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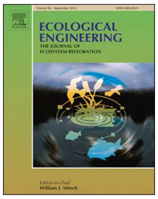

Native species recovery after reduction of an invasive tree by biological control with and without active removal

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ABSTRACT

Removal of invasive species is often an important, if not central, component of many riparian restoration projects, however little is known about the response of plant communities following this practice. In particular, active control of the exotic, dominant tree *Tamarix* spp is often a focus of riparian restoration, much of which occurring against a backdrop of biological control by a folivore beetle. Our research employed controls in both time and space to investigate the impact of active *Tamarix* removal methods in sites subjected to biological control in 40 sites sampled three times over a period of five years. We found that reduction in *Tamarix* cover was much greater over time with active means of removal, however the native understory increased both with and without active removal. Importantly, change in the relative cover of understory native species was significantly negatively correlated with change in *Tamarix* cover, with those sites that received a combination of low-disturbance-mechanical, chemical and bio-control showing greater increases in native understory dominance than those sites with biological control alone or high-disturbance mechanical control. Sites with only biocontrol still contained 10% live *Tamarix* cover > 7 yr since the beetle was released there. Taken together, these results suggest that the reduction of this exotic tree, even by biological control that leaves some canopy intact, can facilitate recovery of the native plant community. As such, this study supports the *Field of Dreams* hypothesis that states that once niches are restored, native plants should be able to recolonize.

1. Introduction

Invasive trees can have substantial negative impacts both economically and ecologically on the systems in which they occur (Richardson and Rejmánek, 2011), thus restoration of degraded ecosystems often involves extensive noxious species removal efforts (González et al., 2015). Ecological restoration theory has suggested that plant communities may recolonize ecosystems once their ecological niches have been restored (*Field of Dreams Hypothesis*; Palmer et al., 1997). However, experience in the field has shown that the ecological impact of removal efforts can be both negative and positive (Mason and French, 2007; Gooden et al., 2009; Loo et al., 2009). This is due to several factors, including the extent to which control of the target is successful and the degree and type of disturbance incurred on an ecosystem by the removal method. Human-caused disturbances have long been associated with plant invasions, due to changes in both physical and chemical flux (Sher and Hyatt, 1999). Because of this, the removal of one invasive species can stimulate the establishment of other invasive species, referred to as secondary invasion (Pearson et al., 2016). Pearson et al. (2016) suggested that the space vacated by the first alien was the most important factor explaining the responses of secondary invaders, but specific case studies also showed that the type and intensity of management disturbance can promote the establishment of certain weeds. Invasive plant removal techniques can determine the responses of natives as well (Flory and Clay, 2009). Successful restoration is often defined by the recovery of native or otherwise desirable vegetation, however such species may or may not respond positively to the removal of the invasive target, due to the combined and interacting influence of remnant target individuals, the removal method, and secondary invasions.

Available techniques for removal of invasives are numerous. However, their effectiveness is usually compared in mesocosms or at small scales in experimental fields, and not in real large-scale restoration projects (Flory, 2010). While there is a great need for restoration practitioners to rigorotusly test he effects of exotic plant control methods (Clewer and Rieger, 1997; Byers et al., 2002), the truth is that

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most restoration projects are not even evaluated, as they are not designed to conduct scientific research but rather to meet management goals (Bernhardt et al., 2007). Projects combining removal techniques of different types and intensity of disturbance could help us better understand key ecological processes, such as assembly rules in plant communities (Trowbridge, 2007). However a limitation of existing studies is the confounding effects of target reduction and disturbance; in most cases it is not possible to determine whether the response of the plant community to the removal method is due to decreased competition or some unrelated feature of disturbance by the removal method itself.

Furthermore, studies that do exist to assess the ecological impact of noxious species removal in actual restoration projects tend to be at a small geographic scale and without much replication over time or space (e.g., Mason et al., 2007; Sher et al., 2008; Loo et al., 2009; Flory, 2010). Because of the potentially great influence of both geographic location and inter-year variability, understanding of these systems benefits greatly from a BACI design; that is, with comparisons of the same sites Before versus After (B vs. A) as well as between different treatments (Control vs. Impact) at the same point in time (Stewart-Oaten et al., 1986). However funding and other limitations make such monitoring very unusual (Bernhardt et al., 2005; González et al., 2015).

Monitoring the impact of restoration of river systems can especially benefit from comparisons in both time and space, due to the very strong effects of each on biotic systems associated with rivers (González et al., 2015), and because treatments are rarely if ever randomly assigned. In the American Southwest, removal of invasive *Tamarix* spp. (saltcedar, tamarisk) and other weedy trees is often a central feature of restoration of riparian habitat, with the goal of increasing native species cover (Taylor and McDaniel, 1998; Sher, 2013). *Tamarix* invasion is highly associated with the damming and channelization of rivers in this region, and it has been argued that recovery of the native flora is unlikely to occur after removal of invasives if the underlying hydrological issues are not also addressed (González et al., 2017a). Here, we use a well-replicated BACI design to consider the response of a riparian plant community both without ("control") versus with ("impact") active removal of an invasive tree at 40 sites both before and after that active removal by two methods in sites with no concurrent hydrological improvements.

