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UNDERSTANDING PATTERNS AND FUNCTIONAL IMPACTS OF AN INVASIVE TREE AND ITS BIOLOGICAL CONTROL IN A RIPARIAN SYSTEM

A Dissertation
Presented to
the Faculty of the College of Natural Sciences and Mathematics
University of Denver

In Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy

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by
Annie L. Henry
March 2021
Advisor: Anna A. Sher

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Author: Annie L. Henry
Title: UNDERSTANDING PATTERNS AND FUNCTIONAL IMPACTS OF AN INVASIVE TREE AND ITS BIOLOGICAL CONTROL IN A RIPARIAN SYSTEM
Advisor: Anna A. Sher
Degree Date: March 2021

ABSTRACT

Invasive species have become an inextricable part of the landscape, particularly in riparian plant communities, and removal is often a key component of restoration programs. Biological control (biocontrol) is a method of removal that is often both efficient and effective. However, the impact of biocontrol on target species and indirect effects from invasive species removal can be hard to predict. While monitoring the impact of invasive species removal usually involves some species-based assessment such as changes in diversity, historically dominant species or native species, these strategies do not typically provide insight into the mechanisms underlying plant community response to removal.

My research that I present here seeks to expand our understanding of the drivers underlying variations in impact of a biocontrol beetle (*Diorhabda* spp.) on a dominant invasive tree (*Tamarix* spp.) in the southwestern United States. I used spatial modeling to uncover underlying structure in the response of *Tamarix* to *Diorhabda*. I found evidence for compensatory growth in response to defoliation. I also showed that a large portion of spatially structured variation in *Tamarix* cover was not associated with abiotic conditions, suggesting that biotic factors may be more important in determining the impact of biocontrol.

Biocontrol defoliation creates a natural gradient of invasive species cover across the landscape. I examined *Tamarix* dominated sites across a large geographic extent to understand how both the abiotic environment and varied levels of *Tamarix* influence the functional composition of underlying plant communities. I found that *Tamarix* cover encourages shade tolerance, sexual reproduction and short life cycles in the understory plant community. To better understand the long-term effect of *Tamarix* defoliation and the response to a specific defoliation event, I examined traits and functional diversity over the course of 8 years, up to 14 years after initial defoliation. This study provides evidence that understory plant communities stabilize after an initial defoliation event and supports the previous findings on plant community functional response to *Tamarix*. My research adds to the body of knowledge regarding the role of environmental filters in structuring the plant communities and aids land-managers in anticipating plant community response to invasive species removal.

ACKNOWLEDGEMENTS

I would like to thank my advisor, Anna Sher and my committee: Shannon Murphy, Robin Tinghitella, and Jing Li, as well as my committee chair Michael Daniels. I would also like to thank Eduardo González for his invaluable mentorship throughout my doctoral program. I thank my additional co-authors Bérenger Bourgeois, Wright Robinson and Patrick Shafroth. I would like to thank my research assistants Grace Fierle, Carlie McGuire, April Rose, Maddie Sligh, Lisa Clark, Alex Goetz, Kayleigh Kearnan, Kyla Reiner and James Sheinbaum. I would also like to acknowledge all those who advised on these chapters or contributed to datasets, including but not limited to Emily Palmquist, Eric Tabacchi, Melissa Islam, Lindsay Reynolds, Tim Higgs, George Gerhart, Tim Graham, Philippe Janssen, Jayne Belnap, Steven Lee and Sasha Reed.

This work was supported by funding from the University of Denver, Pustmeuller Fellowship, Val A. Browning Foundation, Utah Department of Agriculture and Food, Utah Weed Supervisor's Association (APHIS funds), Tamarisk Coalition and the National Park Service, Marie Curie International Outgoing Fellowship within the 7th European Community Framework Programme (ESFFORES project grant number 299044) and the U.S. Geological Survey, Invasive Species Program and the National Science Foundation Dynamics of Coupled Natural and Human Systems award (project number 1617463). Finally, I would like to thank my family and friends for their support, particularly Marcus Perman.

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Summary

Spatial modeling has proven to be useful in understanding the drivers of plant populations in the field of ecology but has yet to be applied to understanding variation in biocontrol impact. In this study, we employ multi-scale analysis (Moran's Eigenvector Maps) to better understand the variation in tree canopy exposed to defoliation by a biocontrol beetle (*Diorhabda* spp.). The control of the exotic tree *Tamarix* in riparian areas has long been a priority for land managers and ecologists in the American Southwest. *Diorhabda* spp. was introduced as a bio-control agent beginning in 2001 and has since become an inseparable part of *Tamarix*-dominated river systems in the southwest. Between 2013 and 2016 tamarisk dieback was assessed at 79 sites across Grand County, Utah, arguably the epicenter of *Diorhabda* impact in the U.S. Canopy cover of *Tamarix* was between 73 and 81% at these sites, with the percent that was live cover fluctuating by year with a minimum of 42%. Using a traditional general linear model, we found that readily and commonly measured environmental factors could explain only up to 26% of the variation in *Tamarix* live canopy each year. The number of defoliations was correlated with an increase rather than a decrease in percent live canopy, suggesting compensatory growth. Spatial structure alone explained 22–40% of variation. We found fine scale spatial structure at less than 10 km and broad scale spatial structure from 10 to 30 km. Combining both traditional and novel spatial statistical methods we increased that percentage to 43–63%, depending on year. These results suggest that scientists and land managers must look beyond commonly measured environmental variables to explain nonrandom biocontrol impact in this system. In particular, this study points to the potential for biotic interactions and variation in flood cycles for further exploration of the identified spatial structure.

Introduction

Ecological phenomena display geographical patterns as a result of the underlying abiotic conditions being spatially structured (spatial dependence) or through contagious biotic processes in the community (true spatial autocorrelation, SAC; Borcard et al., 2004; Fortin et al., 2006; Legendre, 1993; Legendre and Legendre, 2012). This spatial structure was, until recently, largely ignored in ecological studies. However, a new analytical framework has been developed to incorporate spatial structure into the analysis of ecological systems (Moran's Eigenvector Maps; Legendre and Legendre, 2012). Recent studies have demonstrated the value of identifying spatial patterns of ecological communities to increase understanding of community drivers (Andersen et al., 2011; Sharma et al., 2011). An understanding of spatial structure may be particularly valuable in the context of restoration outcomes and invasive species community dynamics (Bourgeois et al., 2016; Muster et al., 2014; Venugopal et al., 2016). Early in the study of biological control (biocontrol), spatial patterns were also recognized as an important element to understanding this management tool (Levins, 1969). The impact of invasive species removal through biocontrol presents a particularly difficult scenario to predict, given that biocontrol effects are both spatially and temporally variable. However, to our knowledge, no published study has incorporated spatial modeling to better understand patterns of biocontrol impact. Here we combine traditional approaches with a new modeling tool to explore patterns of defoliation by a biocontrol herbivore.

Determining the drivers of the response by invasive plant species to biological control based solely on environmental conditions without regard for spatial patterns may be insufficient due to the complexity of interactions between small- and large-scale processes. Biocontrol has a myriad of potential drivers, from top-down factors such as predation to bottom-up factors such as soil nutrients and competition among target plant species (Seastedt, 2015). While environmental conditions can influence the effects of a biocontrol herbivore on its target plant, other factors such as population genetics and dispersal, which may be heavily spatially structured, also play a role. For example, gene flow among species of both the biocontrol agent and target species before and after the introduction of the biocontrol agent can make biocontrol impact more difficult to predict (Seastedt, 2015). Additionally, it is difficult to predict how far and in what manner an agent will disperse in a new environment (Nagler et al., 2014).

One family of spatial models that has proven particularly useful in ecological studies is Moran’s Eigenvector Maps (MEM; Borcard and Legendre, 2002; Dray et al., 2006). These models are based solely on a matrix of geographic distances between sites, rather than complex mathematical modeling, making them more accessible than other spatial modeling options. Additionally, they allow for the quantification of the relative role of spatial structure and environmental conditions in shaping ecological communities at multiple scales (Borcard and Legendre, 2002). For this, a matrix of geographical distances between sites is submitted to an ordination whose eigenvectors represent independent spatial processes acting at decreasing scales. The eigenvectors can then be used as explanatory variables to determine the spatial drivers of the phenomena of interest. In these methods, prior knowledge about the system or a given hypothesis can also be used to define the relationships between sites (i.e., the type of geographical distances used) or the directionality of spatial processes (Asymmetric Eigenvector Map framework; Blanchet et al., 2008).

In this study, we apply MEM analysis to examine the defoliation of an invasive tree by a biocontrol beetle in riparian corridors and intermittent watercourses of the Southwestern United States: *Tamarix* spp. (tamarisk, saltcedar). *Tamarix* was introduced in the early 19th century as a bank stabilizer, windbreak and ornamental. Although naturalized prior to the widespread practice of hydrological engineering (Birken and Cooper, 2006), river regulations and thus changing flood regimes partially facilitated the dominance of *Tamarix* (Stromberg et al., 2007). In the Southwestern U.S., it is now the third most common woody species and second highest tree cover in the (Friedman et al., 2005). Given the difficulty of distinguishing species in terms of biology and ecology, *Tamarix* refers to the two most common species in the U.S. and their hybrids – *T. ramosissima* and *T. chinensis* (Di Tomaso, 1998; Gaskin, 2013). *Tamarix* reproduces throughout the growing season, with wind and water dispersed seeds that are sensitive to desiccation, and thus no seed bank is maintained (Di Tomaso, 1998; Hultine and Dudley, 2013). *Tamarix* has been called a “paradox plant” as it has seemingly contradictory life history traits (Sher, 2013): It is both long-lived and produces large amounts of small seeds, is both drought and flood tolerant, and is an excellent competitor as a mature tree while easily overtopped as a seedling. *Tamarix* is a passenger of degraded ecosystems (*sensu* MacDougall and Turkington, 2005), but once established it drives tenacious changes in the ecosystem including higher soil salinity, increased fire frequency, and altered river geomorphology (reviewed in Johnson, 2013). As a costly invasive species (Zavaleta, 2000), its control has been a high priority in the American Southwest.

In 2001, a biocontrol beetle (*Diorhabda* spp*.)* was released as a potentially low ecological impact, low-cost and effective method of reducing *Tamarix* dominance compared to herbicide application or mechanical removal or burning (DeLoach et al., 2003). Several ecotypes were selected for variation in diapause onset and length, and the number of generations per season. Since their release, ecotypes have further adapted their critical day length (hours of daylight at which half the population enters diapause) to match their new environment (Bean et al., 2013a). Adults emerge from diapause after several warm days in the spring to coincide with *Tamarix* greening. Most populations of these beetles complete two generations per growing season.

Diorhabda adults and larvae feed exclusively from *Tamarix* foliage, resulting in leaf desiccation and defoliation (DeLoach et al., 2003; Lewis et al., 2003). They are gregarious, and swarms are known to intensively defoliate entire stands of trees at a time

(Bean et al., 2013a). Following such an event, *Diorhabda* tend to abandon the stand, resulting in areas that were heavily defoliated in one year having small or absent populations of larvae in the following year (Jamison et al., 2015). Conversely, areas that are only partially defoliated tend to retain an overwintering population, affecting the spatial distribution of beetle populations in future years (Jamison et al., 2015). Adult beetles are attracted to new food sources by sensing chemical compounds in tree foliage that are released through feeding activity as well as aggregation pheromones produced by mature males (Cossé et al., 2006, 2005). They have been measured to travel up to 65 kilometers in one dispersal event (Jamison et al., 2015; Nagler et al., 2014).

One defoliation event does not usually kill a stand or even a tree; leaves will often regrow on some or all of the defoliated branches depending on degree of carbon starvation (Bean et al., 2013a). Multiple defoliation events are generally required to cause branch or whole-tree mortality, however the number of defoliation events that is required for this to occur varies greatly (Bean et al., 2013a). Some studies suggest that the variation in number of defoliation events required to kill a tree is related to resource allocation governed by tree genetics or response to water availability (Hultine et al., 2013; Williams et al., 2014). Specifically, trees that allocate more resources to root growth and nutrient storage may be more resilient to herbivory than trees that invest more in above ground growth and leaf production (Williams et al., 2014). Recent studies show that beetle defoliation may affect ecosystem processes such as evapotranspiration, although at lower rates than were anticipated prior to release (Nagler et al., 2018).

The establishment and spread of this biological control is not without concern, however, given that *Tamarix* has become wildlife habitat. Beetle defoliation potentially threatens several species of passerine bird, lizards, and small mammals that use *Tamarix* in the absence of suitable native species (Bateman and Ostoja, 2012; Sogge et al., 2008). Thus, the importance of understanding patterns of defoliation is beyond the impact on the *Tamarix* itself.

In general, studies examining the response of *Tamarix* to biocontrol are highly variable (Hultine et al., 2015; Kennard et al., 2016; Nagler et al., 2018). Despite 15 years of biocontrol, the impact of *Diorhabda* on *Tamarix* remains inconclusive and nearly impossible to predict (González et al., 2017b; Hultine et al., 2015; Kennard et al., 2016; Sher et al., 2018). To date, variation in defoliation and mortality has been primarily studied in terms of environmental factors influencing tree response (but see Jamison et al., 2015), but no consensus has been reached about what environmental conditions mediate tree mortality in *Tamarix* stands. For example, Hultine et al. (2015) found a positive relationship between soil salinity and canopy dieback, but no correlation with the number of defoliation events or drought stress. In contrast, Kennard et al. (2016) found that defoliation was positively correlated with soil percent sand and negatively correlated with drought stress.

In this study, we quantified the relative roles of environmental variables versus spatial structure in determining the defoliation patterns of *Tamarix* by *Diorhabda* on a river catchment scale, including ephemeral washes, using percent live canopy per stand as the dependent variable. Exploring the spatial component is important both to improve our predictive power and because it can point to sources of variability not previously considered, including those relating to the beetle itself. Specifically, we asked the following: (1) How much variation in percent live canopy can be explained by environmental variables and if so, which environmental variables? (2) Is percent live canopy spatially structured and constrained by the river network? If so, at which spatial scales are these patterns observed and what is the structure? (3) Are the environmental variables driving live canopy also spatially structured (i.e. do they relate to the significant spatial patterns), and at which spatial scales are environmental drivers operating? By addressing these questions, we aim to improve our understanding of variation in beetle-caused *Tamarix* defoliation, pointing to testable hypotheses for future studies.

Methods

Site Description and Data Collection

A total of 79 defoliation monitoring sites were established throughout the landscape of Grand County, Utah (Figure 1-1), arguably the epicenter of *Diorhabda* spp. beetle impact in the Southwestern U.S. (Tamarisk Coalition, 2016). The Northern tamarisk beetle (*Diorhabda carinulata)* was released at 12 locations (Figure 1-1) between 2004 and 2006 throughout the study area and has since expanded across the western United States. This region has an average high temperature of 22.1 ºC and low temperature of 5.6 ºC with average annual precipitation in rainfall of 241 mm and snowfall of 152 mm (U.S. Climate Data, 2016). Sites were established at every known *Tamarix* population within Grand County that was (1) accessible and (2) large enough to accommodate the sampling design (described below). Distances between adjacent sites ranged from .2 (an exception) to 12.5 km. All sites were individual stands, with the exception of two sites that were each a combination of two, smaller, adjacent stands in order to meet the size requirement while maintaining good geographic coverage across the study area. The resulting study area reached from the Book Cliffs (mountain range running East to West along the northern edge of study area) to the Colorado River or Green River, representing a wide variety of ecosystem types, including ephemeral washes, cattle stock ponds and two rivers with permanent flow. As such, this location provided the diversity in environmental variables that exist where *Tamarix* occurs without confounding other spatial variables such as climate.

Field sampling was conducted once per growing season at each site. Canopy cover was measured using the point intercept method (Bonham, 1989). At each site, a baseline of 60 to 100 meters was placed from a GPS-mapped point that was consistent from year to year running along the edge of the *Tamarix* stand. Permanent transects were established perpendicular to the baseline using a stratified random method. The length of the baseline plus transects equaled 160 meters. Each year of sampling, canopy status was recorded using the point intercept method at every half-meter along each transect. This point was scored as “live” if it intersected a live branch at any point vertically from the ground to the top of the canopy. A live branch was one that had evidence of having leaves that season (i.e. brown foliage was still considered live and branches that re-sprouted were also counted as live). If only dead branches were intersected at the point vertically from the ground to the canopy, the point was scored as dead. A point was recorded as “dead” if all intercepted branches were bare of leaves, with no evidence of greening for the season (Kennard et al., 2016). Dead branches may remain on the trees and thus be counted as dead in subsequent years. If no canopy of any kind was intersected, the point was scored as “open”. These points served as intermediate data used to calculate site-level canopy measures. Percent live canopy (the primary response variable of interest) was determined using the total points “live” divided by total points sampled that intersected *Tamarix* (“live” or “dead”). Canopy cover was calculated as the number of points that intersected *Tamarix* divided by the total number of points sampled. All 79 sites were sampled for *Tamarix* canopy from 2013 – 2016 for a total of four years of data (Figure 1-1). Given the number of sites, sampling began in late spring once *Tamarix* had greened up and was finished by late summer before autumn browning began.

Twelve site-level environmental variables that could potentially drive canopy status were sampled in 2014 and used in subsequent analyses. These were grouped in three categories: stand characteristics, geographic features and soil characteristics (Table 1-1).

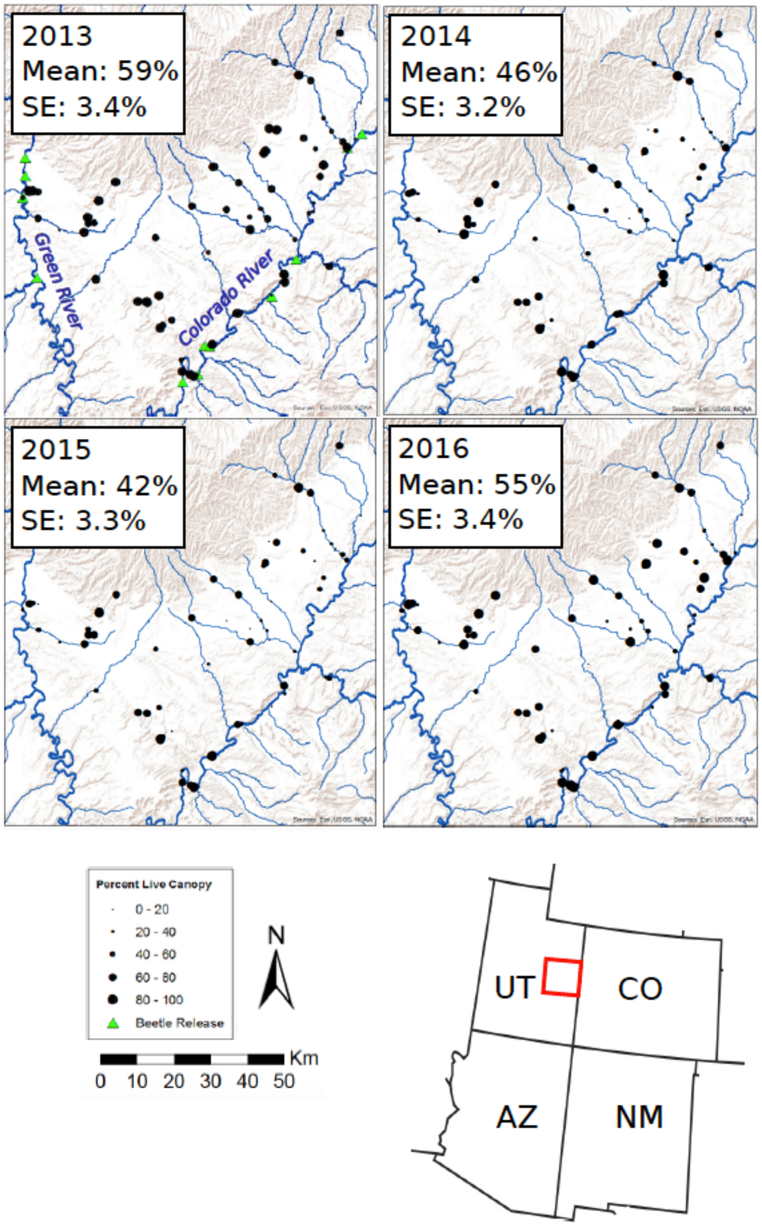

Figure 1-1: Percent Live Canopy. Percent live canopy (as indicated by size of circle) of Tamarix in southeastern Utah for each of the 79 sites recorded annually between 2013 and 2016. The red box in the overview represents the study area. UT-Utah, CO-Colorado, AZ-Arizona, NM-New Mexico.

Table 1-1: Summary statistics for all environmental variables sampled. Mean ± 1 SE are presented for all continuous variables. Counts are presented for categorical and ordinal variables. See text - methods section for explanation of variables.

