

LONG-TERM MONITORING FOLLOWING *TAMARIX* SPP. BIOLOGICAL CONTROL SUGGESTS VARIABLE SUCCESS

Invasive plants can cause a broad swathe of environmental and economic problems. One means to alleviate the intensity of such problems is through the introduction of classical biological control agents. Particularly for woody plants, biological control may take many years, and thus long-term monitoring of biocontrol programs may be useful to evaluate the effects of biological control on target plants and the surrounding plant community. Here, we use long-term monitoring to evaluate performance of the invasive tree *Tamarix* spp. and shifts in understory vegetation up to 22 years following release of *Diorhabda* (Coleoptera: Chrysomelidae) biological control agents. We combine three datasets from sites in Colorado and Utah, and include new data, focusing on *Tamarix* volume and understory vegetation. Average tree volume declined in most sites, though not as substantially as might be expected from shorter-term studies. Cover of both native and introduced plant species decreased, while species richness remained fairly stable. These findings suggest that additional action may be necessary to further reduce *Tamarix* performance and manage for desired plant communities, particularly in some sites. Our study offers lessons for others embarking on long-term monitoring, including implementing experimental controls and establishing shared and consistent approaches to data collection, including detailed metadata.

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1. Introduction

When an introduced plant species becomes a highly abundant invader, it can disrupt ecosystem services in invaded areas and management efforts can be extremely costly (Pearson et al., 2016). A financially feasible option for long-term, self-sustaining and widespread control of an invasive plant is classical biological control (Van Driesche & Center, 2013). Classical biological control (or biocontrol) is the release of a specialist natural enemy from the native range to suppress a target plant (Debach, 1974). In biocontrol programs, the aims may be broader than solely the control of the target plant and extend to supporting native plant communities (Clewley et al., 2012). Because it can take years for populations of biocontrol agents to increase, spread, and impact the target plant (Kennard et al., 2016; Van Driesche et al., 2010), monitoring biocontrol programs beyond the first few years following release is important to evaluate program efficacy (Clewley et al., 2012; Schaffner et al., 2020).

Long-term monitoring of biocontrol agents and their target plants can reveal differences in effectiveness over time and space and is necessary to document potential changes in the plant community over time (Clewley et al., 2012). This information can guide management approaches to make current and future programs more effective. For instance, a long-term study in South Africa found that biocontrol of the aquatic invasive *Salvinia molesta* provided essentially complete control at smaller sites, but was less effective at larger sites, leading to the proposal that periodic rereleases of the biocontrol agent be continued at larger sites (Martin et al., 2018). Long-term monitoring can also illuminate changes in plant communities disrupted by the target plant and indicate that initial or continued restoration is necessary to increase native plant coverage and diversity. For example, in grasslands monitored 14 years following release of a biocontrol agent in the United States, the invasive plant *Euphorbia esula* (leafy spurge) was well controlled (Lesica & Hanna, 2009). However, while native plant species diversity increased, it did not increase to pre-invasion levels (Lesica & Hanna, 2009), indicating that additional restoration efforts may be necessary to support the desired plant community. Long-term monitoring can allow researchers and managers to better capture such nuance, and act accordingly to reach management goals.

Thus, not only does long-term monitoring provide an important measure of target plant control, but it also may increase success of invasive species management by indicating that integrated or secondary measures would aid in control (e.g., periodic biocontrol rereleases, timing of release, site burning in addition to releases, etc.). Further, when biocontrol programs showcase a high degree of success, public support may increase, which can indirectly influence funding and assist in control through reducing instances of target plant reintroduction (Martin et al., 2018).

Despite their potential importance, monitoring programs to evaluate the outcomes of biocontrol programs are often short-lived, due to time and funding constraints (Schaffner et al., 2020). Additionally, experimental controls for biocontrol of invasive plants, such as replicate target plants sprayed with an insecticide are rarely established (though see Szűcs et al., 2019), which can limit conclusions that can be drawn from long-term monitoring studies. Finally, as biocontrol typically is used for widespread invasive plants, monitoring efforts will be most meaningful if they span much of the range of the target plant. To do this in a coordinated fashion requires funding, meticulous planning, and collaboration.

Here, we bring together three monitoring efforts of the biocontrol of the invasive tree *Tamarix* following the 2001 release of *Diorhabda* leaf beetles in the western United States. Specifically, we added data to one published (Kennard et al. 2016) and two unpublished monitoring datasets to ask: (1) After a decade or longer of biocontrol, how do measures of *Tamarix* vigor compare to previous years? and, (2) How has vegetation in the understory of *Tamarix* changed, with respect to cover of native and introduced species, as well as species richness?

We hypothesized that *Tamarix* tree volume would decrease over time following biocontrol introduction due to repeated defoliation by *Diorhabda* and consequent cumulative stress. We hypothesized that understory vegetation cover would increase as *Tamarix* canopy opened and trees potentially died, leaving more sunlight and resources for other plants. Similarly, we hypothesized that species richness would increase due to partial release from interspecific competition with *Tamarix*.

Additionally, we discuss some benefits and challenges of long-term monitoring and suggest best practices for establishing and conducting long-term monitoring.

2. Methods

2.1. Study System

Invasive plants in the genus *Tamarix* (commonly called tamarisk or saltcedar) are small trees that were introduced to North America about 200 years ago (Gaskin & Schaal, 2002). They have since become the third-most common woody species along rivers (hereafter riparian ecosystems) in the southwestern U.S. (Friedman et al., 2005). *Tamarix* contributes to a number of detrimental environmental changes. It competes with cottonwood, willow, and other native species that historically were the dominant woody vegetation in riparian ecosystems of the southwest U.S. (Dudley & Bean, 2012; González et al., 2017; Hultine et al., 2020), as well as with herbaceous species (Hultine et al., 2020). Further, *Tamarix* increases wildfire hazard and induces changes in soil chemistry and ecology, including disrupting vital symbioses between native plants and mycorrhizal fungi (DeLoach et al., 2003; Goetz et al., 2022; Meinhardt & Gehring, 2012). *Tamarix* can alter river hydrology through the stabilization of riverbanks, which degrades habitat quality for native fish species, several of which are endangered (Keller et al., 2014; Miller et al., 2025). Finally, in riparian ecosystems already deeply affected by hydrological changes (e.g., drought, damming), *Tamarix* can better tolerate high salinity and low water conditions than many native riparian plant species (Bay & Sher, 2008; DeLoach et al., 2003). Such tolerance of salinity and arid conditions may amplify the competitive advantage of *Tamarix* as climate change increases the frequency and length of droughts (Selwood et al., 2015).