The restoration of *Tamarix* infested communities is also particularly interesting because it takes place in the context of the release of a biological control insect, the folivore *Diorhabda* sp. (Hultine et al., 2010). When using an insect or pathogen, living biomass of the invader can be reduced with minimal if any disturbance to the soil or other vegetation (Primack and Sher, 2016). This low-disturbance method of decreasing the cover of the target species therefore provides a unique opportunity to isolate the impact of reducing competition for light and other resources, decoupled from the soil-disturbing impacts of active methods. Studies comparing biological control alone versus in combination with active removal in the field are nearly non-existent in the literature (but see González et al., 2017a,b) and have yet been investigated specifically as such. Because all of our study sites were subjected to beetle defoliation at the initiation of the study, it is important to clarify that we will not be testing the impact of biological control relative to no impact at all. Rather, we will investigate the plant community response to degree of canopy reduction by the beetle alone versus canopy reduction by additional means that also involve mechanical and chemical disturbance of the soil. In this way, we hope to measure the impacts of those active means beyond that of reducing competition by the target.

The largest study to date on ecological impact of restoration of river/riparian systems took advantage of data from a variety of studies conducted at different times and by different methods (González et al., 2017a,b). The conclusions of that study were that high disturbance *Tamarix* removal methods were associated with increases in other weeds ("secondary invasion") and both high and moderate disturbance methods were associated with only modest increases in native species cover. However, because this study depended on pre-existing data, comparisons could not be made between before versus after these active removal methods. More importantly, it was not possible to determine whether plant community response was due to changes in cover of the target invader or because of other disturbance caused by the removal method.

Our research measured the response of a riparian plant community before and after to two methods of active removal of an invasive tree with comparisons over both time and space. We are also able to investigate changes in the plant community as a function of the reduction in the target without the disturbance of active removal, because of the backdrop of biological control. In this way, we were able to assess the impact of the disturbance of active removal on the assembly of plant communities, including the recovery of natives and secondary invasions, both as a function of the control of the target tree and as a consequence of the removal method itself. As such, we are testing the *Field of Dreams* hypothesis at a large scale representative of actual restoration projects usually neglected in restoration evaluations.

2. Methods

2.1. Study system

The Dolores River watershed is approximately 388 km long and runs through both Colorado and Utah. The Bureau of Land Management, as a part of the Dolores River Restoration Partnership (DRRP), have engaged in intensive efforts to control exotic *Tamarix* spp trees with the goal of restoring riparian habitat (Parternship, 2010). *Tamarix* in this area are likely to be a hybrid swarm between *T. ramosissima* and *T. chinensis* (Gaskin and Schaal, 2002; Gaskin, 2013). *Tamarix* is a poor competitor in every sense as a seedling (Sher et al., 2000, 2002; Sher and Marshall, 2003; Dewine and Cooper, 2008), but as a mature tree *Tamarix* is a strong effect competitor *sensu* (Goldberg, 1990) by shading neighbors (Sher, 2012; Taylor and McDaniel, 1998), elevating soil salinity (Ohrtman et al., 2012), and using water (Smith et al., 1998; Glenn and Nagler, 2005; Cleverly, 2013). It also promotes and withstands wildfire better than native riparian trees (Drus et al., 2013). Therefore, we expect that lowering the cover of *Tamarix* will correspond with an increase in the cover of desirable understory plants.

2.2. Research sites and treatments

Forty monitoring sites were established in 2010 along the Dolores River, where removal of *Tamarix* was an eventual goal but in nearly all cases had yet to be done (Fig. 1). The Dolores is a river regulated by the McPhee Dam, upstream from all of the sites in this study. Studies have shown that although the dam has reduced the flood frequency and magnitude (Wilcox and Merritt, 2005), flows are still sufficient to support the establishment of some native species of Salicaceae (Coble et al., 2013; Dott et al., 2016). The biological control agent was introduced to this area 2005–2007 and was active throughout the sampling period throughout the region to varying degrees. Approximately half (21/40) of the sites were selected as "impact" sites to have active removal of *Tamarix* above ground biomass in addition to the ongoing biological control, while the remainder would serve as "control" sites in which biological control was the only means by which *Tamarix* cover was reduced. Over the following years, some sites were lost and others added to maintain a sample size of 39–40 each year (Appendix A). Selection of sites, method and timing of removal were determined by the DRRP. Selection was non-random and driven by management objectives as well as practical and logistical constraints.

Active removal was conducted by one of two methods: CHEM ("cut stump" method that involves chainsaw cutting with immediate application of herbicide to the cut surface, 7 sites), and MECH (above ground biomass is removed through either mastication with heavy machinery