Geographic	**Mean**	**SE**			
Absolute Elevation (m)	1349.06	12.35			
River Width (m)	35.89	7.09			
Longitudinal Site Slope (m)	5.47	0.89			
River Category (permanent or ephemeral)	Ephemeral (1) = 59	Permanent (2) = 20			
Soil					
Ec (µS/cm)	1937.04	164.23			
% Sand	45.85	2.54			
pH	8.08	0.02			
Wetland Status	UNK(1) = 8	FACU(2) = 12	FAC(3) = 40	FACW(4) = 13	OBL(5) = 6
Stand Characteristics					
Tree circumference (cm)	41.50	2.41			
Distance from Release Site (km)	12.95	0.97			
Years Since First Defoliated	9.34	0.08			
Cattle Impact (0-3)	0=19	1=10	2=20	3=30	

Stand characteristics

The circumference of the largest tree per transect was measured and averaged for each site. This variable represents a proxy for stand age, with larger trees representing older stands (Brotherson et al., 1984). Hultine et al. (2010b) have shown that older trees have reduced vigor and fewer leaves and so fewer resources to recover from defoliation, thus we expect to see lower percent live canopy in stands with larger (and thus older) trees. The number of years since the first defoliation was assessed from data collected by the continuous monitoring of the sites since beetle release in 2006. We predicted that more years since first defoliation would be associated with lower live canopy, given that Hudgeons et al. (2007) have shown that multiple defoliation events are required to cause tree mortality. If beetles are returning to stands that have re-greened, then stands that were defoliated in earlier years are expected to have higher mortality over time. Using Google Earth, we measured the as-the-crow-flies distance from each site to the nearest release site. We predicted that stands farther from release sites would have lower live canopy based on Jamison et al.'s (2015) finding that average defoliation was a function of distance from release site. Beetles were seen at all sites at least once, indicating that all stands represent a potential food source for the beetles. Cattle impact was assessed on a scale of zero to three, with three being highest impact based on a visual inspection of cattle damage on adjacent plants and presence of excrements in the area. Cattle may graze *Tamarix* seedlings if desirable vegetation is lacking, despite having no nutritional benefit (Di Tomaso, Joseph M. and Kyser, G.B., 2013). Additionally, cattle can cause physical damage to *Tamarix* stands through trampling and branch breakage (personal observation). We therefore predicted that higher cattle presence in a site would be correlated with lower percent live canopy.

Stands with less access to ground water may have a lower capacity to recover from herbivory based on the relationship between tree mortality, resource availability and disturbance studied in other plant species (Bean et al., 2013a). Thus, we measured water availability with several indirect measures, including by surveying understory plants for each transect. Species identification in the field was verified later in an herbarium. Using the PLANTS Database of the U.S. Department of Agriculture we determined the Wetland

Indicator Status of each plant species found for the “Arid West” Ecoregion (USDA-NRCS, 2016). We assigned a wetland status to each site based on the most wetland-dependent plant present at the site (Table 1-1). These categories were used as proxies to indicate low lying areas of floodplains that are more connected to the river than higher and therefore drier areas (Corenblit et al., 2009; Merritt, 2013).

Geographic features

All study sites were plotted in Google Earth. The absolute elevation for each site was recorded. Using the “measure” tool, we calculated the approximate width of the riverbed and the longitudinal site slope. Site slope was measured as the difference in elevation 500 meters upstream from the site and 500 meters downstream from the site. We recorded whether the primary water source was intermittent or permanent based on visual inspection in the field; permanent would be expected to have less drought stress than intermittent. Ephemeral streams were considered intermittent. We anticipated that sites at higher elevation, which had typically greater slope and intermittent water sources, would have a lower percent live canopy due to plant stress associated with water availability. We also measured the distance from each site to all other sites overland and along waterways to create two matrices of distance relationships. Distances along waterways were measured using National Hydrography Dataset shapefiles in ArcMap (USGS 2014; ESRI 2014). All sites were connected along flow lines (including ephemeral washes) using the NHD shapefile.

Soil characteristics

A soil sample was collected from one randomly selected location along each transect. Transect samples were mixed to create a composite site-level soil sample. Soil samples were collected using a soil corer to a depth of ten centimeters. Samples were placed in a paper bag to air dry until returning to the lab where they were dried in an oven at 60°C and processed to measure soil texture, salinity and pH. Soil texture was measured as the percentage of sand (> 63µm) present, pH was determined using a 1:1 water solution and soil salinity was measured as the electrical conductivity of the soil (González et al., 2014). We predicted that sites with higher soil salinity would have lower live canopy, given that a previous work on *Tamarix* response to *Diorhabda* beetles found dieback positively correlated with salinity in two of the three years surveyed (Hultine et al., 2015).

Statistical methods

To address our first question of whether environmental factors explain variability in live canopy we used a general linear model with stepwise selection, variables selected based on Akaike information criterion (AIC), maximum likelihood fit and normal distribution to test the relationship between percent live canopy in each year and environmental conditions. Sites were at least a half kilometer from the nearest neighboring site, while most were separated by several kilometers or more. Nevertheless, this type of analysis may lead to type I error due to pseudo-replication related to the spatial dependency of environmental variables. To account for and incorporate this spatial dependency into our analysis, the results of the linear model were then considered in the context of the following spatial analyses.

To determine spatial patterns in present live canopy we used MEM (Borcard and Legendre, 2002; Dray et al., 2006). In preliminary analyses we incorporated down river directionality in the modeling of spatial processes using Asymmetric Eigenvector Matrices (AEM, (Blanchet et al., 2008). However, the AEM increased the complexity of the model but did not improve our ability to explain patterns of *Tamarix* live canopy (results not shown), therefore we proceeded only with MEM that do not use directionality. We used two defined relationships – overland proximity (using Euclidean distance, henceforth referred to as MEM overland) and proximity along waterways (MEM waterway). Using overland distances for the MEM overland model and distance along waterways for the MEM waterway model, we generated sets of spatial variables for each model called spatial eigenfunctions (Borcard et al., 2004; Dray et al., 2006; Legendre and Legendre, 2012). For this, a site-by-distance matrix based on either raw overland distances or raw distances along waterways was submitted to a Principal Component Analysis. The resulting eigenvectors corresponded to the spatial eigenfunctions representing independent (i.e., orthogonal) spatial structure acting at decreasing scales. For both models, raw distances as well as two geographic weighting functions were tested representing linear and concave-down spatial relationships (Dray et al., 2006). The weighting function with the highest adjusted R^2 was used (raw distances for the overland model and concave down for the waterway model).

The live-canopy data were checked for linear trends prior to analysis using MEM. MEM requires the response variable to be detrended if a linear trend is found. A linear spatial trend in the response variable indicates that there is some spatial structure that is larger than the extent of the study design area and so must be removed to identify patterns at a finer level (Borcard et al., 2004; Sharma et al., 2011). We found a linear trend for our live-canopy data and so removed it to be analyzed separately using variation partitioning. The spatial eigenfunctions were then used as explanatory variables of this detrended live-canopy data using a general linear model, forward selected to determine which significantly explained variation in live canopy (Andersen et al., 2011; Borcard et al., 2004; Dray et al., 2006).

To explore the shape and scale of significant spatial patterns, we plotted the significant eigenfunctions on a map of the study sites. For the MEM overland model, the significant spatial variables were plotted and then visually inspected to identify broad and fine relative spatial scales. Scales were identified simply by visually exploring the size of clusters in the plot and assigning the spatial variables as broad or fine relative to each other (Borcard et al., 2004; Borcard and Legendre, 2002). These two sub-sets of spatial variables made up a large-scale spatial structure and a fine-scale spatial structure to be used in variation partitioning (see below). For the MEM waterway model, the significant spatial variables were plotted and visually inspected, however, no visual discernment could be made for the scales of these variables.

We used variation partitioning in the R package vegan (Oksanen et al., 2019) to identify the relative importance of environment and spatial structure in *Tamarix* live canopy for each year. For each variation partition we used the undetrended live-canopy data. Variation partitioning was done to identify the exclusive and shared variation of each of the spatial patterns with the environmental variables (Borcard et al., 2011; Sharma et al., 2011). For the overland model (MEM overland), variation partitioning was also done with the sub-models of fine and broad scale and environmental variables, making a total of four components for variation partition: linear, MEM overland (broad and fine), and MEM waterway. Additionally, we compared each significant spatial model to the environmental variables to identify the spatial scale at which environmental variables influence live canopy for each year. MEM methods have not yet been applied to address time series analysis. In this study, we visualized spatial structure from one year to the next by plotting the significant eigenvectors.

Live canopy and environmental data were checked for normality and log-transformed as needed (Figure S1-1, Figure S1-2). Environmental variables were checked for colinearity using pairwise scatterplots (with a 0.6 cut off for correlation coefficients) before including them in the general linear model (Zuur et al., 2010). Model residuals were also checked for normality. All statistical analyses were performed using R version 3.1.2 (R Core Team, 2020).

Results

Mean *Tamarix* live canopy in biocontrol sites varied from 42% to 59% during the four years of this study (Figure 1-1; significant mixed model with live canopy as the dependent variable, year as the fixed effect and site as the random effect (d.f. = 3, F-ratio

= 25.01, $p < 0.0001$). Average live canopy decreased from 2013 to 2015 and increased from 2015 to 2016. The average percent live canopy in 2016 was higher than 2014, but still lower than 2013. Average canopy cover ranged from 73% to 81% depending on year. There was a weak negative relationship between live canopy and canopy cover that was statistically significant in all years except 2013 (linear regression adj. 2013 $R^2= 0.015$, NS; 2014 $R^2=0.16$, $p<0.001$; 2015 $R^2=0.1$, $p<0.01$; 2016 $R^2=0.04$, $p<0.05$). Readily and commonly measured environmental factors explained only 19% to 26% of the variation in *Tamarix* live canopy each year (traditional general linear model, Table 1-2). However, by combining both traditional and novel spatial statistical methods we increased the percentage of explained variation to 43% to 63%, depending on year. The portion of live canopy explained through environmental factors and spatial structure had little overlap (Figure 1-2).

Table 1-2: General linear model with stepwise selection of environmental variables collected in 2014 (Independent variables) and live canopy for each year studied (Dependent variable). n.s. = not significant; the value associated with each significant variable is the coefficient showing the direction and strength of the relationship. Significance codes: 0.0001 '***' 0.001 '**' 0.01 '*' .05 '.' 0.1 ' '

Live Canopy (year)	**2013**	**2014**	**2015**	**2016**
Geographic				
Absolute Elevation (m)	n.s.	n.s.	0.133***	0.113**
River Width (m)	n.s.	n.s.	n.s.	n.s.
Longitudinal Site Slope (m)	0.068*	n.s.	n.s.	n.s.
Stand Characteristics				
Tree circumference (cm)	-0.084**	-0.101***	-0.0842**	-0.101**

Distance from release site (km)	0.103**	0.116***	n.s.	n.s.
Years since first defoliated	0.097**	0.075*	0.0844*	0.0895*
Total Adj. R^2	0.228***	0.2562***	0.1988***	0.190***

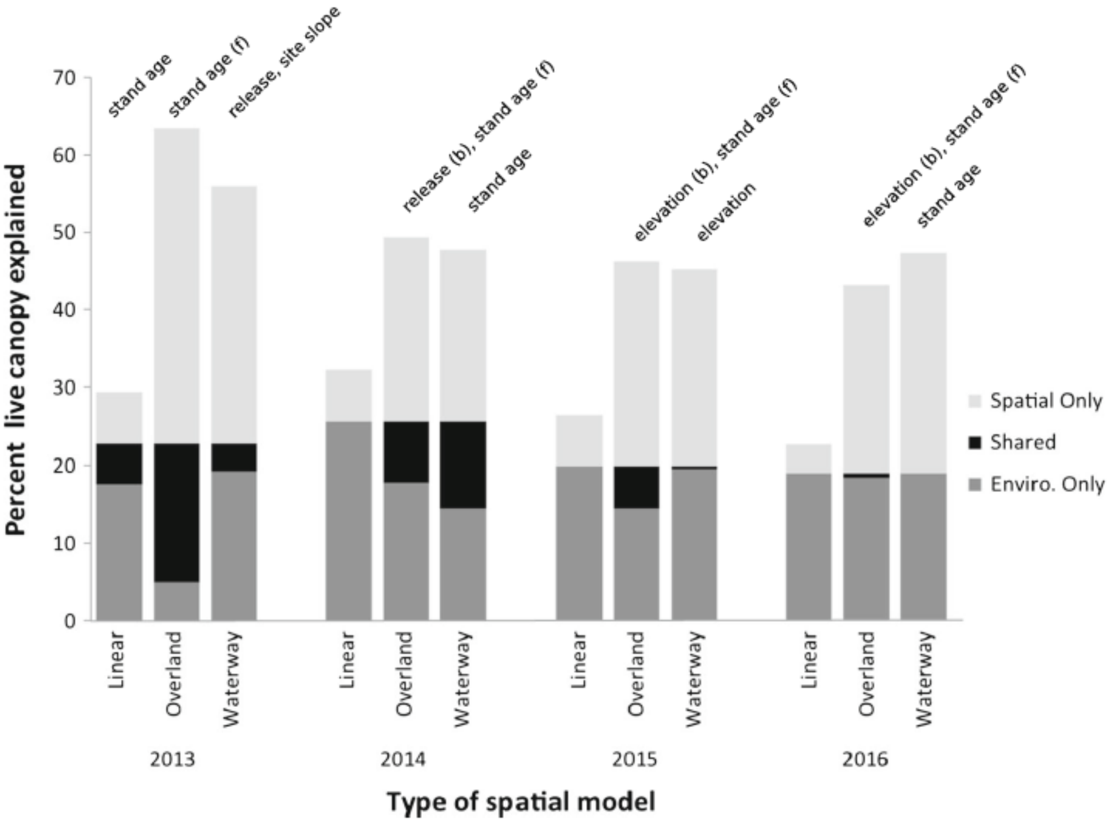

Figure 1-2: Percent live canopy explained using variation partitioning with live canopy as the response variable and spatial eigenvectors and environmental variables as explanatory variables. Each bar represents one regression model using variation partitioning. The different shading within each bar shows the percentage of live canopy explained by spatial variables alone (light grey), environmental variables alone (dark grey), and the shared percent explained by both spatial and environmental variables (black). The text above each bar is the environmental variable that overlaps significantly with the spatial model. For the overland models, the relevant scale was identified for the environmental variable: broad (b) or fine (f).

Environmental variables

Environmental variables that were significantly correlated with live canopy were mainly in the group “stand characteristics” (Table 1-2). Live canopy decreased with stand age and increased with the number of years since first defoliated. Steeper longitudinal site slope, larger distance from beetle release site and higher elevation were all associated with higher live canopy in at least one year of the study.

Spatial structure

A significant linear trend was found in all years of study, explaining from 3.6% to 11.9% of variation in live canopy depending on year. The structure of this trend remained consistent from year to year. Both the waterway and overland models explained a large portion of the variation in live canopy in all years (Figure 1-2). The spatial structure of the waterway model was highly variable from year to year as shown by different clusters of similarly sized and shaded squares in Figure 1-3.

The waterway model explained 26% to 48% of the variation in live canopy. The overland model explained 27% to 53% of the variation in live canopy. In contrast to the waterway model, the overland model showed the same structure in each year of the study (Figure 1-3). Distinct broad and fine scale patterns were identified for the overland model. Spatial structure at the scale of less than 10 km consistently explained more of the variation than either broad scale (10-30 km) or the linear trend (Figure 1-3).

Figure 1-3: Plots in geographic space of each spatial model. Each square represents the predicted value of *Tamarix* live canopy for the model. Predicted values are scaled from -1 to 1 and so should be interpreted in relative terms. Black squares indicate positive values. White squares indicate negative values. The size of the square is proportional to the predicted value, with larger squares being farther from zero. Large white squares have the lowest predicted live canopy, while large black squares have the highest predicted live

canopy. Spatial patterns are interpreted from clusters of similar sized and colored squares. Adjusted R^2 value is in the bottom left corner of each plot. The predicted values are derived from all spatial variables significant at the 0.05 level.

Variation partitioning

For each of the spatial relationships examined (linear, MEM overland and MEM waterway), we partitioned the variance with the spatial variables and the environmental variables. That is, the variation was partitioned into the portion of variation explained exclusively by environmental variables, spatial variables as well as the portion of variation explained by both variables. Interestingly, there was very little overlap in the percent of live canopy explained by environmental variables and spatial structure from year to year (Figure 1-2). An exception to this is that the overland model consistently overlapped with the stand age at the fine scale. Shared variation with the two other types of spatial models varied from year to year. Particularly, the MEM waterway model showed no consistent trend in overlap from year to year.

Discussion

To the best of our knowledge, this is the first attempt to understand the spatial structure of a plant biocontrol impact using spatial models. By incorporating spatial structure into our analysis of the influence of environmental variables, we were able to describe a much larger portion of the variability in live canopy in biocontrol sites than using environmental variables alone. We were able to show that environmental variables underlie some of the spatial structure (overlapping in the variation partition) but that most of the variability in live canopy that is described by spatial structure is not related to the measured environmental variables (non-overlapping), which opens new research pathways to understand the factors governing biocontrol effects on plants. We will discuss these results in terms of beetle defoliation, as this is the phenomenon of interest, bearing in mind that live canopy is the variable we measured. While it is likely that most dead *Tamarix* branches in the study area are a result of beetle defoliation based on observations over the past decade by the Weed Department of Grand County Utah (W. Robinson, personal observation), we cannot entirely rule out other causes of dead branches, such as drought stress or self-pruning in response to competition.

Stand characteristics explain a low percentage of variability in *Tamarix* live canopy

Both of the environmental variables that correlated significantly with live canopy --stand age and time since first defoliation-- were under the category of "stand characteristics", not an underlying property of soil, water, etc. This is not surprising given the lack of consensus on what environmental characteristics are important, despite several studies addressing this question. Our study supports the hypothesis proposed by (Bean et al., 2013a) that older stands would be less able to recover from herbivory and have higher rates of mortality. Older *Tamarix* stands have been shown to have reduced vigor, produce fewer leaves and use fewer resources (Hultine et al., 2010b).

More surprisingly, time since first defoliation was associated with higher live canopy, which is counter to the idea that repeated defoliations eventually lead to the death of the tree (Hudgeons et al., 2007). Given that all of our sites have experienced multiple beetle defoliations, our results suggest that stands not only generally recovered over time but also potentially experienced compensatory growth. *Tamarix* is known to often re-sprout within weeks of beetle defoliation (Hultine et al., 2010b) however these are the first results to show that previously attacked stands were greener. The reason for this may also be that the core of beetle defoliation happens during the first few years following their arrival and tends to level off over time (Hultine et al., 2010b; Kennard et al., 2016). As our latest survey year was between 9 and 12 years after the first exposure to beetles (depending on site), we are likely seeing less dramatic beetle impact than would be expected during initial exposure. *Tamarix* persists in this area in high abundance. Given the "boom and bust" cyclical nature of beetle feeding, *Tamarix* decline and recovery to mirror beetle recovery and decline is likely in this area, even after all stands have experienced at least one major defoliation.

Regional scale spatial structure is consistent over time

The temporally-consistent linear trend in live canopy distribution, despite explaining a low percentage of variability, suggests that there is spatial structure on a larger scale than the study area. Previous studies indicate that large scale climatic variation influences *Tamarix* abundance (e.g. geology, soils, valley shape), especially relating to aridity (McShane et al., 2015). The present study suggests these types of factors also influence the impact of biocontrol defoliation on canopy status. This linear gradient could at least partly be responsible for regional differences in beetle impact as well as differing outcomes of studies done to predict beetle impact (e.g., Virgin River, Nevada: Hultine et al., 2015; Colorado River and small tributaries, Colorado: Kennard et al., 2016; Dolores River, Colorado and Utah: Sher et al. 2018).

The overland model had a temporally stable spatial structure

Interestingly, the overland proximity-based spatial structure in live canopy remained visually consistent among the four years surveyed, while the waterway patterns changed substantially from year to year. This suggests that both processes that are more temporally stable at this time scale (e.g. population genetic structure of *Tamarix*), and less so (e.g., flow regime, beetle dispersal) likely influence defoliation patterns.

Several studies argue that variability in *Tamarix* mortality from beetle defoliation is likely related to variation in plant genotypes among populations (Bean et al., 2013b; Hultine et al., 2013; Long et al., 2017; Williams et al., 2014). Novel hybridization (specifically *T. ramosissima* introgression) in the invaded range has been shown to be variable and associated with higher investment in roots and increased defoliation tolerance (Williams et al., 2014). Conversely, although *Tamarix* is exposed to approximately 320 herbivore species in its native range (Long et al., 2017), the absence of any significant herbivory over the last century in the U.S. may have led to weakening anti-herbivore adaptations (Blossy and Notzold, 1995) to varying degrees across the landscape. The mosaic of genotypes created by either of these processes could explain a spatial pattern of beetle defoliation that would remain stable over four years.

Natural selection by the environment, unrelated to herbivore pressure, may also lead to traits that affect response to herbivory and thus a spatial structure that is unlikely to change markedly year to year. In particular, increased ability to exploit resources could make trees more vulnerable to defoliation because of tradeoffs between growth and metabolite storage, the latter of which plays a significant part in herbivore resistance and recovery. Hultine et al. (2013) showed that radial growth rates of *Tamarix* were positively associated with beetle-related mortality. Additionally, (Friedman et al., 2008) showed that cold-adaptation influenced recovery from episodic herbivory in *Tamarix.* Long et al. (2017) argued that despite gene flow (which one would expect to hinder local adaptation), *Tamarix* is remarkably well adapted to local environmental conditions. Thus, given this dynamic between the genetic basis for herbivory response and local adaptation, the more stable spatial structure we observed could reflect genotype distribution caused by selection by local conditions, unequal loss of herbivory defense, random hybridization patterns, or some combination of these.