Due to the significant management challenges posed by the invasion of *Tamarix*, research into a suitable biocontrol agent began in the late 1960s (DeLoach et al., 2003). After extensive testing of plant host range (DeLoach et al., 2003), the leaf beetle, *Diorhabda carinulata* (Coleoptera: Chrysomelidae), was determined to be sufficiently specialized on the genus *Tamarix* and was first released in the western U.S. in 2001 (Deloach et al., 2003). It was re-released in multiple locations between then and 2010 (Bean & Dudley, 2018), at which point interstate, human-assisted spread of the agent was discontinued (Bean &

Dudley, 2018) and federal funding for monitoring shrank after concerns were raised about potential impacts to the southwestern flycatcher, an endangered bird sub-species that uses *Tamarix* as nesting substrate in the absence of sufficient native plant habitat (Bean & Dudley, 2018). It was thought that defoliation by the beetle might increase exposure of nesting birds to predators and heat (Dudley & Bean, 2012). Despite federal constraints on human transport of these beetles, *Diorhabda* continued to spread on their own across the southwestern U.S. (Bean & Dudley, 2018; Clark et al., 2022); thus, it is prudent to evaluate their apparent impact on their target plant as well as potential knock-on effects to riparian plant communities.

2.2. Long-term Monitoring

In 2005, the United States Department of Agriculture published a monitoring plan (USDA APHIS, 2005) that entailed following 25 permanently marked *Tamarix* trees at a site through time and collecting data one or more times per year on features of the trees such as the height and width of live canopy, foliage color, and reproductive status. The understory vegetation was also surveyed to evaluate cover of plant taxa present. The plan was clearly outlined, but some aspects of it were not possible to follow long-term (e.g., "permanently" following individual branches of *Tamarix* is impossible as branches die and fall off trees) or quite difficult (e.g., permanently marking vegetation quadrats in flood plains). The USDA APHIS monitoring plan also included tracking *Diorhabda* beetle population dynamics. *Diorhabda* were present at all sites surveyed in 2023. However, we do not follow up on beetle data in this study, because beetle numbers can fluctuate greatly throughout the season, and we were able to add only one sample point when we returned to sites, so were unable to evaluate fluctuations throughout the season.

In June 2023 we followed up on three monitoring efforts that had six or more years of data (Table 1, Fig. 1). Each of the three monitoring efforts followed the plan outlined by USDA APHIS but used slightly different approaches to data collection, as well as having different start years (Table 1). To maintain continuity, we followed each effort's distinct data collection approach to be able to compare the new data directly to the existing long-term data.

Table 1. Site codes, names, GPS coordinates, number of trees tracked, release years, initial year of data included in this study, and partners or citations for sites where monitoring occurred. CO1, CO6, and CO7 are likely more vulnerable to scour by river flooding, along with many, though not all areas within UT, while other sites are less vulnerable.

Site Code	Location Name[a]	County, State	Latitude	Longitude	Number of Trees	Release year(s)	Year of first data[c]	Ref. or partner
CO1	Echo Park	Moffat, CO	40.528038	-108.982655	25	2006	2006	Norton & Hardin, 2011
CO2	Salt Creek	Mesa, CO	39.21908	-108.8966	25	2005-2007	2008	Kennard et al. 2016
CO3	Horsethief	Mesa, CO	39.165287	-108.843758	40			
CO4	Flume	Mesa, CO	39.150997	-108.781185	25			
CO5	Rattlesnake	Delta, CO	38.758716	-108.242982	25			
CO6	Gateway	Mesa, CO	38.56926	-108.919089	25			
CO7	Bedrock	Montrose, CO	38.289205	-108.898357	25			
UT	Moab[b]	Grand, UT	38.505595 to 39.123484	-109.101896 to -110.146598	60	2004-2007	2011[d]	Grand County Weed Department and RiversEdge West

[a] From Norton & Hardin (2011) and Kennard et al. (2016).

[b] Rather than 25 trees at a discrete site, in the vicinity of Moab more trees were sampled across a broader area, for which we provide the northern, southern, western and eastern limits. For statistical analyses and graphs, these trees together are treated as one site. Table S1 provides coordinates for the individual trees.

[c] See figures that show response through time for additional information about timing of data collection.

[d] Monitoring was initiated prior to 2011 in Grand County, but we only have data from 2011 onwards.

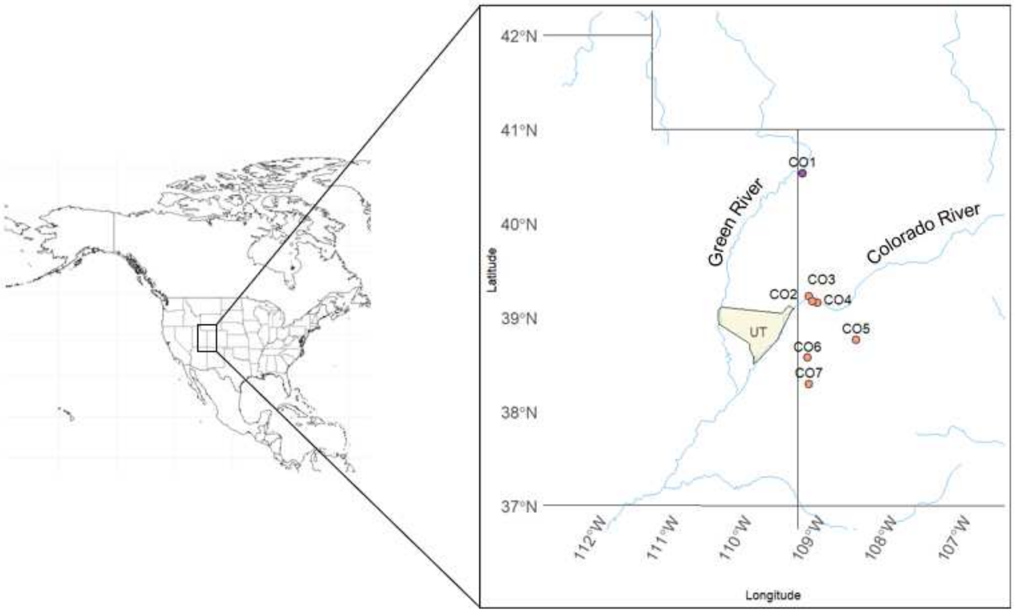

Fig. 1. Map of sites where data collection occurred. The three different colors indicate that a site is part of a particular long-term monitoring effort (CO1 is purple, CO2-CO7 are orange, and UT is yellow).

2.3. Tree Volume

We took three measurements of each tree - height and two widths - to estimate tree volume. At sites CO2-CO7 (Table 1), the height of the tallest green shoot, the maximum width (green shoot to green shoot) and the shortest width were measured following Kennard et al. (2016). At site CO1, following the protocol that had been used there, we measured height, maximum width, and the width perpendicular to maximum width (rather than the shortest width). Tree measurements were not historically taken at the UT site and so were not included in this study. Tree volume was calculated as an ellipsoid using Volume = $4/3\pi \mathrm{abc}$ where a, b, and c are the radii of height, width 1, and width 2, respectively.