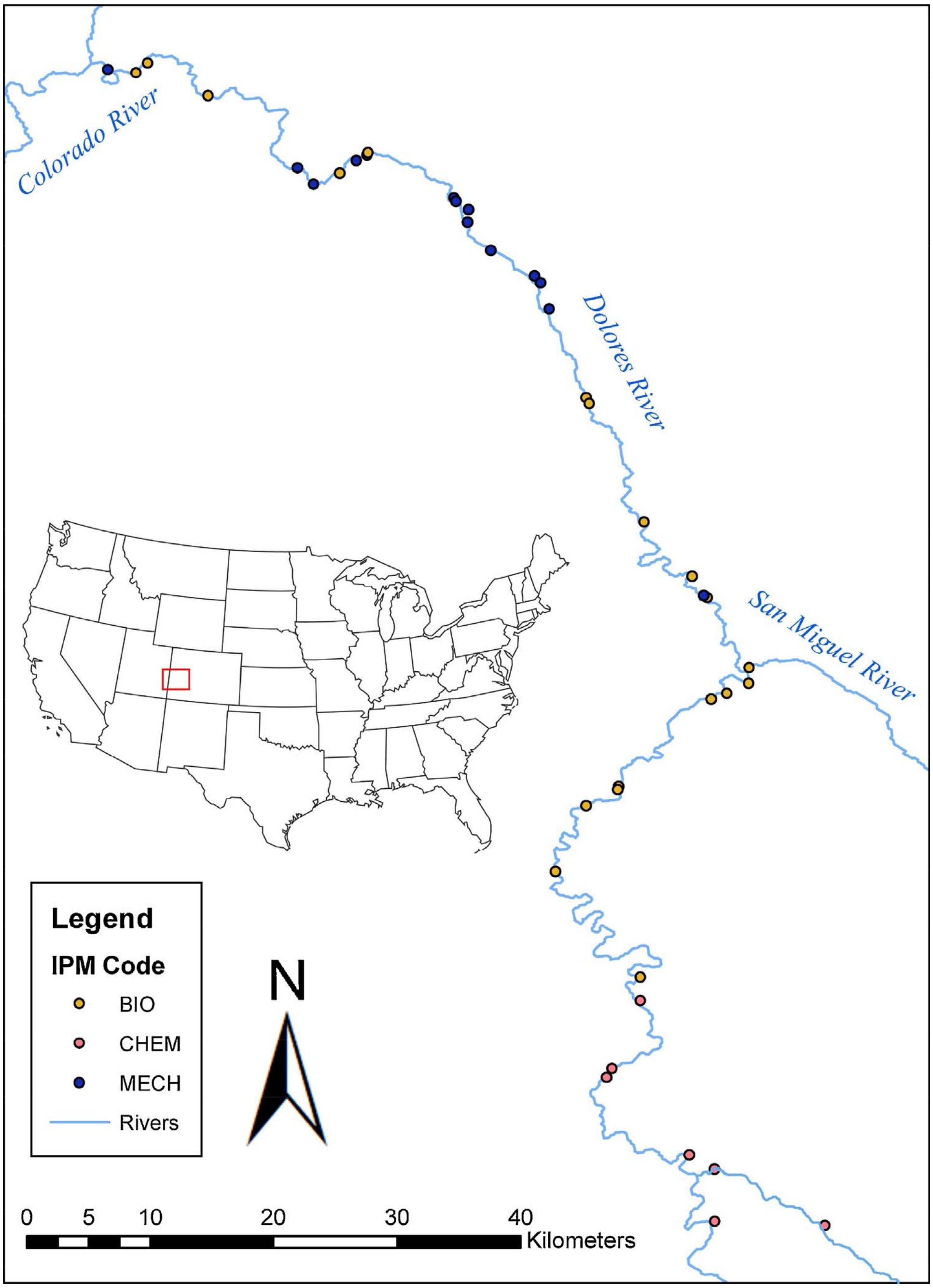

Fig. 1. Sites sampled along the Dolores River in Western Colorado and Eastern Utah.

or a chainsaw-cut followed by a burn, 14 sites). In the remainder "BIO/NONE" sites, *Tamarix* were left standing, with only passive removal by the tamarisk leaf beetle. The MECH treatment generally had the highest physical disturbance of biomass and soil and BIO/NONE had the least. Timing of active removal (i.e. MECH and CHEM) varied somewhat between sites but in all but one case was after the 2010 sampling period and before the 2014 sampling period. In most MECH sites and several of the CHEM sites, there were secondary chemical treatments of both *Tamarix* re-sprouts and/or of understory weeds (Appendix A).

At each site, vegetation cover by species was collected using the line point intercept method in 40 sites in 2010, 2012, and 2014. Thirty of these were sampled all three years, with additional sites lost or added over time (Appendix A). Within each site a permanent, representative 50 m × 80 m sampling area was established, divided into five, 16 m strips perpendicular to the waters edge. These strips were sampled with randomly placed, 50 m long transects sampled at 10 cm intervals for a total of 5000 points per 4000 m^2 site. The portion of each 50 m transect that included hygrophylous versus mesic versus xeric vegetation was also indicated. A plant was recorded if it intercepted a point, regardless of whether it was green or in a state of dormancy. Similarly, *Tamarix* cover was recorded if any portion of a tree was intercepted. Branches defoliated by the biological control beetle often re-green within the same season (Bean et al., 2013), thus it is difficult to assess in the field whether an attacked tree or branch is alive or dead. However, the status of the branch as having green leaves or not was recorded in the final year.

Plants were identified to species in the field when possible, and otherwise collected for identification later at the Kathryn Kalmbach Herbarium at Denver Botanic Gardens. Sampling was done each year in July when the highest diversity could be identified, according to BLM field officers who manage these sites. Bare *Tamarix* branches in July are generally but not always indicative of herbivory by the biocontrol insect, *Diorhabda* spp.

Both species nativity (native vs. introduced) and growth form (tree versus understory) were identified per classifications in the USDA PLANTS database (plants.usda.gov). The primary interest was in the change in vegetative cover for the following dependent variables: the target (*Tamarix*), understory native species, and understory exotic species. Native trees accounted for less than 2% (± 0.4%) total cover and were not expected to change in such a short time period and so were not a group of specific interest.