Understanding the interaction of local adaptation and hybridization is important for understanding the future of biological control in the U.S. as well as its potential in other countries where *Tamarix* acts as an invasive species. This genetic component of *Tamarix* response to *Diorhabda* biological control may be of particular importance in places such as South Africa where there are also native *Tamarix* species present (Marlin et al., 2017).

The waterway model reveals a temporally dynamic spatial structure

Water flow has been shown to be an important force in spatially structuring riparian plant communities (Bourgeois et al., 2016; Cordes et al., 1997), and the present study demonstrates this as well. Although directionality of flow proved unimportant for explaining spatial patterns, the network of the river was as important as overland distances in explaining *Tamarix* live canopy, even if the model differed in its consistency. The variability in the waterway model's structure from year to year is not surprising because the flow of water can change dramatically from one year to the next, and temporal and spatial variability in stream flow is the main driver of biotic communities in river systems (Poff et al., 1997). For example, some ephemeral washes might not get any water at all in low flow years.

We suggest that short-term compensation for flood and drought could be partially responsible for this dynamic structure. If high resource years lead to more growth than carbon storage, trees could be less resilient to defoliation during high-flow years. *Tamarix* has been shown to compensate for water availability through high leaf-level transpiration when water tables are high and lower transpiration when water levels are low (Smith et al., 1998). Such climate variability is likely to cause greater beetle induced mortality in some years over others.

Beetle dispersal is also expected to vary from year to year and so may in part explain the source of unstable spatial variation. Several studies have shown the boom and bust cycles of *Diorhabda* (Jamison et al., 2015; Nagler et al., 2018). Jamison et al (2015) showed that large defoliation events led to abandonment of heavily defoliated sites. This gives *Tamarix* the opportunity to re-sprout following defoliation. Given that there is no implicit confinement of this dispersal to river corridors, we anticipated finding evidence of beetle dispersal in our overland model. If beetle dispersal was predominantly characterized by an overland movement, we would expect to see an overland model that varied from year to year. This hypothesis was based on the fact that adult beetles are known to fly vertically into the air and drift on wind currents establishing satellite populations via this long range dispersal events known as Levy flights (Nagler et al., 2014). Once away from the stand, they use both aggregation pheromones as well as volatile compounds in *Tamarix* to find new *Tamarix* stands (Cossé et al., 2006). (Nagler et al., 2014) showed defoliation at sites 22.5 km from their initial site, with no defoliation in between in one season, suggesting long-range dispersal. These dispersal strategies make overland movement possible, and likely.

However, in the present study it is the waterway model, not the overland model, that varies from year to year. Therefore, beetle movement along connected stands of *Tamarix,* generally seen at their densest along river ways, and use of rivers as a movement corridor for beetle dispersal is more likely. This hypothesis is supported by Ji et al. (2017) who found that dispersal of *Diorhabda sublineata* was primarily driven by *Tamarix* abundance and stand connectivity, both of which were at their highest along major waterways. Our finding that live canopy is lower in stands with higher canopy cover further supports Ji et al.'s (2017) finding that herbivory may be more intense in denser stands of *Tamarix.* Clearly, more direct study of beetle movement is needed to confirm this hypothesis.

Spatial models reveal patterns of live canopy not explained by environmental factors

While stand age explained a small portion of the fine scale overland spatial structure of *Tamarix* percent live canopy, no other measured environmental variables corresponded to the spatial patterns observed. This non-overlapping portion of spatial structure is of particular interest because it reinforces the idea that other factors besides environmental condition measured by classic factors (e.g., distance to river, soil salinity, etc.) related to the invasive tree are causing the variation. As discussed above, the temporally stable elements may be explained by other tree-related factors such as genetics, while those that changed year to year are more likely to be due to factors influencing beetle movement or other underlying contagious biotic processes of tree and beetle (true spatial autocorrelation).

However, it is also possible that the environmental variables themselves were poor, either because they did not measure the environmental conditions accurately or different ones would have had better predictive power. We measured the environment primarily as a proxy for plant stress; we know that host plant quality affects the intensity of and response to herbivory and may vary among and within sites (Awmack and Leather, 2002), however, it is possible that our environmental factors did not accurately predict this. For example, our variables of elevation, class of river, distance to river, and presence of wetland species are commonly used proxies for water availability but are not direct measures of actual water availability, nor of *Tamarix* response to water. Furthermore, other measures of water may be more biologically relevant, such as deviation from historical flood regime (Merritt and Poff, 2010). Perhaps most importantly, a focus on tree-related environmental factors ignores those that may be influence beetle performance, movement and other behavior. Although some of the typically measured variables such as soil texture may have direct relevance to the ground-burrowing *Diorhabda*, there are others such as density of insect predators, which are not. These beetle-related environmental factors are likely responsible for at least some of the unexplained spatial variability.

Limitations and benefits Moran's Eigenvector Maps in ecological studies

Despite the uncertainty of the underlying causes of the spatial patterns, the distinct spatial structure suggests that the patterns of defoliation are not random. The high percent of variability explained only by spatial structure shows that in cases where measured environmental factors are unable to explain ecological patterns, spatial models offer a tool for better understanding the variability in the system. In particular, MEM appear of great interest for the description of spatial patterns as it is relatively easy to implement and allows for the use of different connectivity matrix, distances and weighting functions between sites. MEM analysis can be used to conduct spatial analyses with binary dependent variables, making it useful for distribution studies. While our point level data was in fact binary, we scaled up to the site level in this analysis because all explanatory variables were at the site level. A binomial analysis could be useful however in a study designed to understand very fine scale spatial structure. Regardless of data type, MEM results often overestimate the variation explained solely by spatial components and should thus be put in perspective qualitatively rather than quantitatively (Gilbert and Bennett, 2010; Hawkins, 2012; Kuehn and Dormann, 2012; Tuomisto and Ruokolainen, 2006). Therefore, further studies based on different statistical approaches or experimentally testing hypotheses in the field may be required to fully understand the spatial mechanisms at play in *Tamarix* biocontrol. Despite these limitations, the doubling of explained variation when accounting for spatial processes leaves no doubt here about the existence of strong spatial processes structuring *Tamarix* canopy exposed to biocontrol.

One of the issues this study addresses is the difficulty of designing studies with spatially independent samples, given that spatial structure exists in most ecological phenomenon and at all scales (Legendre, 1993). Despite this, studies that account for this spatial structure are rare in ecology. The present study shows the value of identifying such spatial structure in a system that we know little about. Rather than being a source of noise to be removed or compensated for, spatial patterns in ecological systems provide valuable information in their own right and should therefore be incorporated into ecological studies (Legendre, 1993). The risk here and in other studies that use classic statistics in ecology is that the significance of the statistical test may be overinflated. However, in the present study, the environmental variables measured display little spatial dependence and can therefore be treated as independent samples. This demonstrates the use of MEM as a tool for assessing spatial independence in study design, as well as understanding the spatial structure of the study system.

Comparing ground surveys to remote sensing methods

While accurate and informative, conducting ground surveys to assess large-scale patterns in biocontrol impact is time and labor intensive and not always realistic. Remote sensing to detect beetle defoliation provides a particularly enticing opportunity to test hypotheses proposed here, as they can provide data at much larger scales as well as potentially capture more of the temporally fluctuating nature of biocontrol, even if at a lower resolution than was possible for this current study that employed extensive ground surveys (Ji et al., 2017; Nagler et al., 2018). Several studies have shown that results from satellite imagery accord with ground surveys, although several types of imagery may be necessary for full and accurate coverage (Hultine et al., 2015; Nagler et al., 2018, 2014). In particular, remote-sensing studies primarily concerned with *Tamarix* defoliation for its influence on ecosystem processes such as evapotranspiration must combine imagery types to ensure accurate measurement of defoliation (Nagler et al., 2012). Leaf Area Index (LAI), as calculated using remote sensing tools, can be used as an estimate of percent green cover in *Tamarix* stands. This method has been successfully used in several recent studies (Nagler et al., 2014 and others cited therein). The use of multiple types of imagery is also important for calculating a Leaf Area Index that would accurately compare to a visual inspection of defoliation using field methods. This is because when beetles defoliate, the leaf mesophyll is consumed, and the supporting twig is left, which may interfere with the ability to detect a decrease in apparent LAI (Nagler et al., 2014).

Additionally, using satellite imagery, Hultine et al. (2015) showed that ground surveys at the tree scale could be accurately scaled up to the stand scale. However, we would caution against scaling up too far, given the patchiness shown in the present study at less that 10 km. Further, Nagler (2018) found through satellite imagery confirmed by on the ground surveys, that *Diorhabda-Tamarix* interactions were highly variable among sites even in the same river system, making high resolution sampling important for accuracy.

Conclusions

In this study we have shown empirical evidence for compensatory growth in *Tamarix* in response to *Diorhabda* herbivory. Additionally, we have provided support for the hypothesis proposed by Bean et al. (2013a) that older *Tamarix* stands are at greater risk for mortality in response to beetle herbivory. Both of these points are important for management applications. First, managers can target sites for follow up treatment in the years following heavy defoliation to account for potential compensatory growth. Secondly, in regard to habitat loss due to *Tamarix* mortality, managers can prioritize older stands for active revegetation measures in anticipation of *Diorhabda* impact.

In our spatial analysis, we have demonstrated the importance of fine scale spatial structure (less than 10 km) and suggest that future studies focus more on local or stand scale variation in beetle impact to drivers of biocontrol impact, rather than attempting to find broad-scale, regional generalizations. We have quantified both stable and dynamic spatial patterns that are not related to commonly measured environmental variables. To this end we encourage future studies to focus on fluctuations in water availability. While these data are difficult to gather, our results reinforce the idea that they are likely important for understanding biocontrol in semi-arid riparian ecosystems. Additionally, we suggest genetic variability among populations of both *Tamarix* and *Diorhabda*, as well as the biotic interactions between these species outweigh commonly measured environmental factors in predicting the impact of biocontrol herbivores on invasive plant species.

Finally, from a methodological standpoint we have shown that spatial analyses such as Moran's Eigenvector Maps provide relevant statistical tools to discern otherwise hidden patterns in ecological systems, with applications to both fundamental and applied ecology including understanding biocontrol impact. In the present study we were able to describe previously unknown spatial structure in this system, helping to guide future studies of target response to biocontrol.

Data availability

The data associated with this paper have been deposited in a Dryad digital repository doi:10.5061/dryad.2ts54jj

Citation Information

Henry, A.L., González, E., Robinson, W.W., Bourgeois, B. and Sher, A.A., 2018. Spatial modeling improves understanding patterns of invasive species defoliation by a biocontrol herbivore. Biological Invasions, 20(120): 3545-3562.

Chapter 2 Cover of an invasive tree covaries with environmental factors to explain the functional composition of riparian plant communities

Summary

Invasive species are a major cause of biodiversity loss worldwide, but their impact on communities and the mechanisms driving those impacts are varied and not well understood. This study employs functional diversity metrics as well as guilds - suites of species with similar traits - to assess the influence of an invasive tree (*Tamarix* spp.) on riparian plant communities in the southwestern United States. We asked: 1) What traits define riparian plant guilds in this system? 2) How do the abundances of guilds vary along gradients of *Tamarix* live cover and abiotic conditions? 3) How does the functional diversity of the plant community respond to the gradients of *Tamarix* cover and abiotic conditions? We found nine distinct guilds primarily defined by reproductive strategy, as well as height, seed weight, specific leaf area, drought and anaerobic tolerance. Guild abundance mostly varied along a covarying gradient of local and regional environmental factors and *Tamarix* cover. Guilds relying on sexual reproduction, in particular those producing many light seeds over a long period of time were more strongly associated with drier sites and higher *Tamarix* cover. *Tamarix* itself appeared to facilitate more shade tolerant species with higher specific leaf areas than would be expected in resource

poor environments. Additionally, we found a high degree of specialization (low functional diversity) in the wettest, most flood-prone and lowest *Tamarix* cover sites as well as in the driest, most stable, highest *Tamarix* cover sites. These guilds can be referred to when anticipating plant community response to restoration efforts and in selecting appropriate species for revegetation.

Introduction

While it is well known that invasive species are a major cause of biodiversity loss worldwide, the impact of invasive species on the functional composition of communities is varied and not well understood (Vilá et al., 2011). Invasive species may affect communities by altering resource availability and contributing to changes in disturbance regime. The impact of invasive species on ecosystem function has been identified as a fundamental research need to help inform policy and management practices (Drenovsky et al., 2012). However, few studies have identified the impact of invasive species on the functional composition and structure of the resident community itself (Foxcroft et al., 2017; Vilá et al., 2011).

Functional diversity is an important aspect of a plant community, influencing the resilience and stability of that community in response to shifting abiotic conditions. A wide range of trait values reflects varied co-existing strategies in response to the abiotic environment, whereas low functional diversity reflects a high degree of specialization in the community potentially making that community's stability vulnerable to altered disturbance regime or resource availability (Lozanovska et al., 2018; Scott and Merritt, 2020).

One way to understand the functional composition of a community is using trait-based analyses. Compared to taxonomic approaches, trait-based approaches to studying plant communities can provide a more mechanistic understanding of response to environmental change, such as invasive species dominance or removal (Díaz et al., 2016; Drenovsky et al., 2012). Trait-based approaches focus on the morpho-physio-phenological characteristics of organisms rather than species identity to directly relate plant community response (response traits) to environmental filters (Díaz et al., 2007). Traits can be used to identify groups of species with similar strategies for dealing with environmental pressures, referred to as guilds (Diehl et al., 2017; Stromberg and Merritt, 2015) or to quantify the average and range of community strategies through functional diversity components (Laliberté and Legendre, 2010; Lozanovska et al., 2018). Both of these methods make it possible to identify ecological mechanisms of community response to species invasion and subsequent invasive species removal, in addition to providing guidance in selecting species for restoration efforts (Aguiar et al., 2011).

Over the past decade, trait-based approaches have been increasingly applied to riparian ecosystems and riparian plant communities in particular (Bejarano et al., 2018; Diehl et al., 2017; Lozanovska et al., 2018; Scott and Merritt, 2020; Stromberg and Merritt, 2015). Riparian ecosystems are highly vulnerable to species invasion (Friedman et al., 2005; Richardson et al., 2007) in part due to human-caused changes in flow regime and water availability (Mortenson and Weisberg, 2010; Naiman et al., 2005). As a consequence, many riparian corridors are increasingly dominated by not typically riparian, upland and non-native species (Catford et al., 2014, 2011; Mortenson and Weisberg, 2010). Thus, the primary objective of riparian trait studies to date has been to identify plant community responses to hydrogeomorphic conditions (Bejarano et al., 2018; Diehl et al., 2017; Lozanovska et al., 2018; Scott and Merritt, 2020; Stromberg and Merritt, 2015). Communities in topographically low-elevated fluvial landforms have been defined by ruderal strategies and anaerobic tolerance such as high specific leaf area, short height, reproductive efforts focused on many light seeds and disturbance dependent resprouting of above ground biomass (Aguiar et al., 2018; Stromberg and Merritt, 2015). Less frequently flooded terraces have been characterized by resource conservative strategies and drought tolerance such as low specific leaf area and fewer, heavier seeds (Aguiar et al., 2018; Stromberg and Merritt, 2015). To date, however, no riparian trait-based study has explicitly incorporated the influence of woody invasive species that so often dominate riparian ecosystems on plant community functional composition. Additionally, despite several studies employing a trait approach, herbaceous species are often not included in defining riparian plant guilds (Díaz et al., 2016), likely due to the effort required to collect trait data for many species. Given that herbaceous species usually comprise a much larger portion of species richness and are more varied across the landscape than woody species, this represents a large gap in our understanding of riparian plant community guilds (Viers et al., 2012).

Accounting for the complexity of invasive species interacting with varied environmental contexts has been identified as a major barrier to understanding the mechanisms behind invasive species impact on plant communities (Foxcroft et al., 2017). Plant communities with varying abundances of invasive non-native shrubs in the *Tamarix* genus (tamarisk, saltcedar) make an ideal study system for understanding the co-varying impacts of the regional and local abiotic conditions and invasive species on plant community traits. While the establishment of non-native *Tamarix* was in part facilitated by altered hydrological regimes due to dam regulation and water use (Merritt and Poff, 2010), once established, it can further alter soil salinity, fluvial processes, riparian plant composition, and wildlife habitat (Auerbach et al., 2013; Merritt and Shafroth, 2012; Ohrtman et al., 2012; Shafroth et al., 2005). The role of *Tamarix* as either passenger or driver of ecosystem change has never been definitively elucidated and today's consensus is that the responses to and effects on the ecosystem are intimately connected (Sher, 2013).

Regionally, *Tamarix* cover is more dominant in drier areas with less precipitation (González et al., 2017b; Hultine and Dudley, 2013). We would expect the traits of plant communities in overall lower precipitation areas to be different as well, reflecting a more resource conservative strategy. Local factors such as the distance to the nearest water source and the height above the river water level (both affecting flood frequency) also determine available resources and disturbance patterns, influencing the ability of *Tamarix* to thrive as well as driving the understory plant community response traits (Keddy, 1992; Sher, 2013). For these reasons, we expect *Tamarix* cover to covary with local and regional factors and that all these factors combine to drive guild cover and functional diversity.

Understanding *Tamarix*-dominated plant communities is critical because of the spatial extent of *Tamarix* (Jarnevich et al., 2013). *Tamarix* is now dominant in most riparian corridors of the southwestern U.S. (Friedman et al., 2005) where its control is commonly the object of riparian management (González et al., 2015, 2017b; Shafroth et al., 2005; Sher, 2013). In 2001 *Diorhabda carinulata* (northern tamarisk beetle), a specialist insect herbivore feeding exclusively on *Tamarix,* was released as a biocontrol agent (DeLoach et al., 2003). The varying impact of *Diorhabda* on *Tamarix* canopy cover (Nagler et al., 2018) provides a gradient of *Tamarix* cover that allows us to examine the impact of varied cover on the plant community.

Here, we use a trait-based approach to understand the functional composition of riparian plant communities in river reaches with varied levels of *Tamarix* cover. Specifically, we ask 1) What traits are most important in defining riparian plant guilds? Based on previous work in riparian plant communities, we hypothesize that the guilds present in these plant communities will be primarily defined by their resource acquisition traits and disturbance tolerances (Stromberg and Merritt, 2015). 2) How do the abundances of each guild and the traits defining guilds vary along a gradient of invasive tree cover and abiotic conditions? Given that *Tamarix* increases stress in a plant community by increasing soil salinity and shading, but also occurs in disturbed areas we hypothesize that stress and disturbance will be stronger filters in heavily *Tamarix* dominated plant communities than in communities where it is less prevalent. We predict that guilds defined by stress tolerance with low specific leaf area and opportunistic guilds with low seed weight will be more likely to occur in more heavily *Tamarix* dominated sites as well as sites higher above the water and in hotter, drier regions. 3) How does the functional diversity of the plant community respond to combined gradients of invasive tree cover and abiotic condition? We hypothesize that *Tamarix* adds novel environmental filters, making plant communities more specialized. We therefore predict that functional diversity measures will decrease as *Tamarix* cover increases in conjunction with local and regional co-varying factors. This study is the first to explicitly compare guilds from all woody and herbaceous species across a range of invasive tree cover in a riparian system, integrating both regional and local abiotic influences. We discuss the implications of our results for the management of *Tamarix*-dominated riparian zones. Appropriate species selection has been identified as a key component of revegetation success in riparian systems (Sher et al., 2010). Not only describing but understanding how an invasive species have changed the plant community is a crucial first step in effectively conserving and restoring ecosystem function.

Methods

Study area

We selected 95 sites ranging from low *Tamarix* cover, native-dominated plant communities to plant communities with overstories made up entirely of *Tamarix*. Sites were within the Upper Colorado River Basin along the main stem of the Colorado, and two of the main tributaries: Dolores and Green rivers, as well as in small order streams in the Colorado catchment (Figure 1-1). We divided the study area into six regions based on river and geographic location: Colorado river in Utah, Colorado river in Colorado, the

Dolores river above and below the San Miguel river and the green river north and south. The San Miguel is a free-flowing river that empties into the Dolores and flows south of the confluence and so the river and plant communities are expected to be different north and south of this point. All three rivers are regulated by dams and water diversions (Merritt and Poff, 2010). Each site corresponded to a single geomorphic unit, such as a channel margin, floodplain, terrace, off-channel depression or sandbar, which captured general differences in site characteristics such as flood regime. These sites were from a large-scale study assessing the response of vegetation to *Tamarix* removal across the southwestern United States (González et al., 2017b). Sites used in the current study were exposed to *Diorhabda* biological control for five to nine years at the time of sampling, with no other mechanical or chemical removal methods used. Thus, there were gradients of *Tamarix* cover that were both dependent and independent of abiotic growing conditions. Time since first defoliation by biocontrol beetles is not necessarily correlated to lower *Tamarix* cover as defoliation is a cyclical process (Henry et al., 2018; Nagler et al., 2018).