2.4. Understory Vegetation

To assess understory vegetation at sites CO2-CO7, following previously used protocols (Kennard et al., 2016), $1\mathrm{m}^2$ plots were placed approximately 1m to the east or west of the trunk of each tree. Kennard et al. (2016) had previously estimated percent cover of each species within both quadrats using the following cover classes: 0–5, >5–25, >25–50, >50–75, >75–95, >95–100%. Understory vegetation could be either over or under 100% of the quadrat to account for overlapping vegetation (Bonham et al., 2004). In 2023, we recorded estimated percent cover in both quadrats without using a cover class. Again following Kennard et al. (2016), we then calculated average cover of each taxon at each tree, using the midpoints of each taxon's cover class for the earlier data, and the exact cover estimate for 2023 (using: (quadrat 1 species 1 % cover + quadrat 2 species 1 % cover)/2). This provided one set of cover measurements per tree, to match the data available from Kennard et al. (2016).

At site CO1, we again used two $1\mathrm{m}^2$ plots per tree, but in this case placed them as close as possible to the base of the tree, on the north and south side of the trunk, following previously used protocols (Norton & Hardin, 2011). Percent cover of different taxa was recorded as for sites CO2-CO7.

At UT, the protocol was to measure understory vegetation using the Point Intercept method, rather than using $1\mathrm{m}^2$ plots. This approach has been shown to provide comparable data (Hanley, 1978). A single 30.48-meter (100-foot) transect was placed underneath and through a *Tamarix* stand at a subset of trees (10). Starting at the zero-meter mark, point intercepts were recorded every 1.52 meters (5 feet), for a total of 21 points. Standard methods for estimating percent cover of each species at each point were used (number of hits for each species or ground cover class/total number of points per transect).

Plants were identified to genus, and to species when possible; additionally, we determined whether plants were native or introduced (Ackerfield, 2015; Natural Resources Conservation Service, 2026). In the analyses described below, we focused on total cover of native taxa and total cover of introduced taxa. This excludes a small percent of cover that could not reliably be identified as native or introduced. The maximum percent cover of unknown species at one single tree was 31.25%, however the mode and median were much smaller (both were 1.25%). The incidence of unknown observations, out of total observations, was 3.04%. Understory vegetation and species richness results do not include *Tamarix* cover.

2.5. Statistical Analyses

To merge the three datasets, we used the package dplyr (Wickham et al., 2023), and functions loop, cast, mutate, and join in R. We double-checked all merges and performed quality control with any updates or changes to a dataset. All analyses were conducted using R version 4.4.2 (R Core Team, 2024). Statistical significance was determined as a *P*-value below 0.05.

We ran analyses on three types of response variable: tree volume, percent cover of understory vegetation, and species richness. Our main goal in these analyses was to determine whether and how the response variable changed through time.

To analyze tree volume and percent cover of understory vegetation, we used repeated measures mixed effects models to account for a repeated measures design (i.e., repeat observations on the same tree(s) over time) using lmer from the lme4 package (Bates et al., 2015) with a square root transformation to improve normality of residuals. We treated year as a categorical factor, which allows the response variable to fluctuate over time non-linearly. We present ANOVA Type III Analysis of Variance results using Satterthwaite's method to calculate degrees of freedom.

To analyze species richness data, we used glmmTMB in the glmmTMB package (Brooks et al., 2017) with a Poisson distribution and a log() link function. We checked QQplot residuals to evaluate model fitness in the DHARMA package (Hartig, 2024). Overall fit was good, but where there were minor deviations of fit, we tested the negative binomial distribution as an alternative to the Poisson; the results were qualitatively similar, thus we present all results from the models with a Poisson distribution. We again treated year as a categorical factor, which allows the response variable to fluctuate over time non-linearly. We tested significance using a Wald chi-square test.

For all types of response variable, we first ran analyses that included all sites (excluding UT for tree volume analyses, as tree volume was not measured in that area) with site, year and their interaction included as fixed effects, and tree nested within site as a random effect. Given significant year by site interactions (see Results), we then evaluated each response variable site-by-site, with models including year as a fixed effect and tree as a random effect. To test hypotheses regarding change over time following the introduction of the biocontrol agent, we ran custom contrasts on the emmeans() (Lenth, 2024) for each response variable at each site. Each contrast (besides site CO4, tree volume, described below) reports the estimated difference in mean response for each variable between the final year of the study period and the average of the first three years, on the analysis scale (square root or log scale). Note that the contrast for tree volume at one site, CO4, had two rather than three years for early time point, as flooding prevented access in 2009.

3. Results

3.1. Tree Volume and Mortality

Tree volume was influenced by year ($F_{17,2301} = 19.0$, $P = < 0.00001$), site ($F_{6,187} = 8.2$, $P = < 0.00001$) and a significant interaction between year and site ($F_{74,2301} = 6.6$, $P = < 0.00001$). Models on each site showed significant changes in tree volume through time (Figure 2, Table 2). Contrasts showed that tree volume decreased significantly in four of the seven sites and increased in one site (Table 2). Thus, our hypothesis that tree volume would decrease following introduction of the biocontrol agent was supported in more than half the locations.

We also looked at tree mortality. Of the 190 trees whose volume had been measured – thus, not including the UT site – 36 were dead within the time period of the study. Five of those 36 trees were dead definitively not due to effects from beetle defoliation (i.e., they died due to chemical spray, mulching, or removal by a railroad company), so were not counted towards overall tree mortality. Thus, of the 36 trees that were dead eventually, 31 trees were used to measure overall tree mortality, which was 16.32% ((31/190)*100).