2.3. Data analysis

We used mixed linear models to investigate the change in *Tamarix* cover, native understory species cover, and exotic understory species cover between 2010 and 2014 (i.e., Before vs. After) and between treatments (i.e., Control vs. Impact) with site as a random variable. In 2012, most but not all impact sites had active removal, and so was not included in this analysis. All data were tested for normality and log transformed where necessary. Species richness was compared between 2010 and 2014 using a paired *t*-test with site as replicate.

To determine whether the difference between removal methods could be explained on the basis of their efficacy of removing the target, we performed a general linear model on the relationship between change in *Tamarix* cover (2010 – 2014) and change in relative native plant cover (i.e., as a percent of total cover) by removal method. Change in relative cover allows us to determine whether there was an actual shift in the plant community from more exotic-dominated to more native-dominated.

Patterns of change over time between 2010, 2012 and 2014 were tested using a repeated measures ANOVA on the mean site values across the three years comparing the three removal methods for those 31 sites sampled each of these years.

To determine the shift in plant species community composition as a function of removal method and time since restoration (including time since introduction of the beetle), we conducted a redundancy analysis (RDA), a type of ordination, using Hellinger-transformed cover data by species. Hellinger transformations are a recommended approach when species abundance data includes many zeros (Legendre and Gallagher, 2001). An RDA also allowed us to control for those variables that were likely affecting the plant community but were not of interest: annual precipitation, initial tamarisk cover, initial native cover, and width of riparian zone. We then ran a Principle Components Analysis (PCA) on the constrained data (i.e., resulting data after being controlled for variables not of interest), and tested the significance of the RDA using 10,000 permutations.

Because timing of removal of *Tamarix* was somewhat variable between sites, we also used the PCA site scores to explore the change in the plant community composition as a function of years since the treatment was applied, that is, the last year either CHEM or MECH treatments were applied, or for those sites with no active removal, year of the introduction of the biocontrol (BIO). Prior to any active removal, sites were considered biocontrol only and plotted as such. We then ran a mixed model with site as a random factor to test whether the plant community, as described by the site scores, differed between removal methods for each time period.

3. Results

At the 40 sites over the five years surveyed, we identified 126 species, 34 of which were exotic. Despite the higher diversity of native species, most sites were dominated by exotic species considered noxious in Colorado and/or Utah. *Tamarix* was the most common tree and the second most common exotic species (after *Acroptilon repens*, a.k.a. Russian knapweed), and when present *Tamarix* had the highest mean cover of any exotic (25.9%). The third most common species was *Bromus tectorum* (cheatgrass). The most common native species in descending order were *Distichlis spicata* (saltgrass), *Salix exigua* (coyote willow), *Rhus trilobata* (skunkbush sumac), and *Forestiera pubescens* (New Mexico privet). *Salix* and *Forestiera* had the highest mean cover of any species when present (58.0% and 31.5% respectively).

Using data from PRISM Climate Group (http://prismmap.nacse.org/nn/), we also explored climate for these sites. For this reach, mean annual precipitation was negatively correlated with latitude with southern sites being the wettest (linear regression: $p < 0.001$, adj $R2 = 0.47$); because CHEM sites were more southern than the other treatments, on average CHEM sites received 2 cm more rain than MECH (176 ± 3.1 mm vs. 156 ± 6.6 mm, respectively; Wilcoxon $Z = -2.12$, $p = 0.03$). Neither treatment significantly differed from BIO/NONE (164 ± 5.7 mm). Pairwise comparisons of mean maximum daily temperature (34.7 ± 0.21 °C) and mean distance to the river (34.8 ± 8.17 m) among treatments during the growing season found no significant differences, and there was a mix of broad and narrow floodplain widths in each category.

For *Tamarix*, both active removal methods (CHEM and MECH) significantly reduced standing cover over time, whereas biocontrol alone (BIO/NONE) increased cover slightly on average (Before vs.