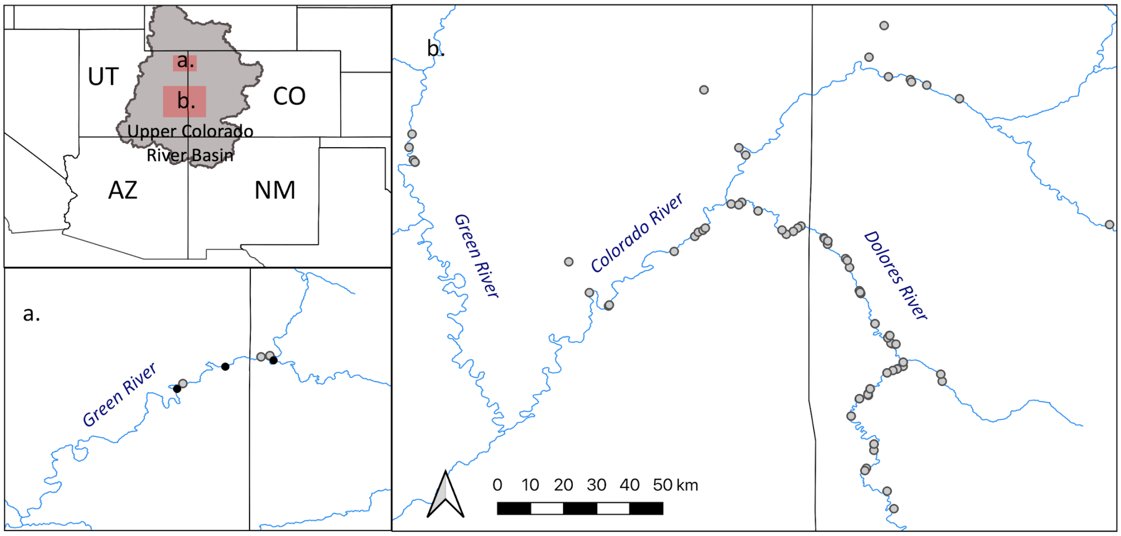

Figure 2-1: Map of study area. Grey points represent study sites. UT-Utah, CO-Colorado, AZ-Arizona, NM-New Mexico.

Data collection

Plant community and traits

We used floristic and environmental data compiled by González et al. (2017) to determine the plant community and abiotic conditions of each site. Sites had been sampled at various times between 2012 and 2014; for those sites sampled multiple years, the present study makes use of only the final year of sampling. We identified 139 taxa (134 species and 5 taxa identified to genus level only) in our sites (Table S2-1). We used species data from González et al. (2017) that was collected using the line intercept method to calculate percent cover (Bonham, 1989).

For these species, we collected data on 14 traits related to resource acquisition, stress tolerance and reproductive strategy using online databases and literature searches (Table 2-1). We chose these traits based on previous studies that have shown them to be relevant for defining riparian plant guilds (Diehl et al., 2017; McCoy-Sulentic et al., 2017; Scott and Merritt, 2020; Stromberg and Merritt, 2015). While functional *traits* are defined as quantitatively measured plant traits used to describe an individual's physiological performance, functional *attributes* are categorical or semi-quantitative estimates that describe a species tolerance to the environment or general morphology (Hough-Snee et al., 2015). In addition to the 14 traits, we compiled data on five attributes (Table 2-1) to get a full picture of plant strategies in response to environmental gradients. For simplicity we will use the term "trait" to refer to both functional traits and attributes in this paper.

We created the plant trait database primarily using plant trait values from Palmquist et al., (2017), the TRY database (Kattge et al., 2020; Table S2-2.1; Table S2-2.2), which is a global database of plant traits, the USDA plants database (USDA, NRCS, 2020), and regional field guides (Whitson et al., 2012). We obtained seed weights from the online database of the Herbarium Catalogue, Royal Botanical Gardens, Kew (Royal Botanic Gardens Kew, 2020). We searched several additional databases if trait values were not found in primary databases: FLOWBASE (Aguiar et al., 2013), eHALOPH (Santos et al., 2016), Fire Effects Information System (FEIS, 2020) and Baseflor (Julve, 2015). Finally, if traits were still not found we conducted a literature search using the species scientific name and trait name as well as common name and trait name in Web of Science and Google Scholar. Reference information can be found in Table S2-3. When we found multiple sources for a trait value, we used the value collected from plants geographically closest or ecologically most similar to the study area (semi-arid riparian ecosystem). For instances where a plant was only identified to genus (five instances), we used USDA plants and regional plant books to identify the most common species in the area and collected trait data for that species. In general, species trait values were similar between species of the same genus in the study area. We will refer to all taxa as species from here forward for simplicity.

We excluded species that were missing eight or more trait values from the database. We ensured that at least 80% of plant cover was represented at each site with the remaining species (not including *Tamarix*) (Pakeman and Quested, 2007). If removing a species reduced cover explained below 80%, we removed that site from the analysis. We removed 14 species and 3 sites, resulting in 125 plant species (Table S2-1) across 95 sites ultimately included in our analysis.

Table 2-1: Traits and attributes (marked with an asterisk*) used to determine riparian plant guilds.

Trait	**Description/units/classes**	**Variable type**	**Dominant life history category**
Specific leaf area (SLA)	Square centimeters per gram (leaf area/dry leaf weight)	Continuous	Resource acquisition/Stress tolerance
Average height at maturity	Meters	Continuous	Resource acquisition/Disturbance tolerance
Growth form	Forb/shrub/tree	Categorical	Resource acquisition

Growth rate	Speed of growth once established: Slow/Moderate/Rapid	Ordinal	Resource acquisition
Salinity tolerance*	Level of soil salinity that reduces plant growth: None/Low/Medium/High	Ordinal	Stress/Disturbance tolerance
Anaerobic tolerance*	Tolerance to anaerobic soil conditions: None/Low/Medium/High	Ordinal	Stress/Disturbance tolerance
Drought tolerance*	Tolerance to drought conditions: None/Low/Medium/High	Ordinal	Stress/Disturbance tolerance
Fire tolerance*	Ability to resprout, regrow, or reestablish from seed bank after a fire: None/Low/Medium/High	Ordinal	Stress/Disturbance tolerance
Shade tolerance*	Tolerance of shade conditions: Intolerant/Intermediate/Tolerant	Ordinal	Stress/Disturbance tolerance
Moisture use*	Ability to use available soil moisture: Low/Medium/High	Ordinal	Stress/Disturbance tolerance
Seed weight	Weight of 1000 seeds in grams	Continuous	Reproduction
Duration	Annual/Perennial	Ordinal	Reproduction
Clonal reproduction ability	Yes/No	Categorical	Reproduction
Vegetative spread rate	Speed of vegetative spread: None/Slow/Moderate/Rapid	Ordinal	Reproduction
Resprout ability	Ability to resprout after damage or fire: Yes/No	Categorical	Reproduction
Median bloom period	Median month during which species typically blooms	Ordinal	Reproduction

Total number of bloom months	Total number of months species typically blooms	Ordinal	Reproduction
Median seed period	Median month during which species typically sets seed	Ordinal	Reproduction
Total number of seed months	Total number of months species typically sets seed	Ordinal	Reproduction

Environmental Variables

We compiled climatic and hydrogeomorphic data from (González et al. (2017) and summarized this information for our study sites (Table 2-2). River metrics of river width and distance to the river water's edge were measured directly in the field or obtained using Google Earth. Topographic elevation of the site relative to the river water channel (relative elevation) was either estimated from interviewing the land manager responsible for the site or measured using a Spectra Precision Laser HL450 Laserometer© with an auto-leveling rotating transmitter (vertical accuracy = 10 cm) at the time of vegetation sampling. Additionally, Google Earth was used to obtain geographic variables of elevation from sea level. Climate metrics were obtained from the PRISM Climate Group website (accessed in 2015). The climate variables of temperature (minimum and maximum during the growing season) averaged over a 30 year period (normal) as well as during the year of sampling and average cumulative precipitation during the growing season over a 30 year period and during the year of sampling were all highly correlated to elevation at sea level and so were removed from the analyses to prevent overfitting. Cumulative precipitation during the growing season (April to

September) of the year of sampling was not correlated to any other variables and so was included in our statistical models. Composite sediment samples were taken from surface sediment at each site to calculate electrical conductivity of a saturated paste for sediment salinity.

Variables were checked for multicollinearity with a correlation matrix (Figure S2-1). Elevation was highly correlated with average precipitation and temperature (adjusted $R^2 \geq 0.7$). Of these highly correlated variables, we only included elevation in our analysis for the simplest model but interpret results in the context of all correlated environmental gradients.

Table 2-2: Average and standard deviation for each environmental variable included in the RDA and regression models. Average precipitation over a 30-year period and minimum temperature were strongly positively correlated with elevation above sea level; maximum temperature was negatively correlated with elevation above sea level (>70%). Of those highly correlated variables only elevation above sea level was included in analysis. Absolute and relative *Tamarix* cover had a 55% correlation. River width and elevation above sea level had a 53% correlation. All other variables correlate with each other at less than 50% (Table S2-4, Figure S2-1). Elevation above river water level was not used in the regression models because of a large number of missing values.

Independent Variables	**Units**	**Scale**	**Min**	**Max**	**Mean (standard deviation)**
Elevation (from sea level)	Meters	regional	1206	1714	1420 ± 121.1
Precipitation (year of sampling)	Mm	regional	83.3	248.4	203.4 ± 37.6
River width	Meters	local	2.1	199.4	43.6 ± 40.5
Distance to river water's edge	Meters	local	0	317	10.78 ± 41.0
Soil EC	uS/cm	local	30	25280	2519.1 ± 4280.4

Elevation above river water channel	Cm	local	12	450	212.5 ± 109.0
Absolute *Tamarix* cover	percent cover	local	0	100	13.0 ± 17.1
Relative *Tamarix* cover	*Tamarix* cover/total overstory cover	local	0	1	0.3 ± 0.3

Statistical analysis

Defining guilds

We used a complete linkage clustering of a Gower dissimilarity matrix based on 125 plant species and 19 traits to obtain plant guilds (Borcard et al., 2011). A Gower dissimilarity matrix is robust against missing values and allows for mixed data types (Gower, 1971). *Tamarix* was not included in the final clustering analysis due to its use as an independent variable in subsequent analyses. However, when included in preliminary clustering, *Tamarix* did alter guilds slightly. Within a range of ecologically relevant group numbers, we used an optimum average silhouette width (ASW) method to estimate the best number of clusters (Kaufman and Rousseeuw, 1990). To better visualize the guilds, we ran a principal coordinate analysis (PCoA; Legendre and Legendre, 2012) on the Gower matrix and depicted the site scores (representing species in this case) in the bidimensional space determined by the two main axes of variability of the species by trait matrix. To understand what traits defined the guilds, we included the weighted average of each quantitative trait value and centroids of qualitative traits in the plot. For each guild, we calculated the average values for each trait (Table S2-5).

To aid in interpreting the guilds, we also calculated centroids of nativity and a modified Wetland Indicator Status variable. We created this new wetland status based on the USDA Wetland Indicator Status: obligate wetland and facultative wetland were grouped as "hydric" species, facultative and facultative upland were grouped as "mesic" species and upland species were labeled as "xeric" (González et al., 2017b). Note that these categories were used to explore the guilds after they were created; they were not included in creating the clusters.

Guild cover along environmental and Tamarix cover gradients

We used redundancy analysis (RDA) to determine if plant community composition expressed as plant functional guilds could be explained by environmental variables and/or by *Tamarix* cover. RDA is a multivariate extension of multiple regression where the response variable is a data matrix, in this case, guild cover for all 9 guilds (Legendre and Legendre, 2012). Guild cover data were Hellinger transformed to account for the abundance of zero values (Legendre and Gallagher, 2001). We used all environmental variables including absolute and relative *Tamarix* cover as explanatory variables (Table 2-2). Variables were scaled prior to analyses. The significance of the RDA was assessed with a permutation test with 999 randomized runs (Legendre and Legendre, 2012). We also ran an analysis of similarities (ANOSIM; Clarke, 1993) on Bray-Curtis distance to determine if the abundance of guilds were significantly different among river regions. We further examined two of the guilds most strongly correlated with the RDA axes using generalized linear mixed effects models with log transformed guild cover as the response variable and the same set of explanatory variables as stated above using region as the random effect.

To understand the role of *Tamarix*, independent of other environmental factors, we conducted additional RDAs and mixed models using either *Tamarix* only or environment only as explanatory factors. We subtracted the full model adjusted R^2 from the sum of the environment and *Tamarix* model adjusted R^2 to identify the overlapping portion of explained variation. We then subtracted the overlapping portion from both the environment and *Tamarix* models to identify the portion explained only by each category of explanatory variable and used Venn diagrams to represent this. For all mixed effects models, we report marginal R^2 (R^2m) - the variance explained by fixed effects only, as well as conditional R^2 (R^2c) - the variance explained by both fixed and random effects.

Functional diversity measures along environmental gradients

Lastly, we calculated two metrics to estimate functional diversity. We calculated guild diversity using Shannon's diversity index. We also calculated functional dispersion – a multivariate metric of the weighted mean absolute deviation of multiple traits (Laliberté and Legendre, 2010) – using all traits included in the analysis. We plotted both indices against the first axis of the RDA to understand how measures of diversity changed along the combined gradient of climate, water availability, soil condition and *Tamarix* cover.

All statistical analyses were performed in R studio (version 1.2.1335) using R version 3.6.0 (R Core Team, 2020). The package "stats" was used to run the cluster analysis using the function “hclust”, the PCoA using the function “cmdscale” (R Core Team, 2020). The package “vegan” was used to calculate the Shannon-Weiner diversity values using the function “diversity”, the RDA using the function “rda”, the ANOSIM using the function “anosim” (Oksanen et al., 2019). The mixed effects models were conducted using the function “lme” in the package “nlme” (Pinheiro et al., 2019). Functional dispersion was calculated using the “dbFD” in the package “FD” (Laliberté and Legendre, 2010).

Results

Defining Guilds

From the 125 species included in the complete linkage clustering, we identified nine riparian plant guilds (Table 2-3). These guilds were defined based on their placement on the PCoA axes as well as average trait values for each guild (Figure 2-2; Table S2-5). The PCoA had a goodness of fit measure of 71.2%. PCoA axis 1 (47.2%) was primarily defined by the ability to reproduce vegetatively and resprout after damage or disturbance as well as duration (annual vs. perennial) and secondarily by spread rate, height at maturity, seed weight, total bloom period, and specific leaf area. PCoA axis 2 (16.3%) differentiated shrubs and graminoids (grasses and grass-like herbs), from trees and forbs and drought tolerant from anaerobic tolerant species.

The first four guilds (Table 2-3) contained plant species that cannot reproduce vegetatively and were differentiated from each other primarily by SLA. Of these four, two guilds were annuals and were further divided into a guild of forbs and a guild of graminoids. “Non-clonal annual forbs” encompassed the largest number of species. It had a wide range of SLA values, contained 65% non-native species and were primarily mesic species. “Non-clonal annual graminoids” were made up of all non-native species and also had high SLA values. Two of the non-clonal guilds were made up of perennials and were differentiated from each other primarily by SLA. The “Non-clonal resource acquisitive” guild had a high SLA and was made up of 40% non-native species, while the “Non-clonal resource conservative” guild had a low SLA and was made up entirely of native species. The next two guilds were both made up of trees. “Non-clonal drought tolerant trees” did not reproduce asexually but were mostly able to resprout following disturbances. These species had low SLA and were drought tolerant. “Clonal anaerobic tolerant trees” were mostly clonal (with the exception of *Populus fremontii*) and also resprouting. They were moderately anaerobic tolerant with medium SLAs. The two tree guilds were separated from the others by height, but height did not play a strong role in defining the understory guilds. The last three guilds all tended to reproduce clonally, not just as a response to disturbance. They were distinguished from each other by seed weight, SLA, moisture use, anaerobic/drought tolerance. “Clonal anaerobic tolerant perennials” were made up of only 10% non-native species and mostly hydric and mesic species. In contrast, clonal drought tolerant perennials were made up of 48% non-native species and contained mesic and xeric species. Finally, “Clonal resource conservative perennials” were made up of mostly native species, both xeric and mesic. Figure 2-3 shows the trait profiles of each guild.

When *Tamarix* was included in the guild analysis, the guilds changed only slightly. All tree species except *Tamarix* were grouped together. An additional guild made up of three species including *Tamarix* was identified and defined by a lack of clonal reproduction and ability to resprout in response to disturbance, as well as low shade tolerance and high salinity tolerance (Table S2-1).

Table 2-3: Riparian functional guilds identified from complete linkages cluster analysis based on a Gower distance matrix of 14 species traits and five attributes. Guilds were named based on primary traits that defined each one. Descriptions summarize traits and tolerances within each guild. n=number of species in guild. Short names are used to refer to guilds throughout text. *Graminoids are grasses and grass-like herbs (sedges and rushes) as defined by the USDA.

Guild Name	**Guild Description**	**Representative Species**	**Short Name**
Non-clonal annual forbs (n=34)	Non-clonal forbs with a wide range of SLA values and anaerobic/drought tolerances. Slow spreading annuals with midweight seeds. Some are able to resprout.	*Salsola tragus* (Russian thistle); *Kochia scoparia* (Common kochia); *Lactuca serriola* (Prickly lettuce)	Annual forbs
Non-clonal annual graminoids (n=4)	Non-clonal graminoids* with a high SLA and a range of drought/anaerobic tolerances. All are slow spreading annuals with light seeds and long bloom periods.	*Echinochloa crus-galli* (Barnyard grass); *Bromus japonicus* (Field brome); *Bromus tectorum* (Cheatgrass)	Annual grams
Non-clonal resource acquisitive perennials (n=5)	Non-clonal forbs and graminoids with a high SLA. All are slow spreading, perennials with light seeds and long bloom periods. Some are able to resprout.	*Taraxacum officinale* (Common dandelion); *Plantago lanceolata* (Narrowleaf plantain); *Elymus canadensis* (Canadian wildrye)	Acquisitive peren
Non-clonal resource	Non-clonal forbs, graminoids and shrubs with a low SLA. All	*Ericameria nauseosa* (Rubber rabbitbrush);	NC Cons peren

conservative perennials (n=16)	are slow spreading, perennials with light seeds and long bloom periods. Some are able to resprout.	*Sporobolus airoides* (Alkali sacaton); *Gutierrezia sarothrae* (Broom snakeweed)	
Non-clonal drought tolerant trees (n=3)	Non-clonal trees, many of which can resprout following disturbance. Drought tolerant with midweight seeds and low SLA.	*Morus alba* (White mulberry); *Malus spp.* (Crab apple)	Drght trees
Clonal anaerobic tolerant trees (n=7)	Clonal, resprouting trees. Moderately anaerobic tolerant with midweight seeds and medium SLA.	*Prunus virginiana* (Chokecherry); *Acer negundo* (Boxelder); *Betula occidentalis* (Water birch)	Anae trees
Clonal anaerobic tolerant perennials (n=21)	Clonal, resprouting forbs, graminoids and shrubs. All are fast spreading perennials with high moisture use, light seeds, a wide range but overall low SLA and high anaerobic tolerance.	*Phragmites australis* (Common reed); *Glycyrrhiza lepidota* (Wild licorice); *Salix exigua* (Coyote willow)	Anae peren
Clonal drought tolerant perennials (n=21)	Clonal, resprouting drought tolerant forbs. Fast spreading perennials with midweight seeds and medium SLA.	*Acroptilon repens* (Russian knapweed); *Cirsium arvense* (Canada thistle); *Convolvulus arvensis* (Field bindweed)	Drght peren
Clonal resource conservative perennials (n=14)	Clonal, resprouting drought tolerant forbs, graminoids and shrubs. Slow spreading with midweight seeds and low SLA.	*Sarcobatus vermiculatus* (Greasewood); *Agropyron cristatum* (Crested wheatgrass); *Atriplex canescens* (Fourwing saltbush)	C Cons peren

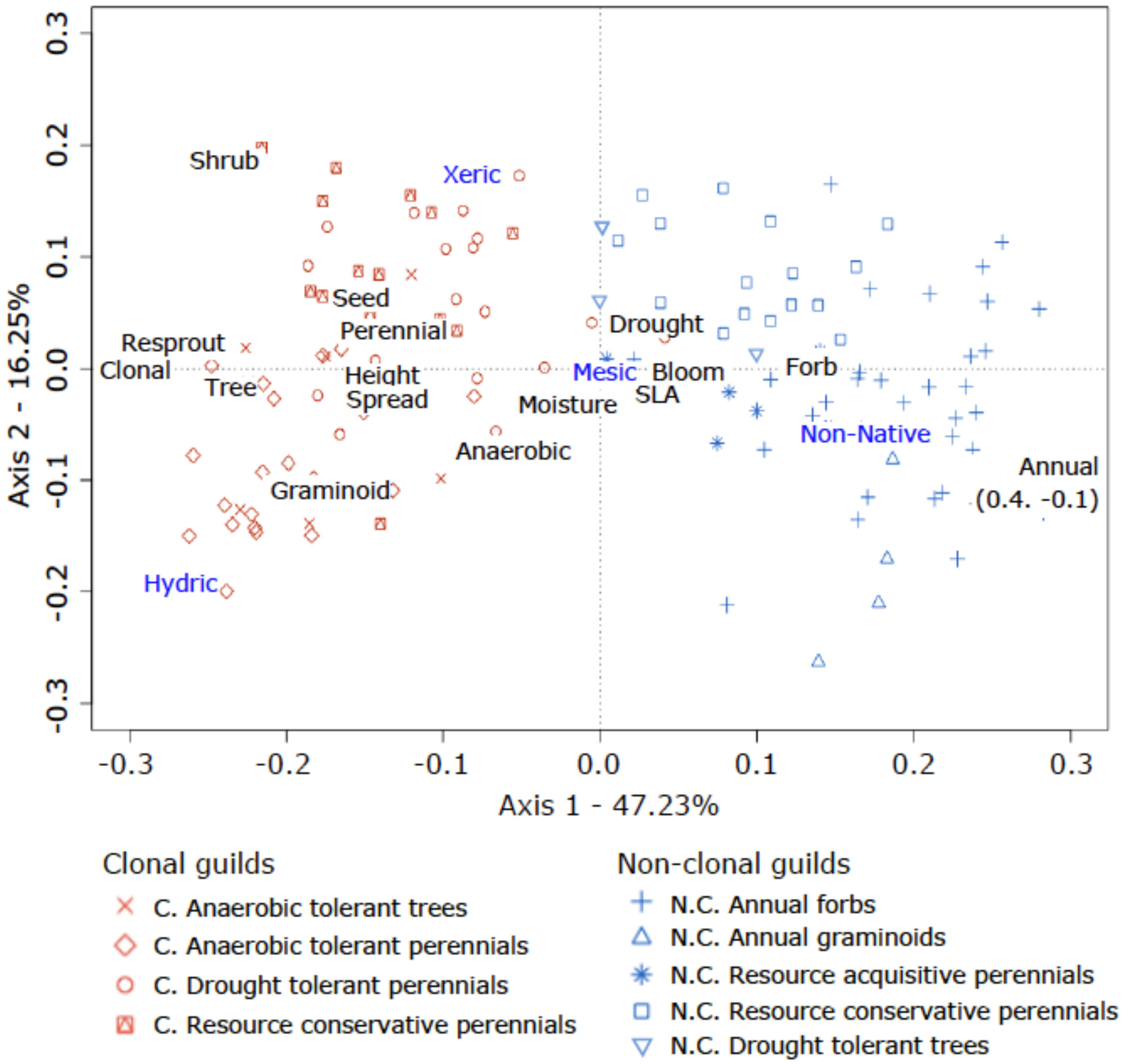

Figure 2-2: PCoA ordination of 125 species based on 19 traits. Colors distinguish the major split of reproductive strategy with clonal guilds in red and non-clonal in blue. Symbols represent guilds. Weighted average traits of continuous traits and centroids of categorical traits are plotted to interpret axes. While all traits were included in the cluster analysis, only the ones with a strong impact on the axes are displayed. All weighted averages and centroids were multiplied by two in order to better visualize the relationship. While the variables “hydric”, “mesic”, “xeric” and native vs. non-native (in blue text) were not included in the cluster analysis, they are plotted to aid in interpretation of the guilds.