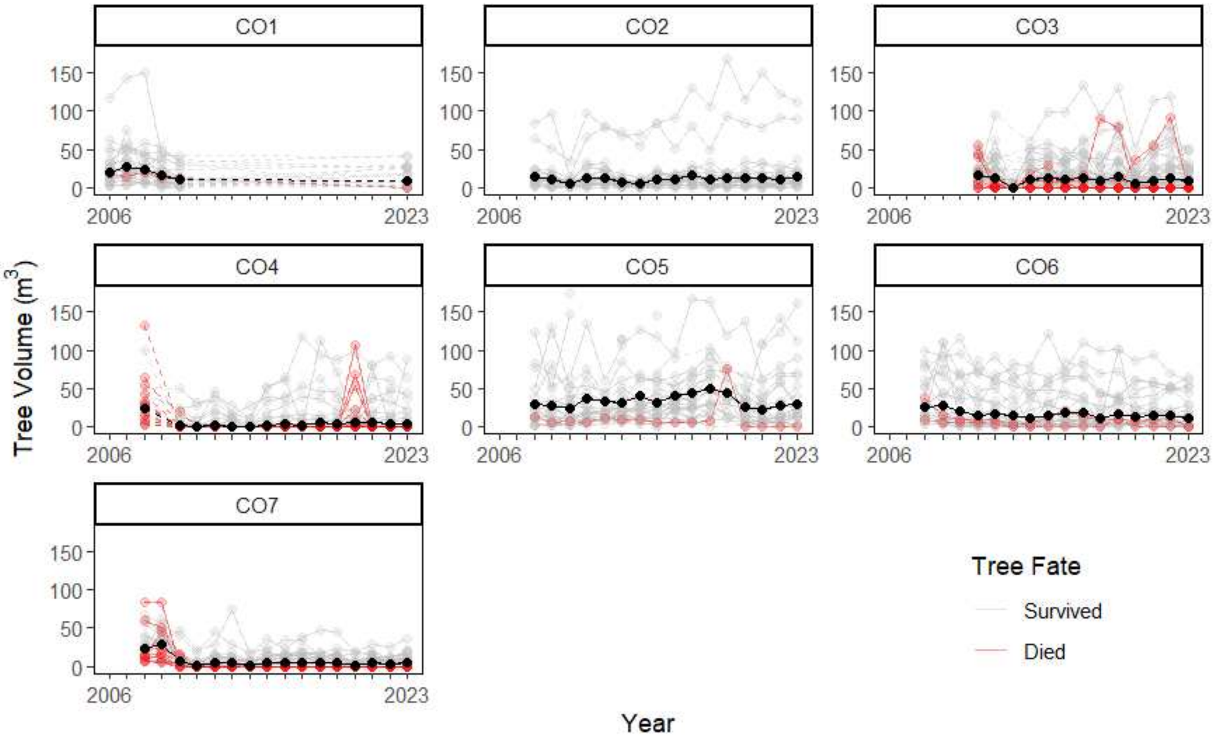

Fig. 2. Changes in tree volume through time. Black lines and dots represent mean tree volume (using emmeans()) back-transformed from the square root scale) at a site. Grey dots and lines in the background represent tree volume through time of individual trees that survived, while red dots and lines in the background represent tree volume through time of individual trees that eventually died during the study period. Dashed lines (whether black, grey, or red) indicate years when data were not recorded at a site.

Fig. 3. Tree 108 at CO1 in 2006, 2010, and 2023. An example of decrease in tree volume; not necessarily representative of an overall pattern.

Table 2. Statistical analysis of tree volume through time at each site from lmer, indicating significant changes through time at all sites. Contrast Estimate reports the difference in square root (mean tree volume) between the first three years and the final year of the study period. Significant changes in tree

volume between those periods are highlighted in bold, and the direction of the change is indicated in the sign of the contrast (negative indicating decreases in volume). The number and percent of trees that died during the study are also indicated.

Tree Volume and Mortality							
Site	F	d.f. (num, denom)	*P*-value	Contrast Estimate	*P*-value	# Trees Dead	% Dead
CO1	12.6	5, 117	< 0.00001	**-1.77**	**< 0.0001**	1.0	4.0
CO2	10.4	15, 359	< 0.00001	**0.65**	**0.0001**	0.0	0.0
CO3	7.1	12, 445	< 0.00001	0.17	0.584	6.0	15.0
CO4	7.5	14, 321	< 0.00001	**-0.92**	**0.034**	13.0	52.0
CO5	4.2	15, 343	< 0.00001	0.28	0.481	1.0	4.0
CO6	6.6	15, 355	< 0.00001	**-1.58**	**< 0.0001**	1.0	4.0
CO7	30.8	15, 360	< 0.00001	**-2.10**	**< 0.0001**	9.0	36.0

3.2. Understory Vegetation: Native vs. Introduced Percent Cover

Native Understory Vegetation

Percent cover of native understory vegetation was influenced by year ($F_{17,853} = 4.9$, $P = < 0.00001$), site ($F_{7,217} = 6.2$, $P = < 0.00001$) and a significant interaction between year and site ($F_{23,853} = 4.5$, $P = < 0.00001$). Examining individual sites showed significant changes in native understory vegetation at all sites through time (Figure 4, Table 3). Contrasts showed that cover of native vegetation decreased in all sites, with four of those decreases being statistically significant (Table 3). Thus, our hypothesis that native cover would increase following introduction of the biocontrol agent was not supported.

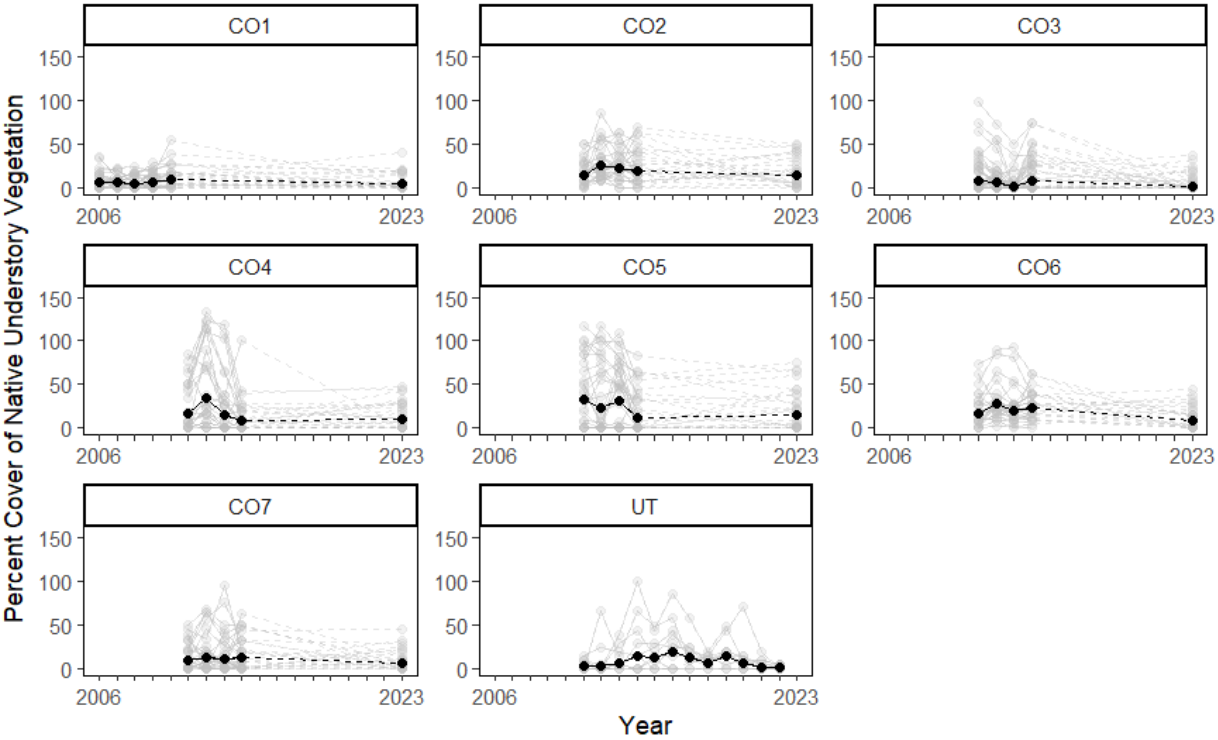

Fig. 4. Changes in percent cover of native understory vegetation through time. Black lines and dots represent mean percent cover of native understory vegetation (using emmeans()) back-transformed from the square root scale) at a site. Grey dots and lines show results for individual trees through time. Dashed lines (whether black or grey) indicate years when data was not recorded at a site.