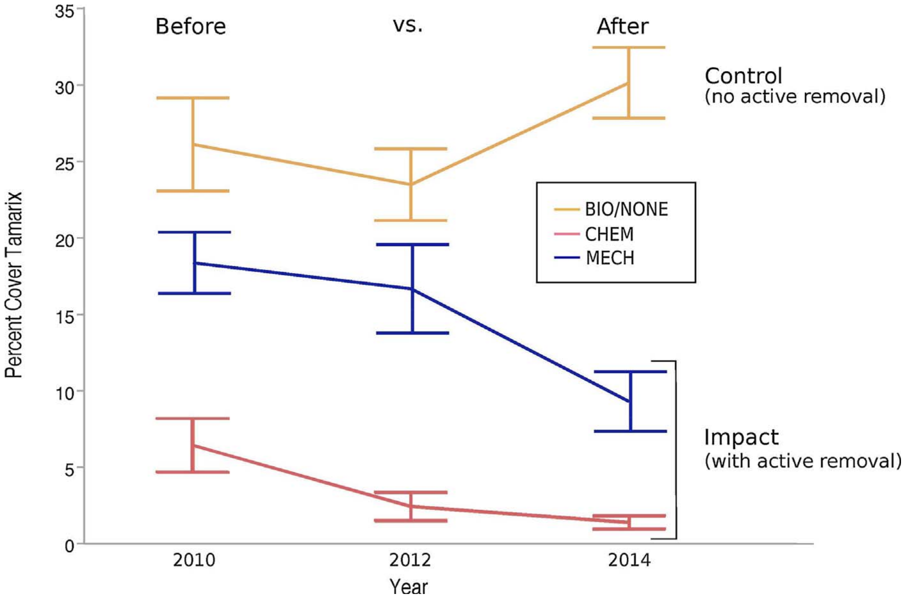

Fig. 2. Mean (± 1 SE) total *Tamarix* cover over five years of sampling by removal method: Biological Control with mechanical and chemical control (CHEM), Biological Control with only mechanical control and delayed chemical control (MECH), and Biological Control only (BIO/NONE). Repeated measures ANOVA: YEAR*method: $F_{4,54} = 3.42$, $p < 0.02$. Due to the BACI design of the study, "Before" sites received active tamarisk removal (in 2010) can be compared with "After" (in 2014) and sites without active removal (BIO/NONE, i.e., "Control") can be compared with those that received active removal (CHEM and MECH, i.e., "Impact").

Table 1
Mixed model comparison of the proportion of Tamarix cover that had green leaves (of total Tamarix cover) between the three Tamarix removal methods: Biological Control with mechanical and chemical control (CHEM), Biological Control with only mechanical control and delayed chemical control (MECH), and Biological Control only (BIO) (Site as random effect, F2,36.1 = 4.10, $p < 0.02$).

Removal method	Total cover	1 SE%	% of total green	1 SE
BIO/NONE	29.9%	2.1%	45.3%	3.4%
CHEM	1.4%	0.4%	57.0%	11.9%
MECH	9.3%	1.9%	71.6%	4.9%

After; Fig. 2). By the final year, BIO/NONE sites had more than six times the *Tamarix* cover of active removal sites, which had only negligible amounts (Control vs. Impact). However BIO/NONE sites also typically began with higher *Tamarix* cover but by the final year had the lowest proportion of cover that contained green leaves (Table 1). Use of a follow-up, foliar spray *Tamarix* treatment produced no statistically significant differences in total *Tamarix* cover, percent green cover, or change in cover using mixed models with site as random variable (mixed model for 2014 with site as random variable; secondary treatment *Tamarix* $F_{2,56.2} = 1.27$).

Understory species cover significantly differed between native and exotic species and between sites with different removal methods over time (Fig. 3). Native species increased in each successive year sampled (Before vs. After) and had a higher percent cover than exotics overall. Although native cover increased most rapidly in sites with CHEM *Tamarix* removal, by the final year of sampling there was no difference between removal methods for native species cover (i.e., no difference for Control vs. Impact). Exotic species decreased in 2012 but rebounded in 2014, with the greatest net increase in CHEM sites. Neither secondary treatment of *Tamarix* nor secondary treatment of targeted understory weeds significantly changed overall exotic species cover (mixed model for 2014 with site as random variable; non-target exotics treatment $F_{2,58.3} = 0.04$).

The change in relative native species cover between the first and last year was significantly negatively correlated with the change in *Tamarix* cover, with the slope of this relationship differing between removal methods (Table 2). The effect of *Tamarix* reduction on native species increase was most dramatic in CHEM sites (Fig. 4). Change in native willow (*Salix exigua*) cover was significantly negatively correlated with change in *Tamarix* cover (mixed model, Adj R-square = 0.61, $F1, 100.1 = 4.61$, $p < 0.03$), but there was no difference between removal methods (results not shown).

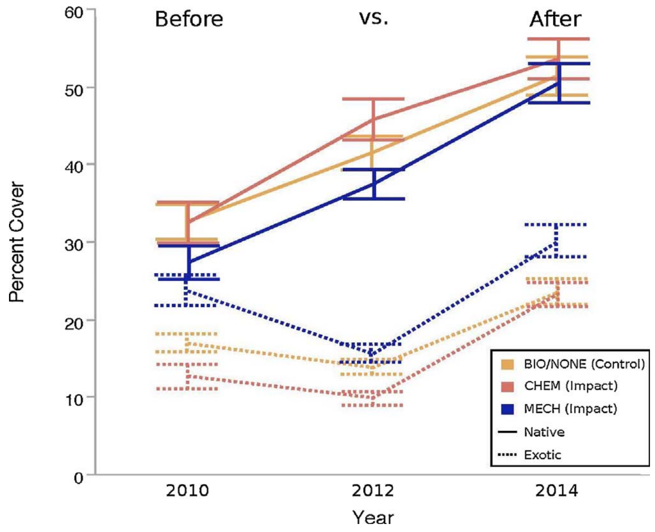

Fig. 3. The mean (± 1 SE) understory species cover for natives (solid) and exotics (dashed) across years for those sites with active removal of Tamarix via selective cutting with herbicide (CHEM), mastication (MECH) and those sites with biological control alone (BIO/NONE). Repeated measures with site as replicate: Year*Method*Nativity Wilks' Lambda F = 3.45; DF = 4110; $p < 0.02$). Due to the BACI design of the study, "Before" sites received active tamarisk removal (in 2010) can be compared with "After" (in 2014) and sites without active removal (BIO/NONE, i.e., "Control") can be compared with those that received active removal (CHEM and MECH, i.e., "Impact").

Table 2
General linear model of change in relative native cover between 2010 and 2014 as a function of change in *Tamarix* cover and *Tamarix* removal method.