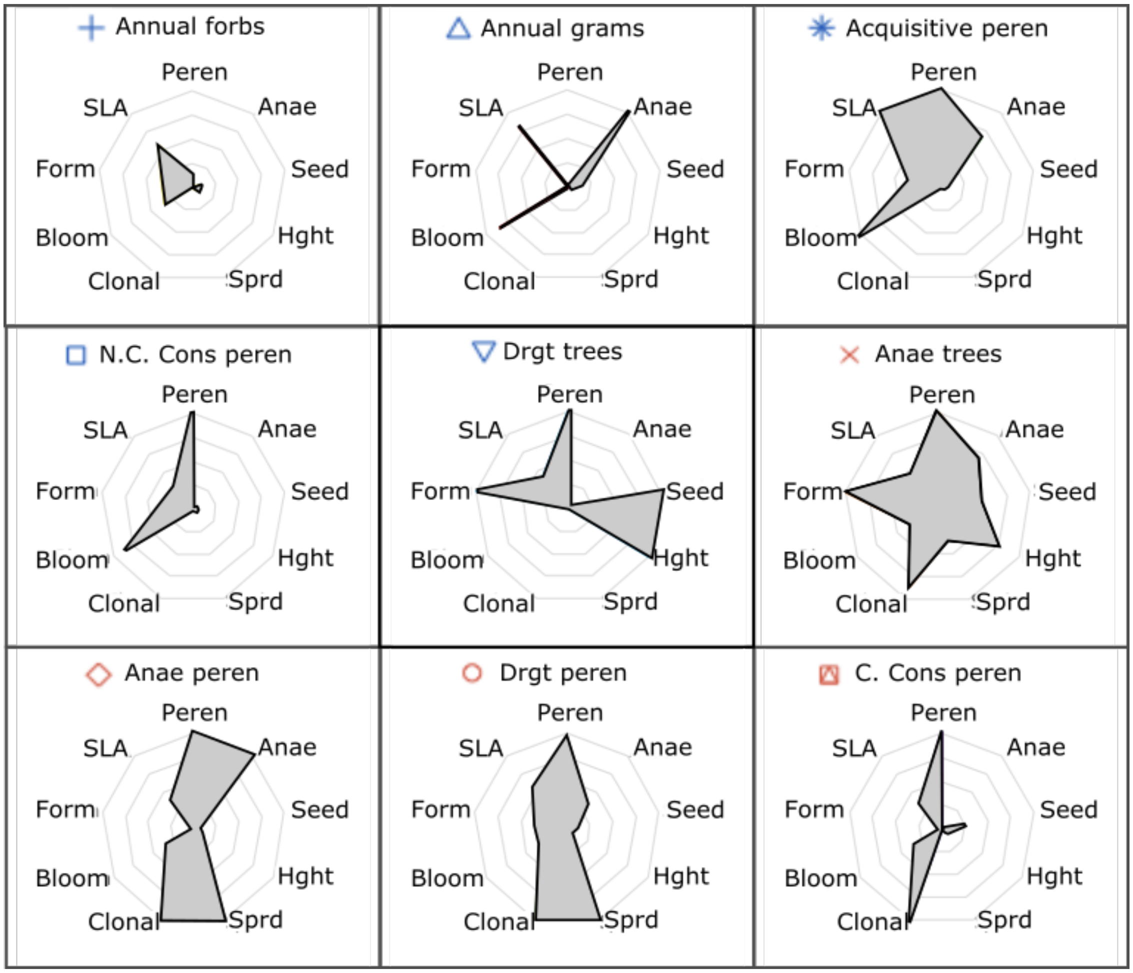

Figure 2-3: Radar plots showing the trait profiles for each guild. Peren (Perennial vs. Annual), Anae (Anaerobic tolerance, Seed (Seed mass), Hght (Height at maturity), Sprd (Spread rate), Clonal (Ability to reproduce vegetatively), Bloom (Total bloom period), Form (life form), SLA (Specific leaf area). The grid lines represent continuous and ordinal values scaled to 0-100. For categorical variables - Peren (0 = annual, 100 = perennial); Clonal (0 = no, 100 = yes). For full guild names refer to Table 3.

Guild cover along environmental gradients

Guild cover varied along a combined gradient of relative and absolute *Tamarix* cover, elevation above river water level, distance to the river water's edge, total precipitation during the year of sampling and elevation above sea level (a.s.l.; RDA1; 23%; Figure 2-4). At low values of RDA1, sites tended to be higher in elevation a.s.l., and so also cooler with higher average precipitation (variables highly correlated to elevation a.s.l.), with low soil salinity, elevation above river water channel, distance to water and *Tamarix* cover. High values of RDA1 were associated with hotter, drier sites, farther from water with higher soil salinity and higher *Tamarix* cover. "Non-clonal annual forbs" (Annual forbs), "Non-clonal resource conservative perennials" (NC cons peren) and "Non-clonal annual graminoids" (Annual grams), increased with increasing RDA1 values. These three guilds had the highest proportion of non-native. Absolute *Tamarix* cover and relative *Tamarix* cover are strongly correlated with the two non-clonal guilds with a high percentage of non-native species - "Non-clonal annual forbs and annual graminoids", while the "Clonal drought tolerant perennials" were more strongly associated with increasing distance to water. At lower values of RDA1 there was a greater abundance of Clonal Anaerobic Perennials (Anae peren). RDA2 (7%) described a gradient of elevation above sea level and soil EC. Higher elevation sites with lower soil EC had higher abundances of both "Clonal resource conservative perennials" (C cons peren) and "Clonal anaerobic trees" (Anae trees). While the gradient of abiotic factors covaried with *Tamarix* cover, *Tamarix* cover alone explained almost 9% of the 31.5% variation in guild cover explained (Figure 4, Table S2-6).

All regions had significantly different guild cover from all other regions except for the Dolores river above versus below the San Miguel river and the Green River - south versus Colorado river in Utah (ANOSIM; Table S2-7), but ANOSIM values were not exceptionally low, which was consistent with some degree of overlap in guild composition (ellipses, Figure 2-4).

Mixed models showed that “Clonal anaerobic perennials” (Anae peren) increased with decreasing relative *Tamarix* cover and distance to water (Table 2-4). Twenty three percent of variation in guild cover was explained by relative *Tamarix* cover alone, while 11% was explained by only distance to river water’s edge. Fifteen percent of variation in guild cover was explained by both relative *Tamarix* and distance to water (Table S2-8). Cover of “Non-clonal annual forbs” (Annual forbs) was significantly positively correlated to relative *Tamarix* cover, and no other variables (Table 2-4).

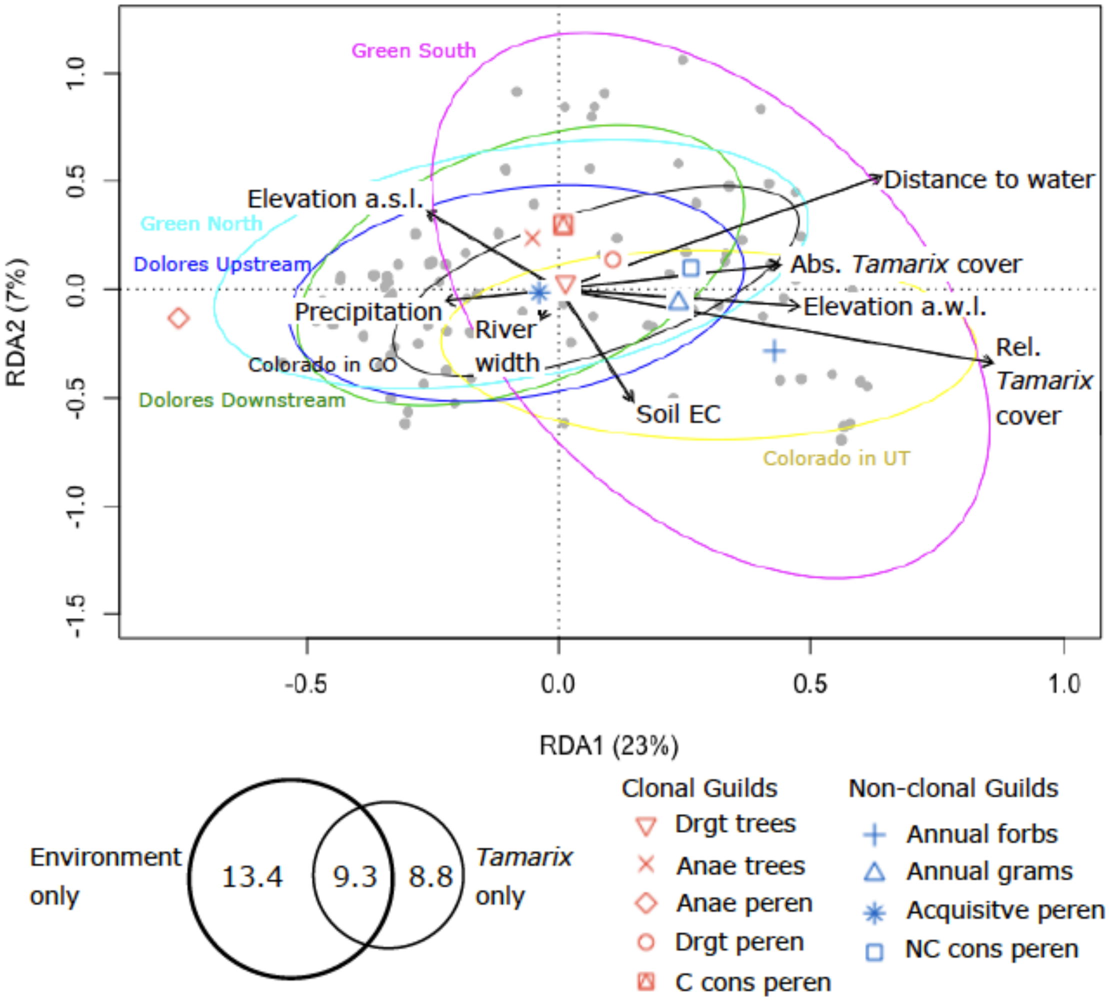

Figure 2-4: RDA of a Hellinger-transformed matrix of guild abundance (scaling=2) with 31.5% of total variability explained (df=8, F=6.41, p=0.001). Ellipses include 70% of the sites in each region. Symbols represent the position of the nine guilds in the bidimensional space determined by the first to axes of constrained variability and were multiplied by 0.8 for visual clarity. Venn diagram shows the portion of variation explained by environmental variables and *Tamarix* (full model details are in Table S2-6). Region abbreviations: Green South - southern reach of Green river, Green North - northern reach of Green river, Dolores Upstream - Dolores river upstream of the confluence with the San Miguel river, Dolores Downstream - Dolores river downstream of the confluence with the San Miguel river, Colorado in CO - Colorado river and low-order tributaries in Colorado, Colorado in UT - Colorado river and low-order tributaries in Utah. Environmental variable abbreviations: Abs.(absolute) and Rel.(relative) *Tamarix* cover, Elevation a.w.l. (above river water level), Soil EC (electroconductivity), Elevation a.s.l. (above sea level).

Table 2-4: Statistical results for general linear mixed models of “Clonal anaerobic perennials” and “Non-clonal annual forbs” - the two guilds most strongly correlated to RDA1, selected by backward and forward selection using the Akaike information criteria. Guild cover of both models was log transformed, as were explanatory variables marked with an asterisk* to improve model residuals.

Clonal anaerobic perennials	**Value**	**Std.Error**	**DF**	**t-value**	**p value**	**R^2m**	**R^2c**
(Intercept)	2.608	0.203	87	12.857	0.00	0.49	0.53
Distance to water*	-0.636	0.133	87	-4.777	0.00		
Relative *Tamarix* cover	-0.822	0.137	87	-6.009	0.00		
Non-clonal annual forbs						0.15	0.15
(Intercept)	2.000	0.118	85	16.877	0.00		
Distance to water*	-0.227	0.127	85	-1.794	0.08		
Soil EC*	0.210	0.135	85	1.560	0.12		
Relative *Tamarix* cover	0.409	0.130	85	3.141	0.00		
Soil EC*:Rel. *Tamarix* cover	-0.204	0.122	85	-1.670	0.10		

Diversity measures compared to RDA axis 1

Guild and overall functional diversity (as measured by functional dispersion) were highest at intermediate levels of stress and disturbance – where RDA1 is near 0 (Figure 2-5). At the highest levels of *Tamarix*, distance from water, elevation above water and EC, both measures of diversity are at their lowest. At the highest elevation and precipitation values where *Tamarix* tends to be lower, both measures of diversity are also low. Intermediate values along RDA1 have the highest levels of diversity. We did not identify any other pattern for functional diversity at RDA2, RDA3 and RDA4 (not shown).

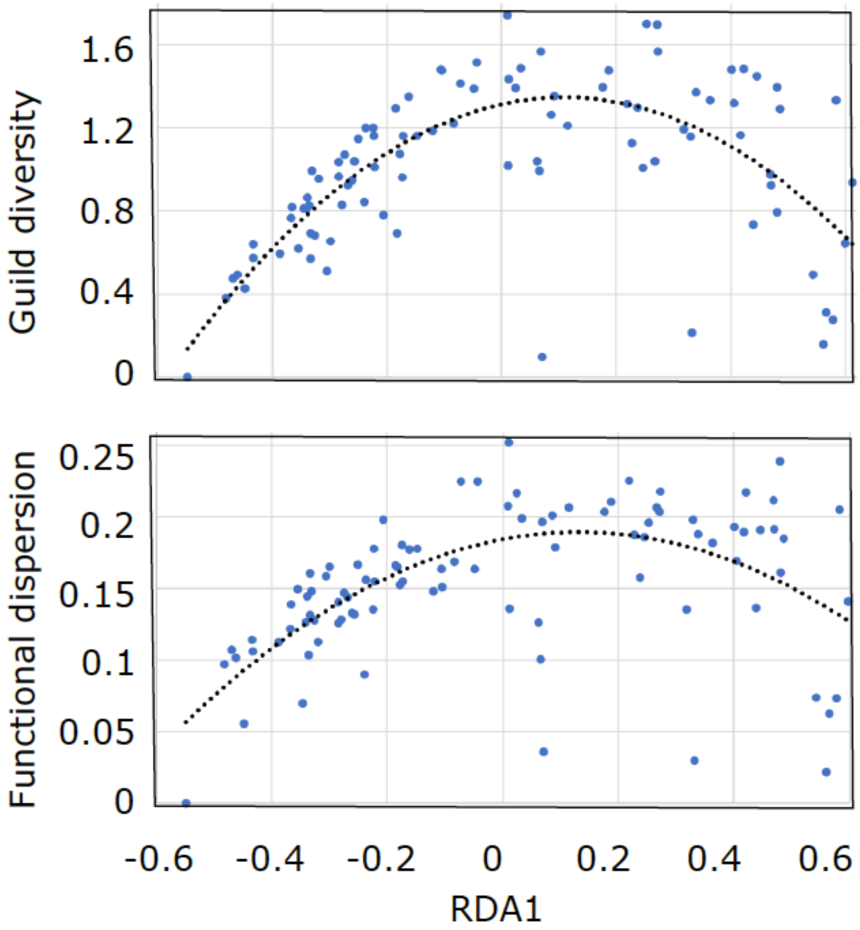

Figure 2-5: RDA1 vs. Guild Diversity and Functional Dispersion (calculated using all traits). A quadratic mixed effects model fit by maximum likelihood was used to determine how RDA1 influenced guild diversity (R^2m=0.43, R^2c=0.62, df=87, t=13.40, $p<0.0001$) and functional dispersion (R^2m = 0.35, R^2c =0.38, df = 87, t=22.17, $p<0.0001$).

Discussion

To the best of our knowledge, this is the first time distinct guilds in riparian plant communities including both woody and herbaceous vegetation have been identified along a gradient of invasive tree cover. The presence of the biocontrol agent *Diorhabda* provided a gradient of *Tamarix* cover without the confounding factors of additional disturbances that other removal methods create. We were able to show that the functional composition of riparian plant communities strongly follows a covarying gradient of climate (represented by absolute elevation and precipitation), local water availability, soil salinity and *Tamarix* cover. Previous studies have shown that *Tamarix* responds to these gradients (e.g., Auerbach et al., 2013; Merritt and Poff, 2010 and many others), making it difficult to differentiate the influence of the invasive species on the plant community from the influence of the abiotic environment. However, we found that there was variability in guild composition explained by *Tamarix* cover that was not explained by environmental variables alone. These results have added to our understanding of how *Tamarix* impacts the plant community in combination with and in addition to the abiotic environment.

Disturbance and stress tolerance traits define riparian plant guilds

Our finding that guilds were primarily defined by reproductive strategies supports our hypothesis that disturbance tolerance strategies are important in riparian plant communities, consistent with previous studies of riparian plant guilds (Aguiar et al., 2018; Bejarano et al., 2018). We found a distinct split in reproductive strategy with clonal, perennial guilds also having heavier seeds, while non-clonal guilds (both annual and perennial) tending toward lighter seeds. Clonal species tend to have a higher investment in below ground biomass and to be more able to survive flooding disturbance than non-clonal species (Martínková et al., 2020). Phenological traits have also been shown to be especially responsive to disturbance (Aguiar et al., 2018); in the present study, median bloom period was not important in defining guilds, but total bloom period was, further suggesting that what is important in defining guilds in our study area is the amount of investment in reproducing by seed as compared to reproducing vegetatively.

Within each of these types of reproductive strategy, we found a range of drought and anaerobic tolerance as well as resource conservative versus resource acquisitive strategies. Two non-clonal guilds ("Non-clonal annual graminoids" and "Non-clonal resource acquisitive perennials") had high SLA values and high anaerobic tolerance, suggesting adaptation to frequently flooded areas, despite not being able to reproduce asexually. "Non-clonal annual forbs" are categorized as drought tolerant, while also having moderately high SLA values suggesting shade tolerance in areas where water is limited. In our study, the importance of height is primarily due to the inclusion of trees. However, for herbaceous species, clonal, perennial guilds tend to be taller than non-clonal guilds. Among herbaceous species, greater height can represent rapid growth between disturbances, or in slow growing species, infrequent disturbance (Westoby, 1998).

The differentiation of these understory guilds provides insight that is not possible when only examining woody species whose growth form can only be broken down into trees or shrubs. Given that most other riparian guild studies have only included woody species, this represents a major contribution to our understanding of riparian plant guilds.