Table 3. Statistical results for percent cover of native understory vegetation through time from lmer, indicating significant changes through time at all but one site. Contrast Estimate reports the difference in mean percent cover of native taxa between the first three years and the final year of the study period, on the analysis scale (square root scale). Significant decreases (negative estimates) in native cover between those periods are highlighted in bold).

Native Understory Vegetation (Percent Cover)					
Site	F	d.f. (num, denom)	*P*-value	Contrast Estimate	*P*-value
CO1	2.7	5, 118	0.024	-0.05	0.853
CO2	2.7	4, 99	0.032	-0.67	0.091
CO3	8.8	4, 156	0.000002	**-0.70**	**0.033**
CO4	8.5	4, 96	0.000007	**-1.37**	**0.004**
CO5	5.3	4, 96	0.0007	**-1.45**	**0.004**
CO6	7.5	4, 95	0.00003	**-1.66**	**< 0.0001**
CO7	0.8	4, 96	0.507	-0.69	0.130
UT	3.1	11, 98	0.001	-1.02	0.173

Introduced Understory Vegetation

Percent cover of introduced understory vegetation was influenced by year ($F_{17,856} = 4.5$, $P = < 0.00001$), site ($F_{7,220} = 17.9$, $P = < 0.00001$) and a significant interaction between year and site ($F_{23,856} =$

8.6, *P* = < 0.00001). Examining individual sites showed significant changes in introduced understory vegetation at six of eight sites through time (Figure 5, Table 4). Contrasts revealed that percent cover of introduced understory vegetation decreased in four sites and increased in one site (Table 4). Thus, our hypothesis that introduced cover would increase following introduction of the biocontrol agent was largely unsupported.

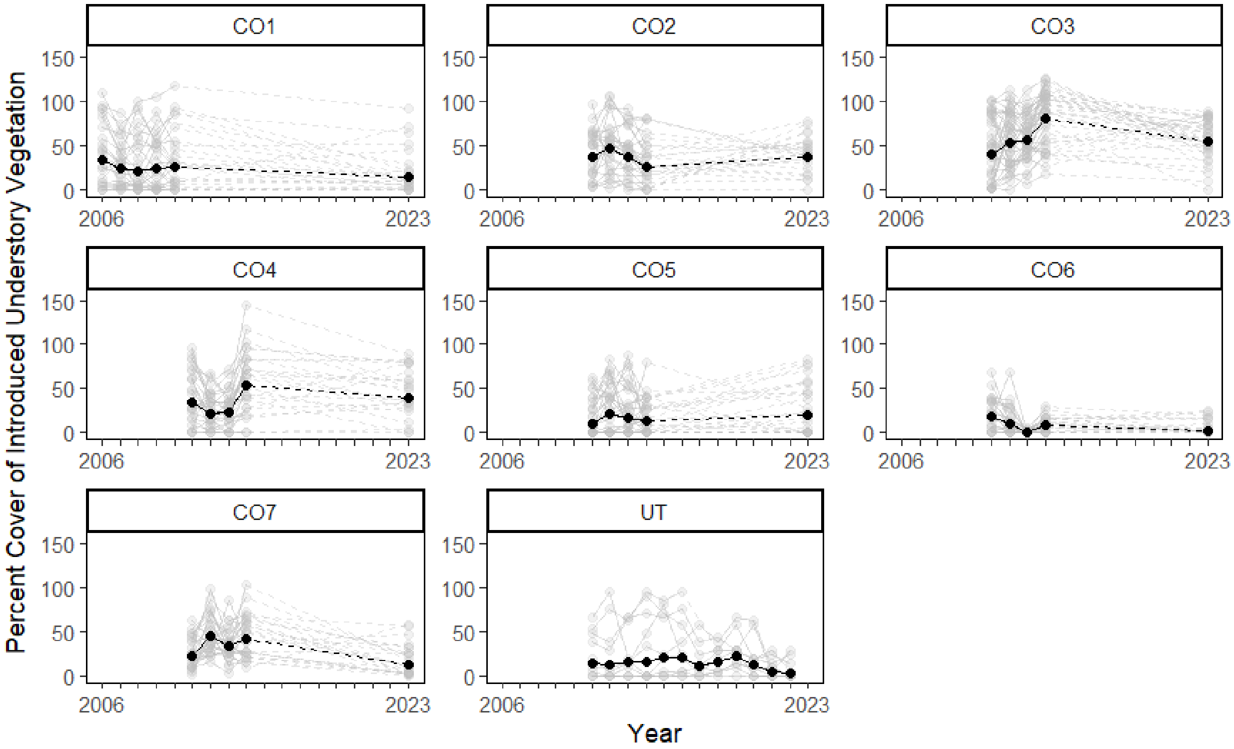

Fig. 5. Changes in percent cover of introduced understory vegetation through time. Black lines and dots represent mean percent cover of introduced understory vegetation (using emmeans()) back-transformed from the square root scale) at a site. Grey dots and lines show results for individual trees through time. Dashed lines (whether black or grey) indicate years when data was not recorded at a site.

Table 4. Statistical results for percent cover of introduced understory vegetation through time indicating significant changes through time at all but two sites. Contrast Estimate reports the difference in mean percent cover of introduced taxa between the first three years and the final year of the study period, on the analysis scale (square root scale). Significant changes in introduced cover between those periods are highlighted in bold, with the direction of the change indicated in the sign of the contrast (negative indicating decreases in cover, positive indicating increases).