Source	DF	F	Prob > F
Change in *Tamarix* cover	1	148.55	< 0.0001
Removal method	2	1.65	0.20
Removal method × Change in *Tamarix* cover	2	24.24	< 0.0001
Whole model	5, 129	36.81	< 0.0001

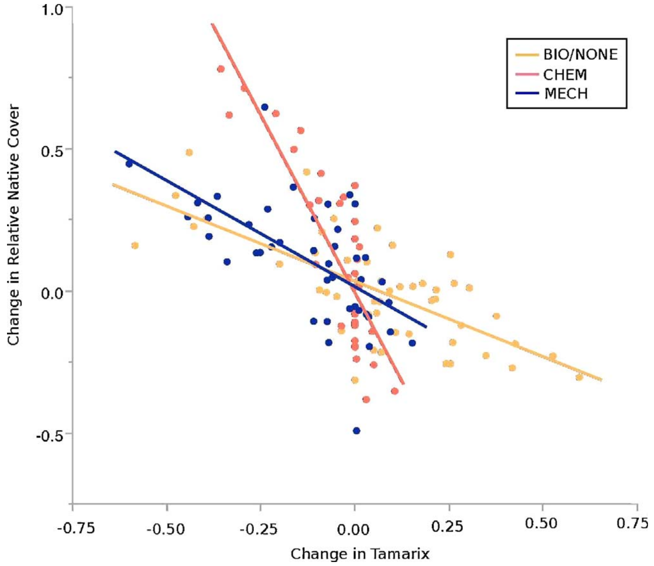

Fig. 4. Change in relative (to total cover) native cover between 2010 and 2014 as a function of change in *Tamarix* cover over the same period for three tamarisk treatment types active removal of *Tamarix* via selective cutting with herbicide (CHEM), mastication (MECH) and those sites with biological control alone (BIO/NONE). A negative slope shows that with a decrease in *Tamarix* cover there is an increase in relative native cover, the steeper the slope the greater that increase. Corresponding statistics can be found in Table 2.

Species richness significantly increased between 2010 and 2014 for all removal categories, with CHEM sites increasing 43% and 101% more than BIO and MECH sites, respectively ($F_{2,27} = 9.6$, $p < 0.001$; Tukey HSD post-hoc comparisons; Table 3).

Plant community composition differed between treatments and over time (Fig. 5). The cumulative proportion explained by the four RDA vectors (i.e. constraining variables of annual precipitation, initial tamarisk cover, initial native cover, and width of riparian zone) was 11.3%. The model overall was highly significant (df = 4, $F = 37.89$, $p < 0.0001$, adj R2 = 0.11). The first four PC vectors on the constrained data explained an additional 13.9%, 9.4%, 7.6%, and 6.9% of

Table 3
One-tailed, paired *t*-tests to test the hypothesis that total site species richness increased from 2010 (before active *Tamarix* removal) versus 2014 (after active *Tamarix* removal) for each of the three site types: CHEM (active removal, low disturbance), MECH (active removal, high disturbance), and BIO (biological control only, lowest disturbance). Analysis performed on log-transformed data to improve normality.

Removal type	Mean increase in richness (± 1 SE)	DF	t-ratio	$p > t$
BIO	61.2 (4.8)	11	17.88	0.0001
CHEM	87.7 (12.9)	5	13.26	0.0001
MECH	43.6 (4.8)	11	28.38	0.0001