Tamarix cover encourages either resource conservative or shade tolerant strategies

With decreasing elevation above sea level (and so decreasing precipitation and increasing temperature), distance to water, soil salinity and *Tamarix* cover (RDA1), cover of non-clonal guilds with a strong focus on sexual reproduction as evidenced by light seeds and long bloom periods also increased. Longer flowering confers a greater tolerance to low predictability of a favorable reproductive period (Bourgeois et al., 2019). One clonal guild was positively associated with RDA1 - “Clonal drought tolerant perennials” but was more strongly associated with distance to water than *Tamarix* cover. It is made up of 48% non-native species and represents the perennial drought tolerant weedy species commonly associated with dry riparian sites. The placement of this guild in the RDA (directly on the trajectory of increasing distance to water) suggests that this guild is present across the landscape regardless of *Tamarix*.

While *Tamarix* covaries with the environmental conditions that favor a more resource conservative strategy, its dominance has created unique filters that the plant community must respond to. In this paper, we show that *Tamarix* favors an understory community defined by classic “weedy” traits of continuous seed production and short life cycles and moderate to high SLA (Bourgeois et al., 2019). High SLA can reflect an ability for rapid resource acquisition, but under a dense canopy can also confer shade tolerance to low growing species (Westoby, 1998). Given that these guilds are associated with lower resource environments, we can interpret the mid to high SLA of the two guilds most strongly associated with higher RDA1 values to be an adaptation to shade rather than rapid resource acquisition. *Tamarix* can create an overstory canopy in resource poor environments where there would not otherwise be one, additionally it has a higher and more frequent litter fall than native tree species and can increase soil salinity (Hultine and Dudley, 2013). That "Non-clonal annual forbs" were only marginally significant in their correlation with distance to water or soil EC but had a very significant positive relationship with *Tamarix* suggests that this guild would not otherwise be so prevalent in these drier riparian sites if it were not for the cover of *Tamarix*. The addition of this novel filter also explains the low diversity at the positive end of RDA1 – lower elevation (and so increasing temperature and decreasing precipitation) distance from water, soil salinity and *Tamarix* cover

Our result that cover of "Clonal anaerobic perennials" was negatively correlated to both distance to water and *Tamarix* cover (and without interactions) shows that this guild decreases with increasing *Tamarix* cover, independent of abiotic conditions. Although *Tamarix* is generally associated with sites farther from water, when it does grow directly along riverbanks *Tamarix* has effects on the plant community that differ from that of the woody species historically dominating these communities. In addition to creating dense canopies of shade and altering soil salinity, *Tamarix*, especially when defoliated, alters the litter mat which may interfere with seed germination (González et al., 2020b). The pattern described here highlights the role of *Tamarix* as both a passenger and driver of ecological change. *Tamarix* can thrive despite an altered flow regime where native vegetation suffers, with its abundance changing along climatic and other regional and local environmental gradients. Once established, it also creates an overstory that is different from the native riverbank plant community.

Functional diversity patterns showed that plant specialization increased at either extreme of a main gradient created by abiotic conditions and *Tamarix* cover. This finding supports the intermediate disturbance hypothesis (Sousa, 1979) from a functional standpoint. Functional diversity, both in terms of guild diversity as well as functional dispersion, was at its highest at intermediate levels of likely flood disturbance and lowest both in sites where one would expect very little or quite frequent flooding.

Applications for conservation of biodiversity

The guilds presented here can be referred to when doing active revegetation in restoration projects to identify species with the most appropriate traits given a site's characteristics or for a desired plant community type (Laughlin, 2014). We determined which guilds contained a large portion of non-native understory species, which could be used to guide managers to choose native species with appropriate traits (i.e., from the same guild) to compete with noxious species in restoration and land management. Restoring plant communities previously dominated by *Tamarix* may require selecting native or desirable species within guilds of likely secondary invaders that could have a strong seed bank in these sites. Removal of *Tamarix* increases light availability, but also makes sites hotter and drier because of increased sun exposure (Bateman et al., 2013). This would likely shift the understory guild dominance from shade tolerant annual forbs and graminoids toward the "Clonal drought tolerant" guild which is made up of many weedy species typical of the riparian southwest (e.g. *Acroptilon repens*, *Cirsium arvense*) but which have a lower SLA and a longer lifecycle and so are more adapted to drier sites. While further studies are needed to test this hypothesis, we recommend beginning revegetation with native species from this guild (e.g. *Artemisia dracunculus, Solidago occidentalis*) to mitigate potential secondary invasions.

Conclusions

This study is the first time that the response of plant communities to the largest plant invasion in North American riparian ecosystems was analyzed using a functional approach. We showed that a well-known covarying gradient of *Tamarix* cover with local and regional environmental variables also explains a large portion of the functional composition of riparian plant communities. Additionally, we showed that *Tamarix* cover creates a unique filter of reduced light availability in areas that would otherwise have little canopy and increased litter fall. While large trees such as cottonwoods are native to this system, they do not form dense, closed canopies the way *Tamarix* does, especially since flow regulation has depauperated their populations. This is an important consideration for *Tamarix* removal and revegetation projects. Further studies are warranted to better understand the drivers of guild abundance in *Tamarix*-dominated sites. In particular, we were not able to include key factors such as flooding frequency and depth to groundwater that would more accurately estimate water availability and disturbance. Additionally, this study represents a snapshot of sites at a particular point of defoliation and so we cannot speak to the impact of biocontrol defoliation itself. *Tamarix* defoliation is cyclical, both intra- and inter-annually and spatially patchy (Henry et al., 2018; Nagler et al., 2018). Understanding the functional impact of defoliation on plant communities will be an important aspect of future research.

This functional framework sets the stage for future research addressing the ongoing changes to this system (and others) such as *Tamarix* removal via active methods as well as the continued unfolding of biocontrol defoliation, further climate change and flow regime alteration. Understanding the relationship between the response traits included in this study and effect traits that ultimately influence ecosystem function will also be a crucial step to anticipate ecosystem service alteration as plant communities change. Traits will also serve to define fundamental properties of *Tamarix*-dominated systems, such as ecosystem stability and complexity, as well as their response to human intervention.

Citation Information

Henry, A.L., González, E., Bérenger, B., and Anna A. Sher. In review. Cover of an invasive tree covaries with environmental factors to explain the functional composition of riparian plant communities. Oecologia.

Chapter 3 Functional diversity is a more sensitive indicator than species diversity of plant community response to biocontrol of an invasive tree

Summary

Monitoring plant community response to invasive species control is a crucial aspect of ecological restoration, but species-based approaches are limited in that they do not reveal the underlying mechanisms driving plant community changes. Particularly, in the case of biological control where the impact on the target species is both spatially and temporally varied and not controlled by land managers, it is important to be able to anticipate broader ecological impacts of invasive species control. This study examines the effect of a defoliating biocontrol beetle on *Tamarix*-dominated plant communities in the southwestern U.S. Using univariate and multivariate functional metrics, we asked, what is the functional response of plant communities over time in areas of *Tamarix* biocontrol? We also sought to determine whether functional and species diversity followed similar trajectories. We found that trait values changed little in response to a second cycle of defoliation, however, specific leaf area and height were both reduced coinciding with a flood that occurred during the study. We found a larger range of height values in sites with less *Tamarix* cover, suggesting that *Tamarix* removal may lead to a more

structurally complex plant community. The range of all trait values as measured by functional dispersion followed a similar trajectory to species diversity but was a much more sensitive indicator of plant community change in response to both time and *Tamarix* cover. This study is the first to report the functional response of the plant community to biocontrol of *Tamarix* and confirms previous studies that higher levels of *Tamarix* cover are associated with more functionally specialized communities. This work is important for understanding the impact of invasive species and for anticipating plant community response in sensitive conservation areas where defoliation of *Tamarix* may lead to changes in ecosystem function.

Introduction

To measure ecological restoration success, it is common to use species diversity, changes in abundance of historically dominant species, or increases in native species richness (González et al., 2015; Wortley et al., 2013). Similarly, these approaches are often used in monitoring the impact of invasive species management via biological control (biocontrol) on the broader plant community (Schaffner et al., 2020; Sher et al., 2018). However, examining responses of the plant community in terms of species composition does not always adequately reveal the mechanisms of species response to biocontrol. This is because species are not a direct response measure of environmental condition, rather their presence is a consequence of the traits they possess (Keddy, 1992). Thus, a trait-based approach provides a direct link to understand the environmental filters driving community assembly. Despite this potential, however, to our knowledge a trait-based approach has never been used to study the long-term response of plant communities to biocontrol before now.

The trajectories of species diversity and functional diversity are context dependent (Mayfield et al., 2010). As such, trait-based approaches are increasingly used to monitor and understand the effects of ecosystem restoration, including invasive species management on biotic communities (England and Wilkes, 2018; González et al., 2015; O'Leary et al., 2018). Among recent restoration projects that use both species and functional approaches, some have found that functional metrics respond more strongly to restoration measures than species-based approaches (e.g., Woodcock et al., 2011), while some studies have found that species diversity measures respond more strongly to restoration (e.g., Pilotto et al., 2019). However, in both cases knowledge of the functional responses provided mechanistic insight that could be further linked to ecosystem function.

In the case of biocontrol of a dominant invasive species, resource availability is altered (increased light and nutrients after removal) and environmental stressors may change (e.g., increased temperature, reduced soil moisture) thus altering the filters that select for specific traits and subsequently, the functional composition of the community (Bateman et al., 2013; Keddy, 1992; Seastedt, 2015). In a species-poor environment, the relaxation of environmental filters caused by the removal of a dominant invasive species may lead to an increase in species diversity (particularly weedy species), without a parallel increase in functional diversity if all the new species are similar (Mayfield et al.

2010). Alternatively, the removal of a dominant invasive through biocontrol may shift the community from shade tolerant species to stress tolerant species that can cope with a hot, dry environment (Suding and Goldberg, 2001). Ultimately, species diversity may be similar, but the trait values may have changed drastically. Even in cases where species and functional diversity do follow a similar pattern, it is still advantageous to use a functional approach to complement an understanding of the taxonomic structure of the community (Funk et al. 2017; Laughlin 2014). Understanding the underlying mechanisms of plant community shifts in response to invasive species removal facilitates effective follow-up management and the ability to predict the cascading effects on broader ecosystem functions.

We examined plant community traits in response to biocontrol defoliation of non-native, invasive *Tamarix*, a Eurasian shrubby tree that has successfully invaded North American riparian systems (Nagler et al., 2011). In 2001 *Diorhabda* spp., a specialist insect herbivore feeding exclusively on *Tamarix*, was released as a biocontrol agent (DeLoach et al., 2003). The rapid spread of *Diorhabda* has generated concern over the plant community and ecosystem impacts of reduced *Tamarix* cover (e.g., evapotranspiration: Nagler et al., 2014, wildlife use: Sogge et al., 2013). The varying impact of *Diorhabda* on *Tamarix* has been geographically unpredictable and can change canopy cover dramatically, altering light availability, microsite temperature and surface evaporation (Bateman et al., 2013; Hultine et al., 2010a; Nagler et al., 2018). Previous research has shown a highly varied response of plant communities to *Tamarix* defoliation (González et al., 2020a, 2020b, 2017a; Kennard et al., 2016; Sher et al., 2018).

The immediate effects of biological control can seem drastic as the biocontrol agent encounters a large food source and defoliates intensively. However, long-term (a decade or more) effects of biocontrol may be less dramatic as the target species and biocontrol agent relationship stabilizes. To date two studies have reported the response of plant communities to *Tamarix* biocontrol defoliation from a taxonomic perspective over a longer period (8-10 years following defoliation (González et al., 2020a, 2020b). González et al. (2020a) reported plant community response to a first cycle of *Tamarix* biocontrol along the Virgin River in AZ and found that *Tamarix* was largely replaced with the native shrub *Pluchea sericea* and that there was a temporary increase in opportunistic understory species. Along the Colorado River near Moab UT, González et al., (2020b) examined the plant community response to a second cycle of defoliation and found a decline and recovery of herbaceous species, but overall, very little change in species diversity during this time.

While these species-based studies have improved our understanding of the impact of biocontrol defoliation on *Tamarix* dominated plant communities, the underlying mechanisms driving these changes remain unclear. In this study we identified functional trajectories of plant communities in response to *Tamarix* biocontrol in a second cycle of defoliation to complement the taxonomic study done by González et al., (2020b) in the Upper Colorado River near Moab, UT. We sought to determine (1) if averages and ranges of key individual response traits as well as multivariate measures of functional diversity changed (A) over time and (B) in response to biocontrol defoliation. Henry et al., (In Review) showed that *Tamarix*-dominated communities tend to be more specialized in terms of reproductive strategies and physiological traits. We therefore hypothesized that as *Tamarix* was removed, communities would become more functionally diverse. Given that *Tamarix* biocontrol has been associated with an increase in microsite temperature and surface evaporation (Bateman et al., 2013) we expected to find more stress tolerant characteristics as a result of defoliation. Alternatively, if the understory plant community has stabilized following the first cycle of defoliation, we would expect little change specifically in response to the defoliation event. We also sought to determine (2) how trajectories of species diversity differ from functional diversity in response to biocontrol. Given that *Tamarix* was defoliated but then recovered in this study area, we hypothesized that overall functional diversity would remain stable, but that specific trait values would change as the environmental filter shifted from shade tolerance to stress tolerance. Therefore, we expected to see a strong correlation between species and functional dispersion.

Methods

Study area

This study includes 10 *Tamarix*-dominated sites along two reaches of the Upper Colorado River near Moab, UT selected for long-term monitoring of vegetation response to biocontrol defoliation (González et al. 2020b; Figure 3-1). The study area has a semi-arid climate with a mean daily temperature of 14° C and mean annual precipitation of 241 mm (U.S. Climate Data, 2019). This section of the Colorado River has been flow regulated since the 1950's and so experiences lower peak flows and decreased summer flows and sediment supply than was historically the case (Rasmussen and Shafroth, 2016). The northernmost reach included in this study is “Cisco Wash to Dry Gulch” (Cisco, hereafter) with two sites. It cuts through a shallow shale and silt-stone valley of variable width and is straight to moderately sinuous. The southernmost reach is “Gold Bar” and extends through sandstone-walled canyon and consists of two large meander bends. The Gold Bar reach has eight sites.

The biocontrol beetle (*Diorhabda* spp.) was released at eight locations in the study area between 2004 and 2006 (Henry et al., 2018). The sites included in the present study had no other control method (e.g., mechanical removal) for *Tamarix* during or prior to the study period. Remote sensing time-series show peak initial defoliation between 2004 and 2008, followed by a recovery until 2010 and a second cycle of defoliation between 2010 and 2013 and subsequent recovery until 2016 (Nagler et al., 2018). There was a sharp decrease in both live and relative *Tamarix* cover as measured in the field from 2010 to 2013, followed by a rebound between 2013 and 2017 bringing cover back to approximately 2010 levels (González et al., 2020b; Figure 3-2a,b). The percent cover of dead *Tamarix* followed an approximately inverse pattern (Figure 3-2c). Therefore, this study captures plant community response to a second cycle of defoliation and recovery of *Tamarix* cover. The variability in *Tamarix* cover and change over time across sites was large (González et al., 2020b). González et al. (2020b) showed that there was a sharp decline in herbaceous species between 2010 and 2012 sampling due to a large flood that affected riverbanks and other low-elevation fluvial landforms such as secondary channels, but otherwise there was little change in species diversity.

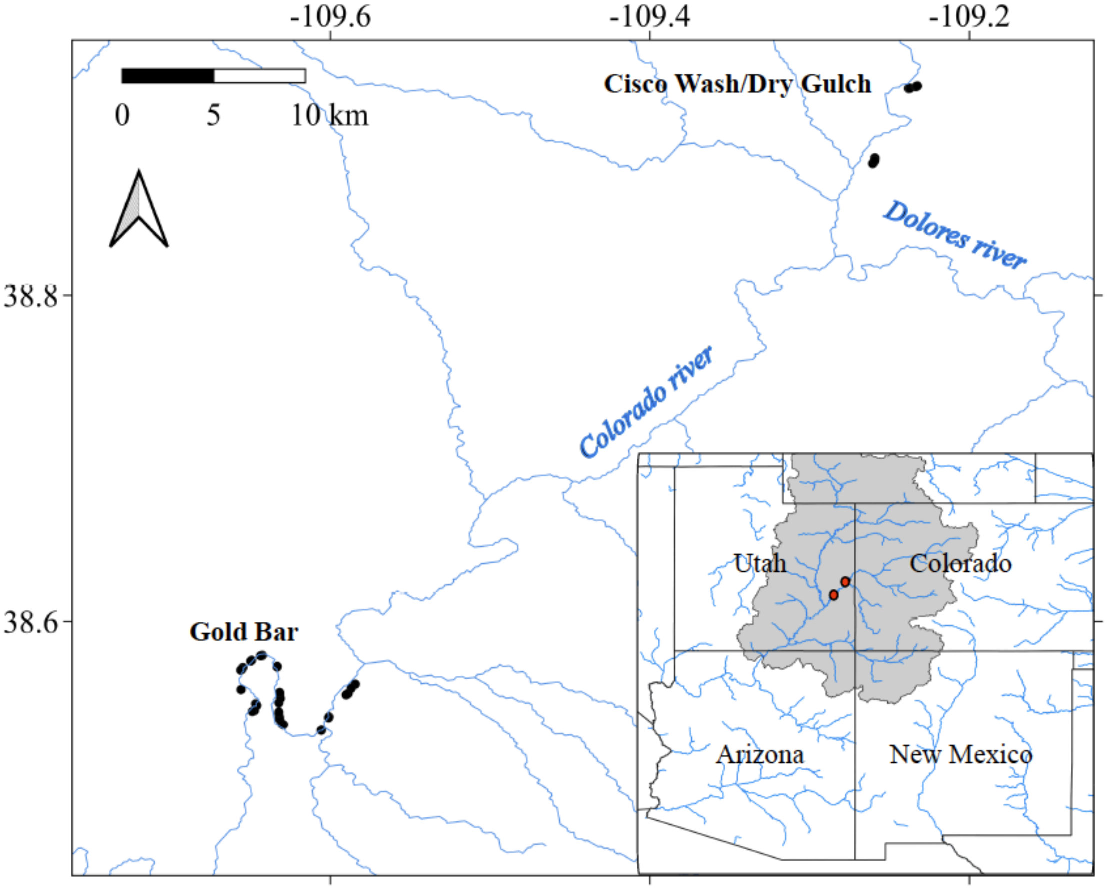

Figure 3-1: Map of study area. Cisco Wash/Dry Gulch contains 2 sites, with a total of 20 transects. Gold Bar contains 8 sites, with a total of 28 transects. Black dots represent transects but are overlapping at this map scale. Grey shading represents the Upper Colorado river basin. Red dots mark the two reaches.

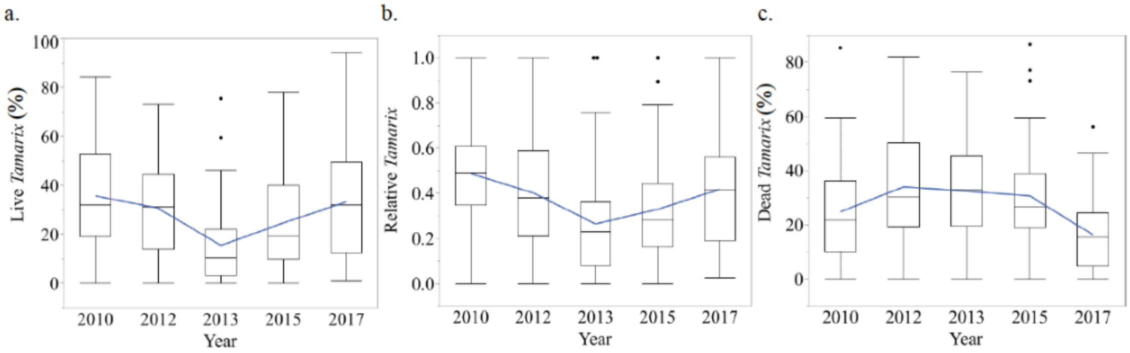

Figure 3-2: *Tamarix* cover for all sites. Included here to show the defoliation cycle from 2010 to 2013 and refoliation from 2013 to 2017 (Nagler et al. 2018; González et al. 2020) and for visual comparison to changes in trait values over time. Relative *Tamarix* is the proportion of *Tamarix* divided by the total cover of overstory species. The horizontal line within the box represents the median cover value; the top and bottom edges of the box represent the first and third quantiles. The whiskers extend to the outermost datapoint that falls within the first or third quartile +/- 1.5*(interquartile range). The blue line connects the mean cover from one year to the next.

Data collection

Field surveys/Vegetation

Within the study area, sites represent depositional surfaces and adjacent floodplains continuing into vegetated terraces on the inside edge of a meander, or vegetated surfaces along straighter sections of river. While a single site was defined as having a homogeneous origin, each site could include different landforms (e.g., floodplain, levee, secondary channel etc.) perpendicular to river. At each study site, we established 1 to 10 transects depending on the size, shape and heterogeneity of the site (20 transects in Cisco, 40 transects in Gold Bar). Only transects that had no *Tamarix* control other than biocontrol were used in the study, resulting in 20 transects in Cisco and 28 transects in Gold Bar. Transects were oriented perpendicular to the channel and were sampled in the fall of 2010, 2012, 2013, 2015 and 2017. The point-intercept method was used to sample vegetation (understory and overstory) along each transect (Bonham, 1989). Points were spaced either every 50 cm or every 1m to achieve a similar total number of points per transect. Live or dead *Tamarix* points were also recorded at each point along transects. Dead *Tamarix* was assumed to be due to beetle presence rather than the effects of other factors such as drought stress or competition, which tend to be minor (González et al., 2020b). The pinpoint data were transformed to percent cover per transect by dividing the number of points with each species by the total number of transect points.