Introduced Understory Vegetation (Percent Cover)					
Site	F	d.f. (num, denom)	*P*-value	Contrast Estimate	*P*-value
CO1	5.1	5, 118	0.0003	**-1.38**	**0.0001**
CO2	3.3	4, 99	0.015	-0.24	0.544
CO3	13.4	4, 156	< 0.00001	0.37	0.209

CO4	11.1	4, 96	< 0.00001	**1.18**	**0.002**
CO5	1.7	4, 96	0.152	0.39	0.447
CO6	26.6	4, 95	< 0.00001	**-0.93**	**0.005**
CO7	19.3	4, 96	< 0.00001	**-2.11**	**< 0.0001**
UT	1.8	11, 98	0.065	**-2.13**	**0.010**

3.3. Understory Vegetation: Total, Native, and Introduced Species Richness

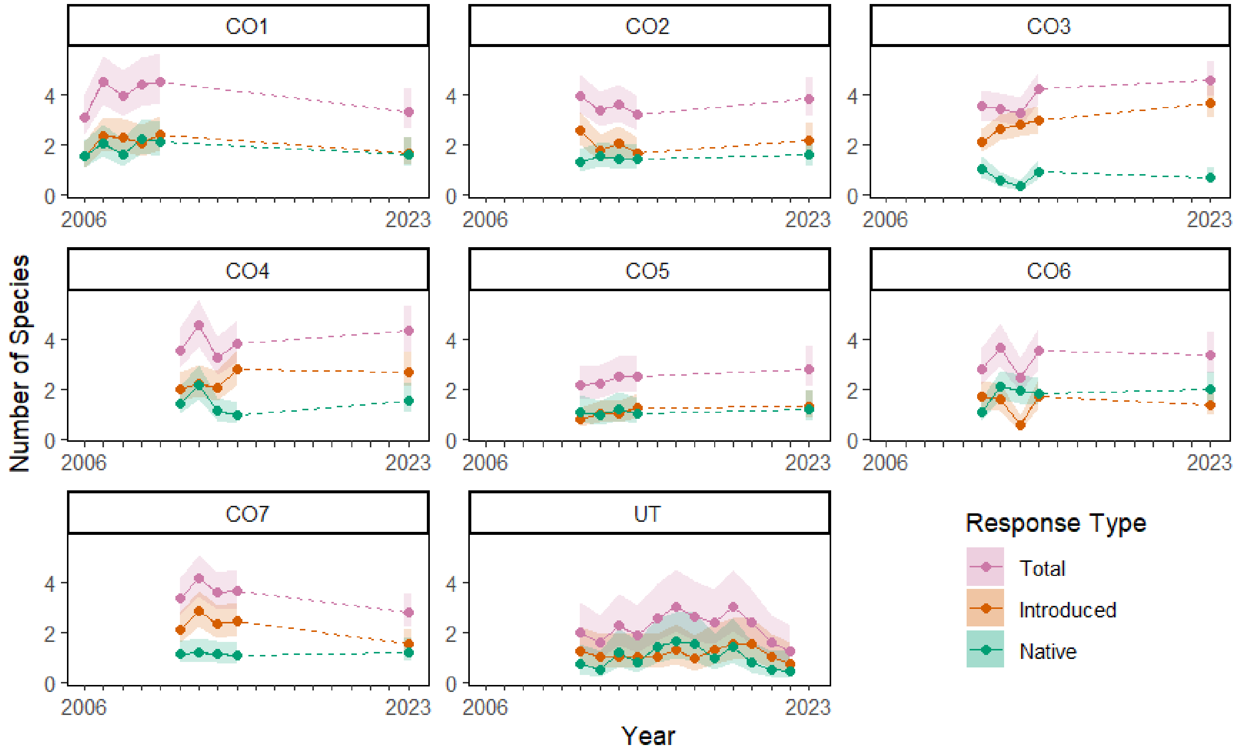

Fig. 6. Changes in species richness (total, native, and introduced) through time. Solid lines and dots represent means of total, native and introduced species richness (using emmeans()) back-transformed from the log scale) at a site. Dashed lines indicate years when data was not recorded at a site. Transparent colors show 95% confidence intervals. CO1-CO7 are in units of the number of species per 1m^2 plot, and UT is in units of the number of species per 21 points along a 30.48m transect, which provides comparable data (Hanley, 1978).

Total Species Richness

Total species richness (sum of native and introduced species) was influenced by year ($\chi^2_{17} = 37.5$, $P = 0.003$) and site ($\chi^2_{7} = 46.9$, $P = < 0.00001$), but there was only weak evidence for an interaction between year and site ($\chi^2_{23} = 32.6$, $P = 0.088$). Examining individual sites showed significant changes in total species richness over time at two sites (Figure 6, Table 5). Contrasts indicated that total species richness increased at one site and decreased at one site (Table 5). Thus, our hypothesis that total species richness would increase following introduction of the biocontrol agent did not receive consistent support.

Table 5. Statistical results for changes in total species richness through time. Contrast Estimate reports the difference in mean total species richness between the first three years and the final year of the study period, on the analysis scale (log scale).

Total Species Richness					
Site	χ^2	d.f.	*P*-value	Contrast Estimate	*P*-value
CO1	12.1	5	0.034	-0.13	0.285
CO2	2.8	4	0.595	0.05	0.653
CO3	13.6	4	0.009	**0.30**	**0.001**
CO4	7.7	4	0.104	0.14	0.210
CO5	2.8	4	0.594	0.20	0.154
CO6	8.4	4	0.078	0.13	0.307
CO7	6.9	4	0.142	**-0.27**	**0.046**
UT	15.6	11	0.157	-0.44	0.163

Native Species Richness

Native species richness was influenced by year ($\chi^2_{17} = 26.8$, $P = 0.061$), site ($\chi^2_{7} = 26.6$, $P = 0.0004$) and a significant interaction between year and site ($\chi^2_{23} = 48.4$, $P = 0.001$). Examining individual sites showed significant changes in native species richness over time at two sites (Figure 6, Table 6). Contrasts revealed that none of the sites experienced a significant change in native species richness (Table 6). Thus, our hypothesis that native species richness would increase following introduction of the biocontrol agent was not supported.

Table 6. Statistical results for changes in native species richness through time. Contrast Estimate reports the difference in mean native species richness between the first three years and the final year of the study period, on the transformed scale (log scale).

Native Species Richness					
Site	χ^2	d.f.	*P*-value	Contrast Estimate	*P*-value
CO1	7.0	5	0.224	-0.05	0.764
CO2	0.7	4	0.952	0.09	0.631
CO3	22.0	4	0.0002	0.15	0.458
CO4	15.9	4	0.003	0.01	0.942
CO5	1.2	4	0.877	0.12	0.546
CO6	8.7	4	0.070	0.20	0.236
CO7	0.2	4	0.994	0.04	0.834
UT	19.6	11	0.051	-0.46	0.350

Introduced Species Richness

Introduced species richness was not significantly affected by year ($\chi^2_{17} = 21.6$, $P = 0.200$), but was affected by site ($\chi^2_{7} = 117.6$, $P = < 0.00001$), and an interaction between year and site ($\chi^2_{23} = 52.0$, $P =$

0.0005). Examining individual sites showed significant changes in introduced species richness over time at three sites (Figure 6, Table 7). Contrasts showed that introduced species richness increased at one site and decreased at one site (Table 7). Thus, our hypothesis that introduced species richness would increase following introduction of the biocontrol agent did not receive consistent support.