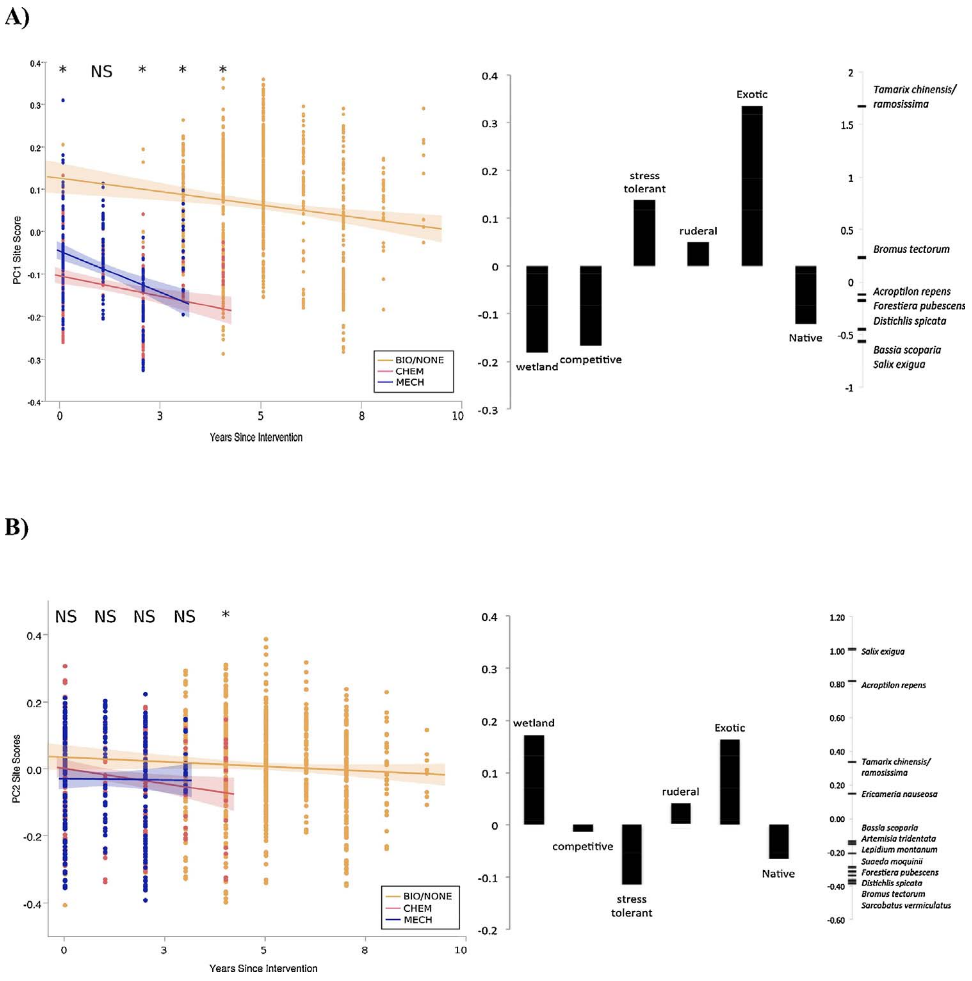

Fig. 5. Plant community composition dynamics with time elapsed since highest disturbance Tamarix removal method at the time of sampling using site scores from first (A) and second (B) RDA constrained Principal Components. Only those species with score along axis 1 greater than 0.1 are represented; mean score for these species by ecological traits (including USDA wetland status of OBL or FACW classified as "wetland") are shown on the right. Each removal method is shown with best fit line: chainsaw followed by herbicide plus Biological Control (CHEM), Mastication plus Biological Control (MECH), and Biological Control only (BIO/NONE). Significant differences (alpha = 0.05) between treatments for each time period are indicated with an *.

the variance respectively. PC1 reflected a tendency for sites to shift from an exotic, stress-tolerant community to a competitive native, wetland community over time, with BIO sites being significantly more characterized by *Tamarix* at all time periods. PCA2 described a gradient from exotic wetland community to a more native, stress tolerant one, but with no differences between treatments or changes over time, except for a single time period in which BIO sites were significantly more exotic-wetland than the active removal sites.

4. Discussion

Consistent with the *Field of Dreams* hypothesis (*sensu* Palmer et al., 1997), we found that reduction of an invasive target tree was positively correlated to recovery of the plant community, as characterized by having more native, wetland species. Furthermore, although active removal introduced novel disturbance to this ecosystem and left space vacated (Pearson et al., 2016), we did not observe dramatic increases in other invasive species.

Our results also demonstrate the value of the BACI (Before After Control Impact) design, given that only considering Before/After or Control/Impact by itself would have had suggested different and even misleading results. This was due in part to the fact that those sites that were the most invaded by *Tamarix* were also those more often left to the biological control alone. Therefore, considering only Control vs. Impact in a single year would have over-estimated the impact of active removal on the target and underestimated its effect on the understory. Furthermore, had we only considered Before vs. After active removal without comparing to control sites, we would have grossly overestimated the importance of active removal on the understory, which changed dramatically over time, but was no different from biological control only sites by the final year. In studies where a BACI design may not be possible or practical, which is the overwhelming majority of studies in restoration (González et al., 2015), one must be cautious about overreaching interpretations, given this risk of misleading data.

As is typical of studies that use sites prioritized for restoration rather than research, we had several sources of variability and confounding variables to contend with, only some of which were addressed by the BACI design. First, our backdrop of biological control was not uniform over time or space, but varied independently of the other variables of interest. Previous research suggests that in this system, biological control movement and impact does not vary predictably with environmental variables (Hultine et al., 2015; Kennard et al., 2016) but instead follows certain spatiotemporal patterns as beetles prefer to forage in dense and connected patches (Ji et al., 2017). That we did observe treatment effects against this considerable statistical "noise" is a testament to how strong/large they were, but we also cannot rule out the possibility that non-random patterns of beetle defoliation contributed to the patterns we observed, as shown by Ji et al. (2017).

4.1. *Control of the target*

Not surprisingly, we found that a combination of biological, mechanical and chemical control was effective in reducing the cover of the target, invasive *Tamarix* (Harms and Hiebert, 2006; Bay and Sher, 2008; Belote et al., 2010; Reynolds and Cooper, 2011; Ostoja et al., 2014; González et al., 2017a). Among the two methods investigated, chain-sawing individuals followed with a systemic herbicide ("cut stump method") achieved faster results than mastication with heavy machinery, but the former is generally more labor intensive, slow and expensive, making it impractical for large infestations (Nissen et al., 2010). In our study this method was selected by managers for those sites with the lowest initial cover of *Tamarix,* thus emphasizing the importance of looking at both the change in cover as well as using initial cover as a covariate when investigating the impact of a removal method. Mastication with foliar application of herbicide in subsequent years was ultimately nearly as effective as cut stump method for reducing *Tamarix* cover, despite some evidence of resprouting. It is likely that biological control contributed to the success of mastication as a control measure, as some have proposed that the *Diorhabda* is preferentially attracted to the lush regrowth that results after mechanical removal (Dan Bean, Pers. Comm.).