We identified 107 taxa (103 species and 4 taxa identified to genus level; Table S3-1). Where taxa were only identified to genus, we identified the most likely species using USDA plants and regional floras and conducted trait data searches on that species. For simplicity we will refer to all taxa as species.

Trait data

We collected data on eight traits that have been previously determined to be important in riparian plant communities (Table 3-1; Henry et al., In Review; Stromberg and Merritt, 2015), following the methods outlined in Henry et al. (In Review). We collected trait data primarily using online databases (e.g., TRY - Kattge et al., 2020 and Palmquist et al., 2017; Table S3-2). When trait values could not be found we conducted literature searches using Web of Science and Google scholar (Table S3-3). These traits characterize resource acquisition, stress tolerance and reproductive strategies of the plants included in this study.

Using the eight traits, we calculated both multivariate indices of diversity and individual indices of the average and range of select traits. We examined specific leaf area (SLA), height at maturity and seed mass individually. These represent the three axes of the Leaf-Height-Seed (L-H-S) scheme proposed by proposed by Westoby (1998). SLA is related to resource conservation and acquisition strategies. High SLA confers the ability to take up and make use of resources quickly, but also is linked to a rapid turnover of plant leaves, allowing for flexibility in environments with unpredictable light and soil resources. Conversely, low SLA is associated with resource conservative strategy (Wright et al., 2004). Height at maturity reflects the amount of growth attempted between disturbance events (Westoby, 1998). Seed mass represents a tradeoff between producing many small seeds and few large ones. Seeds with larger mass tend to be more stress tolerant (Westoby, 1998). Recent studies have found these traits helpful in defining riparian plant community functional response to hydrogeomorphic factors (Brice et al., 2016; Janssen et al., 2020).

We calculated the community weighted means (CWM) and functional dispersion (FDis) for SLA, height at maturity and seed mass for each transect. Seed mass and height were both log-transformed prior to calculating functional metrics to meet the assumption of normality. CWM is defined as the mean trait value of all species in a community, weighted by the abundance of each species (Lavorel et al., 2008). For individual traits, FDis is defined as the weighted mean absolute deviation and so represents the range of values for a given trait present in the community (Laliberté and Legendre, 2010). FDis is also able to incorporate multiple traits representing a multivariate analogue to the weighted mean absolute deviation (Laliberté and Legendre, 2010). We calculated a multivariate measure of FDis using all eight traits for each transect (Table 3-1). These included several reproductive and phenological traits identified to be important in defining plant communities in a previous study including study sites in the same reach of the Upper Colorado (Table 3-1; Henry et al., In Review). The advantage of creating a multivariate index of the weighted range of all trait values is to provide a functional metric analogous to Shannon's diversity index based on species identity. Lastly, we calculated Shannon's diversity based on species cover for each transect in the study area.

Table 3-1: Traits used in study to calculate community weighted means, univariate and multivariate measures of dispersion.

Trait	Description/Unit/Classes	Variable type
Specific leaf area (SLA)	Square centimeters per gram (leaf area/dry leaf mass)	Continuous
Height at maturity	Meters	Continuous
Seed mass	Mass of 1000 seeds in grams	Continuous
Clonal reproduction ability	Yes/No	Categorical

Resprout ability	Ability to resprout after damage or fire: Yes/No	Categorical
Duration	Annual/Perennial	Categorical
Vegetative spread rate	Speed of vegetative spread: None/Slow/Moderate/Rapid	Ordinal
Total number of bloom months	Total number of months species typically blooms	Ordinal

Statistical analysis

We included species with at least half of the trait values present in our analysis. While this led to the removal of seven species, at least 80% vegetation cover was still accounted for at all transects. Subsequent analyses were carried out using the remaining 100 species. We did not include *Tamarix* in our calculation of functional metrics because it was used as an explanatory variable in subsequent analyses.

To identify changes over time and the influence of *Tamarix* cover and defoliation on individual traits, we ran linear mixed effects models using CWM and FDis of each L-H-S trait as response variables and year, live *Tamarix* cover, dead *Tamarix* cover and the interaction of year and live *Tamarix* cover as explanatory variables. We also conducted linear mixed effects models with the multivariate FDis metric and Shannon's diversity as the response variables and the same explanatory variables listed above to identify changes in the overall diversity of plant strategies and species diversity in response to *Tamarix* defoliation. Random variables were transect (nested within site), site (nested within reach; included to avoid pseudoreplication), and reach. The significance of all models was checked by comparing the full model with all fixed and random effects to a null model including only random effects (Bolker et al., 2009; a maximum likelihood ratio test). For each model we report the marginal (variation explained by fixed effects only) and conditional (variation explained by fixed and random effects) adjusted R^2. Lastly, we tested the correlation of Shannon's diversity index with the multivariate functional dispersion using Pearson's correlation coefficient.

All analyses were done in R studio (version 1.2.1335) using R version 3.6.0 (R Core Team, 2020). Functional metrics were calculated using the "dbFD" function of the package "FD" (Laliberté et al., 2014). Mixed effects models were conducted using the function "lme" of package "nlme" (Pinheiro et al., 2019). Pearson's correlation coefficient was calculated using the function "pairs.panels" of the package "psych" (Revelle, 2019).

Results

Change in L-H-S traits with *Tamarix* cover and year

Overall, there was a slight, statistically significant increase in height CWM (community weighted mean) over time (Figure 3-3a) and with increasing *Tamarix* cover (Figure 3-3b). SLA decreased between 2010 and 2012 and then returned to 2010 levels by 2015, independent of *Tamarix* cover (Figure 3-3c,d). Changes in seed mass CWM varied depending on *Tamarix* cover, however the amount of variation in seed mass explained by the fixed effects of this model was very low (Figure 3-3e). Height dispersion decreased as live *Tamarix* increased and this relationship was statistically significant in 2017 (Figure 3-4a). SLA dispersion decreased from 2010 to 2012 independent of *Tamarix* cover (Figure 3-4b,c). Full model details can be found in Table S3-4.

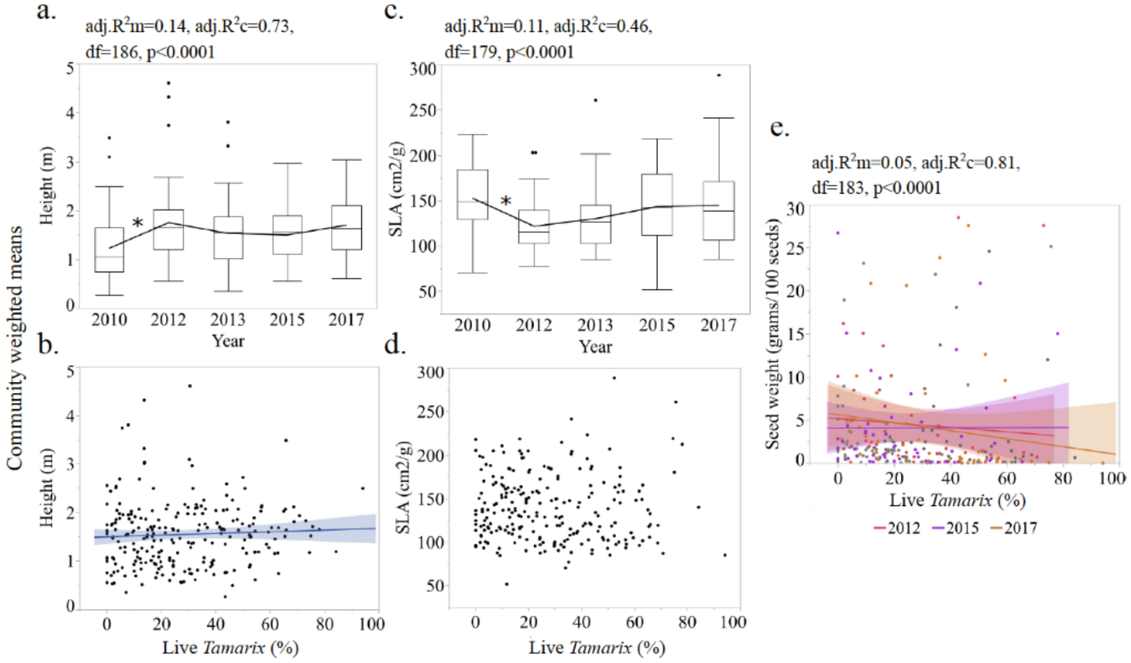

Figure 3-3: Community weighted means over time and across percent live *Tamarix*. Where there were no interactions between year and *Tamarix,* CWM is plotted against both explanatory variables. Where there were significant interactions, only 1 plot is shown with CWM and live *Tamarix* on the axes and an overlay of the year for which a significant interaction was present. a) Height CWM increases slightly over time with a significant difference between consecutive years 2010 and 2012. b) Height cwm increases slightly as *Tamarix* cover increases. c) SLA CWM decreases significantly from 2010 to 2012 but recovers fully by 2015. d) There was no significant relationship between SLA CWM and *Tamarix* cover. e) There was a slight decrease in seed weight with increasing *Tamarix* cover that was significant in 2012, 2015 and 2017. Note: trend lines are not shown if specific year or interaction were not statistically significant. Height and seed mass were log transformed in mixed models and have been back transformed for plotting. Three values were excluded from the plot of seed mass CWM because they skewed the axis too far to be legible. An asterisk indicates a significant difference between consecutive years, determined by Tukey's post-hoc test. The shaded portion surrounding each line of best fit represents the 95% confidence interval of the line. Full model details can be found in Table S4.

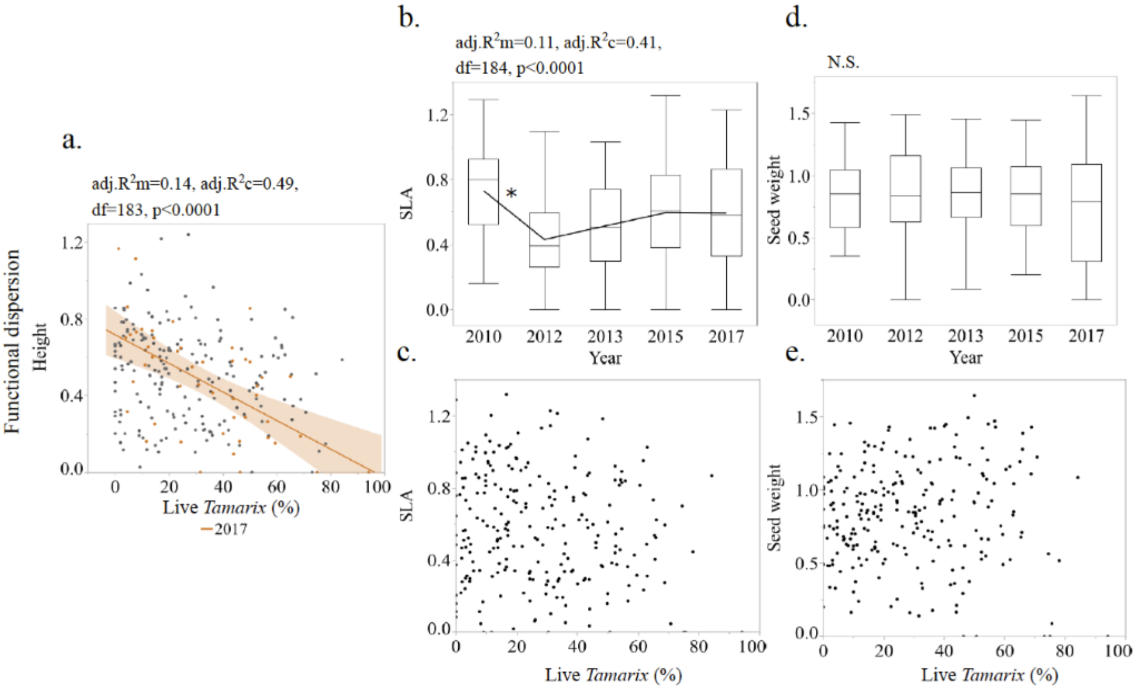

Figure 3-4: Functional dispersion over time and across percent live *Tamarix*. Where there were no interactions between year and *Tamarix*, dispersion is plotted against both explanatory variables. Where there were significant interactions, only 1 plot is shown with dispersion and live *Tamarix* on the axes and an overlay of the year for which a significant interaction was present. a) Height dispersion decreased with increasing *Tamarix* cover. This relationship was significant in 2017. b) SLA dispersion decreased significantly between 2010 and 2012 and remained lower than 2010 values throughout the study period. c) There was no significant relationship between SLA dispersion and *Tamarix*. d,e) There were no significant relationships between seed weight dispersion and year or *Tamarix*. Note: trend lines are not shown if specific year or interaction were not statistically significant. An asterisk indicates a significant difference between consecutive years, determined by Tukey's post-hoc test. The shaded portion surrounding each line of best fit represents the 95% confidence interval of the line. Full model details can be found in Table S4.

Species and multivariate functional dispersion

Shannon diversity and functional dispersion (using all variables included in the study) had a Pearson's correlation coefficient of 0.59 (Figure 3-5). Shannon diversity decreased with both *Tamarix* cover and time (adjusted R^2=0.08; Figure 3-6a,b). Functional dispersion decreased with increasing *Tamarix* cover in 2013 and 2017 (adjusted R^2=0.22; Figure 3-6c). Variation in functional dispersion was more successfully explained by the interaction of *Tamarix* cover and time than the species-based Shannon diversity index (full model details can be found in Table S3-5).

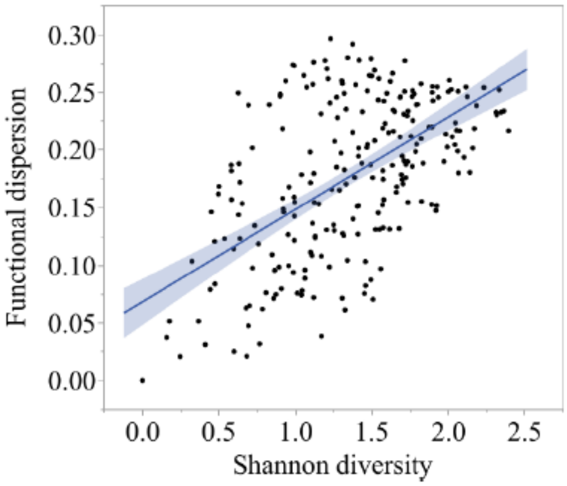

Figure 3-5: Comparison of Shannon diversity to functional dispersion for all 48 transects and five sampling years.

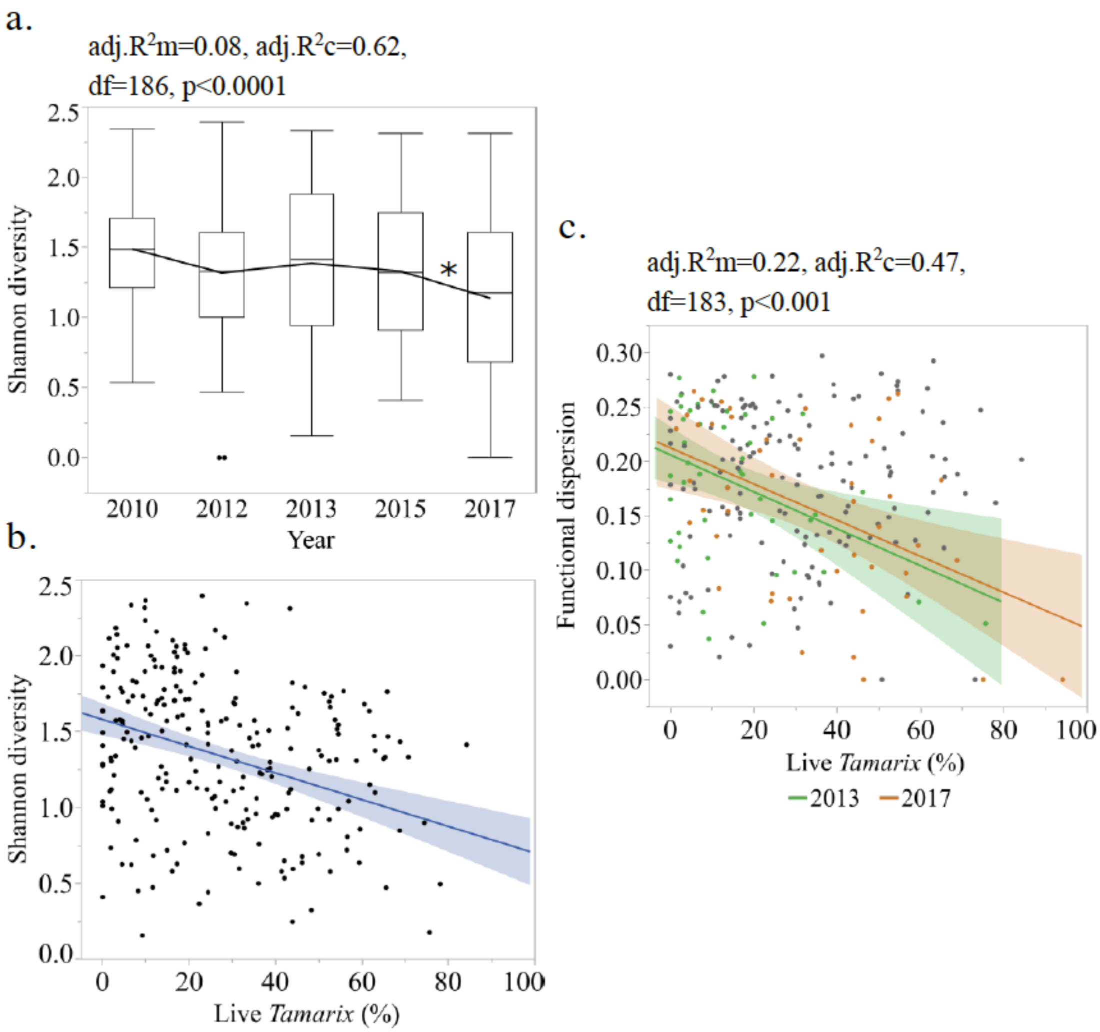

Figure 3-6: Shannon diversity and functional dispersion plotted over time and compared to percent live *Tamarix* to show the differences in response. An asterisk indicates a significant difference between years. The mixed effects model with functional dispersion included significant interactions between year and *Tamarix* cover. Functional dispersion is plotted against percent live Tamarix cover with an overlay of year. While all years had the same general trend, only 2013 and 2017 were statistically significant. Full model details can be found in Table S3-5.

Discussion

This study is the first to examine the functional response of the underlying plant community to biocontrol of an invasive species over time in a riparian system. Overall, there was little fluctuation in the plant community functional traits in response to a specific biocontrol defoliation event. However, there were responses to *Tamarix* cover generally and to a flood event that occurred between the 2010 and 2012 sampling. This lack of response specifically to the defoliation-refoliation event captured in this study provides support for our alternative hypothesis that the community had already stabilized in response to the cyclical occurrences of defoliation events. It is also possible that variability in impact of defoliation over the study area, with some areas not strongly affected, obscured responses in more heavily impacted sites. This highlights the importance of understanding the underlying drivers of biocontrol impact (Bean and Dudley, 2018; Henry et al., 2018; Hultine et al., 2015).

Hydrological events are more important in driving average plant community traits than the *Tamarix* defoliation cycle

Plant community changes in height and SLA between 2010 and 2012, i.e., a year before peak defoliation suggests stronger drivers underlying plant community change than biocontrol defoliation. These changes in trait values are likely due to a large flood in June 2011 that caused an overall reduction in herbaceous species between these sampling periods (González et al. 2020b). The reduction of herbaceous species by flood scouring removed short species with high SLA values, consequently increasing the community's average height and decreasing the community's average SLA. While height remained higher than 2010 levels, SLA returned to pre flood levels by 2015. This recovery further supports the idea that SLA is not strongly influenced by defoliation cycles, particularly given that the dip in SLA occurs before peak defoliation. The coincidence of reduced average SLA with the flood may be because higher SLA species are more likely to occur in the low floodplain. In general, a higher SLA confers greater anaerobic tolerance allowing submerged plants to survive (Phukan et al., 2016). However, occurrence in the low floodplain increases vulnerability to scouring and burial in herbaceous species. The loss of these higher SLA species would reduce the community weighted average SLA. Similarly, herbaceous species which are typically shorter than woody species would also be more vulnerable to flood scouring and burial (González et al., 2020a; Merritt et al., 2010). Their removal via flood scouring and burial would increase the community's average height.

***Tamarix* cover affects the range of trait values expressed rather than the community average**

Our finding that dispersion of height values increases at lower levels of *Tamarix* cover provides some evidence to support our hypothesis that plant communities would become more diverse in response to reduced *Tamarix* cover. While this relationship was only statistically significant in 2017, the other years followed a similar trend but with higher variability. This outcome agrees with previous studies showing that higher *Tamarix* cover leads to more specialized communities (Henry et al., In Review).