Table 7. Statistical results for changes in introduced species richness through time. Contrast Estimate reports the difference in mean introduced species richness between the first three years and the final year of the study period, on the transformed scale (log scale).

Introduced Species Richness					
Site	χ^2	d.f.	*P*-value	Contrast Estimate	*P*-value
CO1	8.4	5	0.137	-0.20	0.243
CO2	6.2	4	0.182	0.04	0.806
CO3	17.2	4	0.002	**0.38**	**0.0002**
CO4	5.7	4	0.225	0.25	0.090
CO5	3.8	4	0.441	0.31	0.137
CO6	16.3	4	0.003	0.17	0.409
CO7	10.7	4	0.030	**-0.46**	**0.009**
UT	5.2	11	0.919	-0.40	0.332

4. Discussion

Classical biological control offers a long-term, financially feasible approach to manage widespread invasive plants (Van Driesche & Center, 2013). While successes of some biocontrol introductions against invasive plants are well documented (Clewley et al., 2012; Szűcs et al., 2019; Van Driesche et al., 2010), tracking the outcomes for long-lived species is challenging. Long-term monitoring offers potential insights into the impacts of biocontrol releases. Here, we present findings from long-term monitoring of *Tamarix*, an invasive tree, as well as understory vegetation, following release of *Diorhabda* leaf beetles for biocontrol. Tree volume and percent cover may vary year to year, in part because different years can represent different environments, particularly with respect to precipitation.

4.1. Tree Volume and Mortality

Interpreting changes in tree volume over time is made challenging by the fact that it was not feasible for early participants in this study to implement experimental exclusions of biocontrol agents (and other insect herbivores) from the trees using insecticides. In the absence of trees protected from beetles, it is only possible to compare metrics of performance through time, which can either under- or overestimate impact. Underestimates can arise if protected trees would have grown and increased in volume over time, providing a starker comparison with trees exposed to biocontrol. Overestimates can arise when using comparisons through time if other environmental changes such as drought that coincide with biocontrol are leading to decreases in size that would have happened even in the absence of biocontrol. Excluding biocontrol agents can be challenging and expensive but doing so is not impossible. For example, they were excluded for tansy ragwort (*Jacobaea vulgaris*) (Szűcs et al., 2019) and melaleuca (*Melaleuca quinquenervia*) (Tipping et al., 2009). These exclusions allowed those authors to confidently demonstrate that biocontrol led to higher mortality and decreased fecundity. Exclusion of *Diorhabda* from *Tamarix* at two sites in 2004 and 2005 demonstrated a 28-66% reduction in canopy cover of untreated trees relative to insecticide-treated trees (Pattison et al., 2010). Having even a few trees protected from insect herbivores can put findings into much better context. For example, if beetles had been excluded from even five to ten *Tamarix* trees at each of two sites, this would have provided a much improved frame of reference.

We tracked the volume of the canopy of 190 trees in seven sites spanning more than 2 degrees latitude. We hypothesized that tree volume would decrease over time following introduction of the biocontrol agent, rather than grow. We found some support for this hypothesis, in that average tree volume decreased over time in the majority of sites. However, there was variability among trees within and among sites, and average tree volume increased in one site. Shorter-term studies focused on the initial years following release of the biocontrol agents showed more substantial decreases (50-63%) (Hultine, Bean, et al., 2015; Kennard et al., 2016). In some cases, initial declines in *Tamarix* cover following release of the biocontrol agent could be temporary, with cover increasing again later (González et al., 2020). In combination, these data suggest that growth can be suppressed in the majority of trees in the short run, in some trees in the long run, and that on average trees may shrink slightly rather than increase in size; but that not all trees that persist will continue to shrink.

We found that over 16% of the trees died, however, without protected trees excluding biological control agents, and with little published information about the lifespan of *Tamarix*, it is difficult to know whether that mortality rate exceeds the background rate in the absence of biological control. Tree longevity is an active area of research, and data suggests that many tree species' life spans are limited only by external conditions (Piovesan & Biondi, 2021). We found two studies that provided information on *Tamarix* longevity in North America. One reports that they can live at least 37 years, and continue to grow, if slowly, at that age (Lesica & Miles, 2001). The other found individual trees that were 75 to 100 years old, that did not show signs of decline due to age (Horton, 1977). If, like many other trees, *Tamarix* longevity is largely regulated by external factors, then 16% mortality over less than 20 years seems substantial. Other studies in this system report mortality relatively soon after biological control releases. In a survey of 900 *Tamarix* individuals across three growing seasons, *Tamarix* trees experienced an increase in mortality from 0% in 2012 to 10% mortality in 2014 (Hultine, Dudley, et al., 2015), while 3-5 years of repeated defoliation was associated with tree mortality of 20-40% (Dudley & Bean, 2012). Our data suggest that tree mortality does not continue at a stable rate over a 20 year or longer period, and substantiates the evidence that mortality varies by environment.

There appears to be little literature that discusses the mortality of mature trees of invasive species in the field following solely biological control (i.e., without other forms of control such as cut stump or girdling) of an approved agent. Therefore, it is difficult to make comparisons of mortality across systems. 16% tree mortality appears relatively low; however, any reduction in *Tamarix* longevity is welcome given its dominance in this system.

4.2. Understory Vegetation: Native vs. Introduced Percent Cover

We hypothesized that understory vegetation cover would increase over time as *Tamarix* canopy opened and trees potentially died, particularly in sites less prone to more intense river scour from flooding. This hypothesis was not supported; percent cover of native and introduced vegetation *decreased* at half of the sites. Six of our eight sites were also used in Kennard *et al.* (2016), which similarly reported that cover of introduced understory plants decreased in half the sites, but increased in the other half. Some potential benefits to native species have been found, with small increases in native cover (Sher et al., 2018), and a large (47%) increase in cover of a native shrub, *Salix exigua* (González et al., 2020). Overall, a strong pattern cannot be drawn between this study and others; native and introduced plant cover experienced both increases and decreases. One reason introduced and native plants decreased in cover in this study may be due in part to insufficient precipitation (Bay & Sher, 2008) or, for native plants, hydrological changes (Bay & Sher, 2008; González et al., 2017). Furthermore, at sites that are primarily gravel or sand bars adjacent to rivers (e.g. Echo Park), low cover of understory vegetation is the historic state, as these gravel bars naturally shift and change with annual spring floods, unless those bars are stabilized by *Tamarix*.