4.2. Response of the understory plant community

Despite the dramatic change it caused to the target, active removal on average did not result in more native species in absolute terms than removal by biocontrol alone by the final year we surveyed. Instead, native plant dominance, that is relative rather than absolute cover, was proportional to the change measured in the target. The degree to which the target was reduced was highly variable among all three treatments, allowing us to test this relationship along a continuum for each of the treatments. Likely this was due in part to the staggered timing of removal, which also allowed us to investigate the effect of time since implementation on plant community composition.

The relationship between relative native cover increase and *Tamarix* decrease suggests that the removal of the invasive tree was directly responsible for the improvement in the plant community through competitive release, rather than both the tree and the understory responding to some other aspect of the removal method. It also is a unique test of the passenger-driver model proposed by MacDougall and Turkington (2005), and points to the role of *Tamarix* being a driver of ecological change (Johnson, 2013). If native species decline was solely due to environmental shifts that in turn promoted *Tamarix,* a passenger model as has been sometimes suggested (Stromberg et al., 2009), then we would not expect that removal of *Tamarix* alone to reverse this trend. However, the stronger recovery of native plants in this reach, in contrast to studies in other rivers, is perhaps only possible because this river, although dammed, has deviated less than other rivers from its original hydrograph (Merritt and Poff, 2010).

Our analysis also suggested that there may be ecological consequences for choice of removal method; the sites with intermediate-disturbance cut-stump method shifted to higher native dominance to a greater degree than either biological control alone or the highly disturbing mastication method. For these sites, the observed shift was achieved by a combination of an increase in native cover with an associated decrease in exotic cover, which was not observed in the other types of sites. We must be cautious in our interpretation of these results however, given the non-random establishment of the cut-stump sites in the south. These sites were no warmer or more likely to flood than others, and there were no significant differences in soil salinity (data from González et al., 2017a, not shown here). However, the fact that these sites were slightly wetter on average would be expected to contribute positively to native plant recovery. Mean precipitation has not been found to be a significant predictor of native plant cover in other published studies on this system (Harms and Hiebert, 2006), but precipitation in a given year (González et al., 2017a), and number of years with above-average precipitation (Bay and Sher, 2008) have. On the other hand, these sites were also above the confluence of the unregulated San Miguel; more northern sites below this might be expected to have an increased likelihood of overbank flooding, most often associated with increases in native plant growth. Finally, it is also possible that the managers of these particular sites were making other choices that differed from other sites besides removal method that were unknown to us. Future research will be necessary to explore the role of the manager on restoration outcomes, and to determine if cut-stump method consistently outperforms other active removal methods.

While disturbances that simply reduce interspecific competition are expected to promote desirable vegetation, as is posed by the *Field of Dreams hypothesis*, changes in physical or chemical flux that differ from historic disturbance are predicted to promote further invasion (Sher and Hyatt, 1999). Contrary to this hypothesis, active removal, which disturbed the soil and introduced herbicides, did not dramatically promote secondary invasion. The sites with the heaviest disturbance removal method, which involved heavy machinery and killing most above ground herbaceous growth, did end up with the highest cover of exotic species, consistent with previous work (González et al., 2017b), but those sites also started with more exotics, and the proportional shifts were identical between active removal methods. The difference between the response of native species versus exotic suggests that even with our highest disturbance removal method, these communities were not reverting to one that favored primary successional, ruderal species. Although we did not find that secondary chemical treatments of weeds significantly changed weed cover, this is likely because chemical treatments were typically targeted at a specific area or species, rather than the entire region we sampled.

The shift of the plant community over time in all sites toward more native wetland species has important implications for habitat for cup-nesting birds, which depend upon the branching structure historically provided by *Salix* trees, and more recently by *Tamarix* (Sogge et al., 2013). In another study performed on the Dolores it was found that *Salix* density benefits from damming due to the associated channel encroachment (Dott et al., 2016). Nonetheless, there has been considerable concern that the release of *Diorhabda* spp. beetles as a biological control would deprive birds of habitat (Sogge et al., 2013; Darrah and Van Riper, 2017). Our results and those recently published (Nagler et al., 2017) suggest that at least along the Dolores, *Salix* is replacing defoliated *Tamarix*, however additional research is needed to determine how quickly the requisite branching structure is forming, whether reduction of *Tamarix* is actually facilitating it, and what the actual impact on birds is across this watershed.

5. Conclusion

There has been debate as to the value of the removal of invasive species when the removal method creates other disturbances in the ecosystem. The specific concern for the removal of *Tamarix* trees has been that we should not expect an improvement of the native plant community without any return of the historical hydrograph (Shafroth et al., 2008), in part because this invader is considered by some to be a passenger rather than a driver of ecological change (Nagler and Glenn, 2013). Our research documents a positive response to the release of competitive pressure by *Tamarix*. This is likely because this river, despite significant changes in the hydrograph since being regulated (Wilcox and Merritt, 2005; Coble et al., 2013), still had periodic overbank flooding for much of its length during the period we collected data. Certainly, observed recovery of mesic species requires that this be so.

These results should not be taken to mean that simple removal of *Tamarix* or any target invasive species will in all cases be sufficient for restoration. However, it does suggest that recovery of a community dominated by natives, without further assistance, can be possible even on a regulated river such as the Dolores. The fact that neither re-invasion by *Tamarix* or other weeds prevented this recovery is, we think, cause for optimism.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ecoleng.2017.11.018.

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