4.3. Understory Vegetation: Species Richness

We hypothesized an increase in species richness but found little evidence of a change in total or introduced species richness through time, and no evidence of a change in native species richness. A shorter-term study found that total species richness increased significantly and did not observe a dramatic increase in introduced species richness (Sher et al., 2018), while a later study found that plant communities changed little over time following biocontrol introductions (González et al., 2020). The differences in findings between these studies may reflect environmental differences across sites and years. Species richness, whether total, native or introduced, appears relatively stable, given previous studies and our largely insignificant results.

4.4. Long-term Monitoring Benefits, Challenges, and Recommendations

Challenges and Recommendations

Long-term monitoring across multiple sites with multiple research groups is quite challenging. Specifically, we found that the research groups differed somewhat in how they collected and formatted data. In the collection of data, despite a shared sampling protocol, the three monitoring efforts differed in their specific approaches due to differing interpretations of the same protocol, and constraints due to the specifics of particular sites as well as resources (both time and funds). The sampling protocol did not provide a spreadsheet for data entry, so naturally, specifics of spreadsheets differed across the groups. These two differences did not prevent us from collecting additional data and combining the datasets, but the process was more challenging than necessary.

File sharing systems and communications are now much easier than they were even 20 years ago, and so most collaborations of this nature today include shared datasheets and frequent meetings, often virtual (e.g., see Borer et al., 2014). Given sufficient funding and staffing, we strongly encourage those practices be adopted in future long-term monitoring of biocontrol systems. Specifically, we encourage collaboratively creating standardized data sheets, providing detailed instructions for all methods, keeping in mind that for long-term work, the original researchers may not always be available to speak with people collecting data in the future. Additionally, the methods should be tested and refined prior to general use.

Benefits

Long-term monitoring of biocontrol agents and their target plants is important because shorter-term changes to the target plant and the surrounding plant community may not be indicative of longer-term trends. For example, for the *Tamarix-Diorhabda* system, initial data indicated a sharp decrease in *Tamarix* size. However, our longer-term data indicate that while, on average, trees continued to shrink, they did so at a slower rate. These results can be used accordingly to update action plans and reach management goals. Further, we found a decrease in both native and introduced plant cover, which suggests additional action may be needed to reach management goals – such as reseeding periodically to increase propagule pressure, planting native species and monitoring their growth, or changing hydrological practices (such as removing dams or allowing pulse flooding) when feasible. Long-term monitoring of biocontrol programs also demonstrates accountability to the public about a practice that is often viewed with some level of apprehension. Additionally, long-term monitoring can help early career researchers and others build their network through the collaboration that is a necessary part of continuing long-term monitoring efforts.

5. Conclusion

Here, we showed that *Tamarix* trees continue to decline in size, though slowly, more than a decade following biocontrol. While the lack of trees protected from beetles limits inference, biologically, this finding makes sense, as herbivory strongly shapes plant performance (Root & Cappuccino, 1992).

Our findings also match other systems well. For example, in a metanalysis of 61 studies, invasive plant biocontrol agents were found to significantly reduce plant size (Clewley et al., 2012). This same metanalysis found that insects in the Chrysomelidae (such as *Diorhabda*) and Curculionidae families were most effective at suppressing target invasive plants (Clewley et al., 2012). Our findings suggest that *Tamarix* will continue to impact riparian ecosystems in the southwestern U.S., though that impact will be tempered to an extent by biocontrol. To better understand the role of biocontrol, even at this late date, trees that exclude beetles using insecticide may prove illuminating. Given continued persistence of *Tamarix*, active restoration may be needed to support recovery of native plants such as willows and cottonwoods or desired understory communities in this system.

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APPENDIX

Table S1. Site names and GPS coordinates of trees where data collection occurred in Utah.

Site/Tree Identity	Latitude	Longitude
DHPSTA1	38.656529	-109.712472
DALTON RD	38.711212	-109.703166
DALTON RD ALT	38.711342	-109.702975
BRDG1 ALT	38.72896	-109.723103
HWY153 BRDG	38.891367	-109.801185
RR44	38.937868	-109.398342
I70MP219	39.123447	-109.171447
WW Exit ALT	39.123484	-109.171436
WWRAMP ALT	39.088272	-109.101896
WW RELEASE	39.08279	-109.12478
I70MP215	39.045526	-109.273752
CISCORAMP	38.970099	-109.250674
FISHFORD ALT	38.924098	-109.247706
TRANSPROP ALT	38.861214	-109.295766
RR32	38.832941	-109.287249
RR24.3	38.771725	-109.324233
RR21 (Ramp) ALT	38.737878	-109.360177
RR20B	38.726609	-109.370007
RR17	38.696327	-109.412738
RR15 (resprout)	38.681799	-109.432225
RR12 (mature)	38.683078	-109.475552
RR12 (cut-burn) ALT	38.682638	-109.477046
RR9 Resprout	38.646677	-109.504866
RR9 Mature	38.646215	-109.504173
RR7	38.640406	-109.478087
RR7(CUT)	38.639537	-109.477851
RR5	38.626489	-109.506311
RR3	38.609575	-109.535591
RR1 (Info. kiosk) ALT	38.604107	-109.558551
RR0	38.604957	-109.57671
CBN3 ALT	38.606319	-109.583855
RR0 (Lion's)	38.603089	-109.576169
I70RANCHRD	38.922591	-109.942139
GR3 Ramp	39.112377	-110.10866
GR2 (farm)	39.070078	-110.138735
GR1 ALT (Hastings)	39.024839	-110.138904

CHAN	38.971654	-110.146598
CG1 (Geyser)	38.937956	-110.135361
CGCAMP	38.937112	-110.135249
CG2 (Wash)	38.928372	-110.129198
PA13	38.579358	-109.58463
PA11 (cut)	38.553157	-109.593811
PA11 (cliff) ALT	38.552572	-109.594804
PA11 (old)	38.552433	-109.59473
WB2 ALT	38.535254	-109.605306
WB2 Cut ALT	38.535372	-109.605215
PA9 (mature)	38.530323	-109.611632
PA9 (cut-burn)	38.530176	-109.611532
PA8.75 (burn-cliff)	38.531025	-109.617249
PA8.75 (burn-river)	38.530857	-109.617229
PA8	38.535958	-109.628188
PA7 (ALT)	38.549665	-109.631291
PA5	38.57811	-109.636006
PA4	38.575229	-109.651177
PA3.5	38.571209	-109.65601
PA3	38.562093	-109.658423
PA1.25 (cut/burn)	38.542815	-109.652925
PA1	38.537394	-109.655056
PAP Lot (resprouts)	38.518662	-109.65213
PA0 Ramp	38.505595	-109.659644