Dispersion of SLA was unaffected by *Tamarix* cover and remained unchanged during peak defoliation years. SLA dispersion was only different between the 2010 and 2012 sampling periods when the flood occurred. Floods disproportionately affect species at low topographical positions, which are more likely to have a larger SLA (submergence tolerance and resource acquisition), reducing overall variability. The scouring and burial of these species would lead to a temporarily more specialized community until the affected species were able to recover.

Functional diversity is more sensitive to *Tamarix* cover than species diversity

The relationship between *Tamarix* cover and functional dispersion was only statistically significant in two years, however, one of these years (2013) was during the peak defoliation event, suggesting that more *Tamarix* defoliation was associated with an increase in the range of phenological and reproductive strategies. *Tamarix* communities are functionally specialized and the decrease in *Tamarix* likely allows for species that can colonize these areas to return. Given that the changes in average or dispersion of L-H-S (leaf-height-seed) trait values did not change during this time, this pattern is likely driven by reproductive and phenological traits rather than L-H-S traits. This makes sense given how strong these traits are in structuring overall plant communities, particularly perennation, blood period and vegetative reproduction, in *Tamarix*-dominated systems (Henry et al., In Review).

While species diversity and functional diversity are closely linked in this context, they are not perfectly correlated. In fact, functional dispersion was shown to be a measure more sensitive to *Tamarix* cover than taxonomic diversity, particularly in a high defoliation year. Both species diversity and functional dispersion decreased with higher levels of *Tamarix* cover. However, while functional dispersion was influenced by the cycle of defoliation and refoliation (as evidenced by the significant relationship in 2013), species diversity did not respond to this cycle.

Our finding that higher levels of *Tamarix* cover is associated with more functionally specialized plant communities is consistent with previous studies in this system (Henry et al., In Review). A global review found overwhelmingly that invasive species negatively impact plant community diversity, although this is conditioned by both the abiotic environment and biotic interactions (Pyšek et al., 2012). Our study suggests that this may be the case in *Tamarix* dominated systems for both species diversity and functional diversity.

Conclusion

We found that measures of species diversity and functional diversity generally followed similar patterns in plant community response to a second cycle of biocontrol defoliation, but that functional measures were more sensitive to the invasive tree cover as well as hydrological factors. We confirmed that *Tamarix* cover is a driver of not only the taxonomic, but also the functional diversity of plant strategies present in a community, making communities more functionally specialized. However, the community response to peak defoliation and refoliation was minor and was a smaller response than to a large flood that only inundated the study sites partially. This may suggest an overall resistance of the plant community to fluctuations in *Tamarix* cover, or that plant communities have gained stability as a result of the first defoliation cycle. Further studies should be done across the full range of *Tamarix* and *Diorhabda* abundance, to better understand the relationship between the often sudden and drastic defoliation events that *Diorhabda* can cause and plant community response. This is particularly important for anticipating community response in sensitive conservation areas, for example, endangered southwestern willow flycatcher breeding habitat where *Tamarix* often occurs and is used for nesting.

Citation Information

Henry, A.L., González, E., Shafroth, P.B., and Anna A. Sher. In Prep. Functional diversity is a more sensitive indicator than species diversity of plant community response to biocontrol of an invasive tree.

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Appendix: Supplemental Figures and Tables

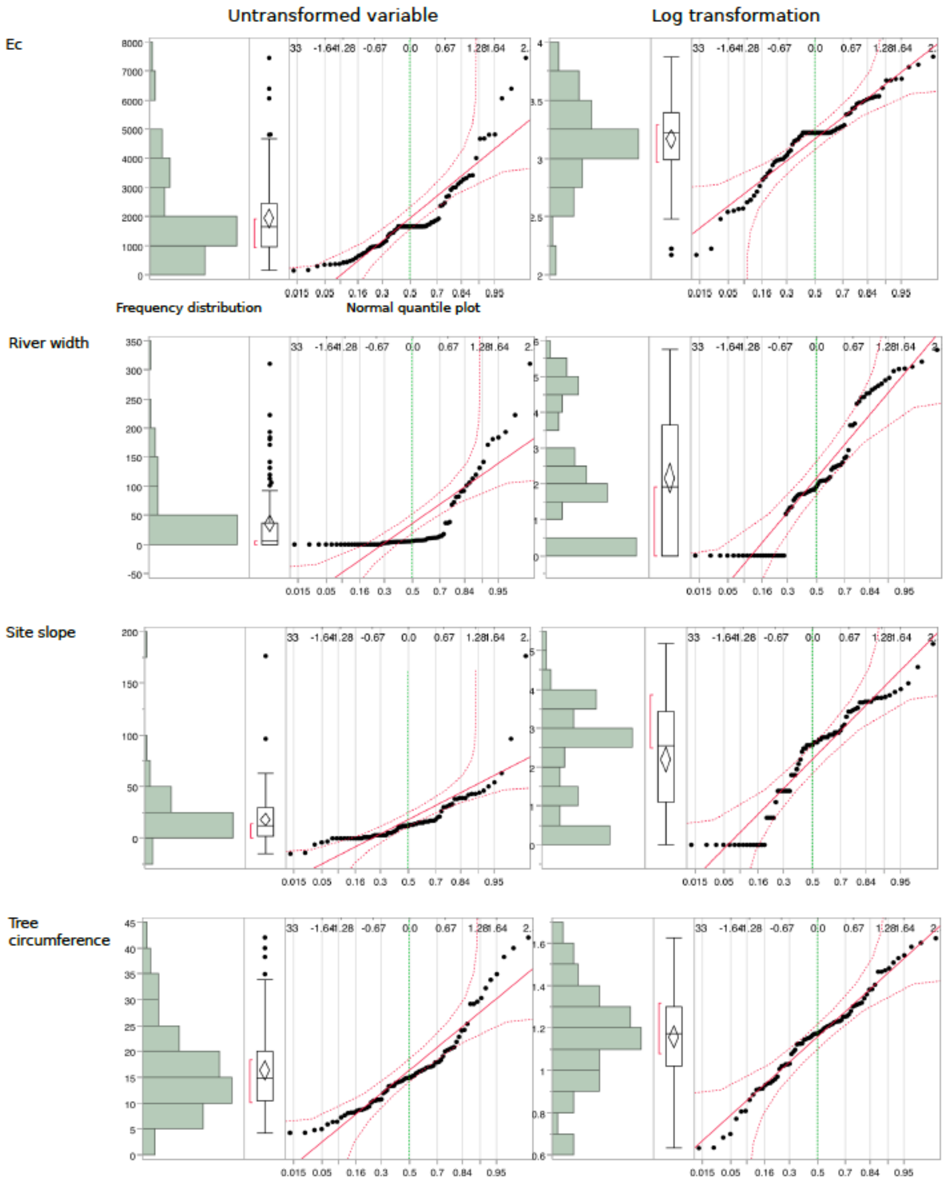
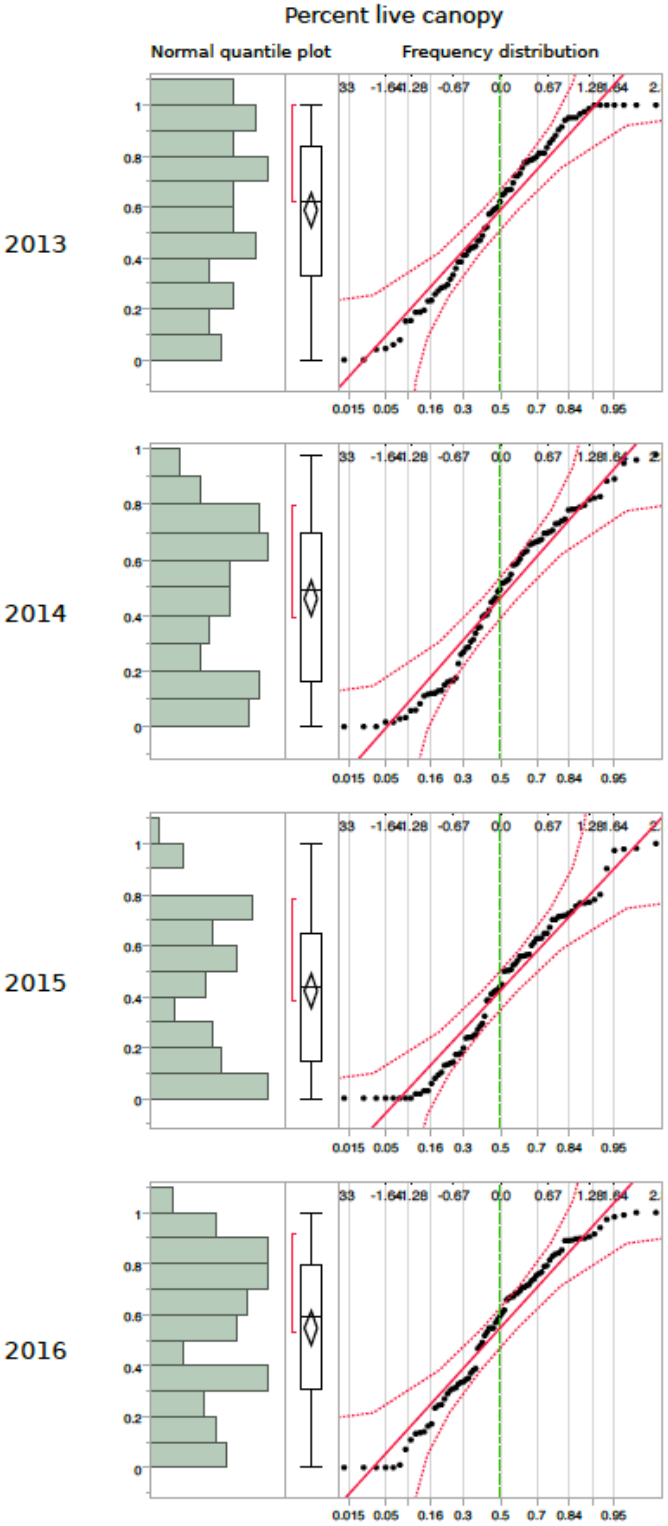


Figure S1-1: Environmental variable transformations. This figure shows the frequency distribution and normal quantile plots for the environmental variables that were log transformed.


Percent live canopy
Normal quantile plot
Frequency distribution
2013
2014
2015
2016
0
0.2
0.4
0.6
0.8
1
33
-1.64
1.28
-0.67
0.0
0.67
1.28
1.64
2.
0.015
0.05
0.16
0.3
0.5
0.7
0.84
0.95

Figures S1-2: Distributions of percent live canopy in each year. This figure shows the frequency distribution and normal quantile plots for percent live canopy in each year. Table S2-1. Species list. This table contains all species listed by guild identity and then alphabetically. Species marked with an asterisk were part of the *Tamarix* guild when *Tamarix* was included in the cluster analysis. USDA code, common name and nativity are also listed.

Species	USDA code	Common name	Nativity
Non-clonal annual forbs			
Amaranthus albus L.	AMAL	Prostrate pigweed	Non-native
Amaranthus retroflexus L.	AMRE	Redroot amaranth	Native
Arctium minus Bernh.	ARMI2	Lesser burdock	Non-native
Atriplex patula L.	ATPA4	Spear saltbush	Non-native
**Carduus nutans* L.	CANU4	Nodding plumeless thistle / Musk thistle	Non-native
Chenopodium album L.	CHAL7	Lambsquarters	Non-native
Chenopodium berlandieri Moq.	CHBE4	Pitseed goosefoot	Native
Chenopodium fremontii S. Watson	CHFR3	Fremont's goosefoot	Native
Chorispora tenella (Pall.) DC.	CHTE2	Crossflower / Purple mustard	Non-native
Cichorium intybus L.	CIIN	Chicory / Cornflower	Non-native

Cirsium vulgare (Savi) Ten.	CIVU	Bull thistle	Non-native
Conyza canadensis (L.) Cronquist	COCA5	Canadian horseweed	Native
Datura stramonium L.	DAST	Jimsonweed	Non-native
Descurainia sophia (L.) Webb ex Prantl	DESO2	Herb sophia / Fixweed	Non-native
Erodium cicutarium (L.) L'Hér. ex Aiton	ERCI6	Redstem stork's bill	Non-native
Grindelia squarrosa (Pursh) Dunal	GRSQS2	Curlycup gumweed	Native
Gutierrezia microcephala (DC.) A. Gray	GUMI	Threadleaf snakeweed	Native
Halogeton glomeratus (M. Bieb.) C.A. Mey.	HAGL	Saltlover	Non-native
Helianthus annuus L.	HEAN3	Common sunflower	Native
Helenium autumnale L.	HEAU	Common sneezeweed	Native
Helianthus petiolaris Nutt.	HEPE	Prairie sunflower	Native
Bassia scoparia (L.) A.J. Scott	KOSCT	Common kochia	Non-native
Lactuca serriola L.	LASE	Prickly lettuce	Non-native

Lepidium perfoliatum L.	LEPE2	Clasping pepperweed	Non-native
Machaeranthera tanacetifolia (Kunth) Nees	MATA2	Tansyleaf tansyaster	Native
Melilotus alba (L.) Lam.	MEAL12	Sweet clover	Non-native
Plantago patagonica Jacq.	PLPA2	Woolly plantain	Native
Portulaca oleracea L.	POOL	Little hogweed / Common purslane	Non-native
Salsola kali L.	SAKA	Russian thistle / Tumbleweed	Non-native
Sisymbrium altissimum L.	SIAL2	Tall tumblemustard	Non-native
Sonchus asper (L.) Hill	SOAS	Spiny sowthistle / Sow thistle	Non-native
Tragopogon dubius Scop.	TRDU	Yellow salsify	Non-native
Verbascum thapsus L.	VETH	Common mullein / Wooley mullein	Non-native
**Xanthium strumarium* L.	XAST	Rough cocklebur / Cocklebur	Native
Non-clonal annual graminoids			

Bromus japonicus Thunb.	BRAR5	Field brome / Japanese brome	Non-native
Bromus tectorum L.	BRTE	Cheatgrass	Non-native
Echinochloa crus-galli (L.) P. Beauv	ECCR	Barnyardgrass	Non-native
Polypogon monspeliensis (L.) Desf.	POMO5	Annual rabbitsfoot grass	Non-native
Non-clonal resource acquisitive perennials			
Castilleja angustifolia (Nutt.) G. Don	CAAN7	Northwestern Indian paintbrush	Native
Elymus canadensis L.	ELCA4	Canada wildrye / Canada wildrice	Native
Plantago lanceolata L.	PLLA	Narrowleaf plantain	Non-native
Plantago major L.	PLMA2	Common plantain / Wide leaf plantago	Non-native
Taraxacum officinale F.H. Wigg.	TAOF	Common dandelion	Native
Non-clonal resource conservative perennials			

Achnatherum hymenoides (Roem. & Schult.) Barkworth	ACHY	Indian ricegrass	Native
Aristida purpurea Nutt.	ARPU9	Purple threeawn / Threeawn	Native
Artemisia tridentate Nutt.	ARTR2	Big sagebrush	Native
Chrysothamnus linifolius Greene	CHLI3	Spearleaf rabbitbrush	Native
Ericameria nauseosa (Pall. ex Pursh) Britton	CHNA2	Rubber rabbitbrush / Rabbitbrush	Native
Descurainia pinnata (Walter) Britton	DEPI	Western tansy mustard	Native
Gutierrezia sarothrae (Pursh) Britton & Rusby	GUSA2	Broom snakeweed / Snake weed	Native
Heterotheca villosa (Pursh) Shinners	HEVI4	Hairy false goldenaster	Native
Ipomopsis aggregata (Pursh) V.E. Grant	IPAG	Scarlet gilia	Native
Lepidium montanum Nutt.	LEMO2	Mountain pepperweed / Whitetop	Native
Machaeranthera canescens (Pursh) A. Gray	MACA2	Hoary tansyaster	Native
Mirabilis multiflora (Torr.) A. Gray	MIMU	Colorado four o'clock	Native
Sporobolus airoides (Torr.) Torr.	SPAI	Alkali sacaton	Native

Sporobolus cryptandrus (Torr.) A. Gray	SPCR	Sand dropseed / Spike dropseed	Native
Stanleya pinnata (Pursh) Britton	STPI	Desert prince's-plume / Prince's plume	Native
Suaeda moquinii (Torr.) Greene	SUMO	Mojave seablite / Bush seepweed	Native
Non-clonal drought tolerant trees			
Fraxinus spp.	FRAXI	Ash	Native
Malus spp.	MALUS	Crabapple	Native
Morus alba L.	MOAL	White mulberry	Non-native
Clonal anaerobic tolerant trees			
Acer negundo L.	ACNE2	Boxelder	Native
Betula occidentalis Hook.	BEOC2	Water birch	Native
Cornus sericea L.	COSE16	Red osier dogwood	Native
Populus spp.	POPUL	Cottonwood	Native

Prunus virginiana L.	PRVI	Chokecherry	Native
Salix nigra Marshall	SANI	Black willow	Native
Ulmus pumila L.	ULPU	Siberian elm / Chinese elm	Non-native
Clonal anaerobic tolerant perennials			
Agrostis gigantea Roth	AGGI2	Redtop	Non-native
Pascopyrum smithii (Rydb.) Á. Löve	AGSM	Western wheatgrass	Native
Apocynum cannabinum L:	APCA	Indian hemp / Dogbane	Native
Baccharis salicina Torr. & A. Gray	BASA	Willow baccharis / False willow	Native
Schoenoplectus maritimus (L.) Palla	BOMA7	Cosmopolitan bulrush	Native
Distichlis spicata (L.) Greene	DISP	Saltgrass / Inland saltgrass	Native
Eleocharis spp.	ELEOC	Spikerush	Native
Equisetum arvense L.	EQAR	Field horsetail	Native
Glycyrrhiza lepidota Pursh	GLLE3	American licorice / Wild licorice	Native

Juncus arcticus Willd.	JUARL	Mountain rush	Native
Muhlenbergia asperifolia (Nees & Meyen ex Trin.) Parodi	MUAS	Scratchgrass	Native
Panicum virgatum L.	PAVI2	Switchgrass	Native
Phalaris arundinacea L.	PHAR3	Reed canarygrass	Native
Phragmites australis (Cav.) Trin. ex Steud.	PHAU7	Common reed	Native
Salix exigua Nutt.	SAEX	Coyote willow / Narrowleaf willow	Native
Schoenoplectus pungens (Vahl) Palla	SCPU10	Common threesquare	Native
Schoenoplectus tabernaemontani (C.C. Gmel.) Palla	SCTA2	Softstem bulrush	Native
Sorghastrum nutans (L.) Nash	SONU2	Indiangrass	Native
Spartina pectinata Bosc ex Link	SPPE	Prairie cordgrass	Native
Toxicodendron rydbergii (Small ex Rydb.) Greene	TORY	Western poison ivy	Native
Typha angustifolia L.	TYAN	Narrowleaf cattail	Native

Clonal drought tolerant perennials			
Acroptilon repens (L.) DC.	ACRE3	Hardheads / Russian knapweed	Non-native
Ambrosia psilostachya DC.	AMPS	Cuman ragweed	Native
Artemisia dracunculus L.	ARDR4	Tarragon	Native
Artemisia ludoviciana Nutt.	ARLU	White sagebrush	Native
Asparagus officinalis L.	ASOF	Garden asparagus	Non-native
Asclepias speciosa Torr.	ASSP	Showy milkweed	Native
Cirsium arvense (L.) Scop.	CIAR4	Canada thistle	Non-native
Clematis ligusticifolia Nutt.	CLLI2	Western white clematis	Native
Convolvulus arvensis L.	COAR4	Field bindweed	Non-native
Comandra umbellata (L.) Nutt.	COUM	Bastard toadflax / Blueberry (Hisham)	Native
Dalea candida Michx. ex Willd.	DACA7	White prairie clover	Native
Lepidium densiflorum Schrad.	LEDE	Common pepperweed	Non-native
Lepidium draba L.	LEDR	Whitetop / Hoary cress	Non-native

Lepidium latifolium L.	LELA2	Broadleaved pepperweed / Tall whitetop	Non-native
Opuntia polyacantha Haw.	OPPO	Plains pricklypear	Native
Sonchus arvensis L.	SOAR2	Field sowthistle	Non-native
Solidago canadensis L.	SOCA6	Canada goldenrod / Goldenrod	Native
Solidago occidentalis (Nutt.) Torr. & A. Gray	SOOC4	Western goldentop	Native
Sonchus palustris L.	SOPA10	Marsh sowthistle	Non-native
Symphyotrichum ericoides (L.) G.L. Nesom	SYER	White heath aster	Native
Urtica dioica L.	URDI	Stinging nettle	Non-native
Clonal resource conservative perennials			
Agropyron cristatum (L.) Gaertn.	AGCR	Crested wheatgrass	Non-native
Atriplex canescens (Pursh) Nutt.	ATCA2	Fourwing saltbush	Native
Bouteloua curtipendula (Michx.) Torr.	BOCU	Sideoats grama	Native

Carex spp.	CAREX	Sedge	Native
Elymus trachycaulus (Link) Gould ex Shinners	ELTR7	Slender wheatgrass	Native
Forestiera pubescens Nutt.	FOPU2	Stretchberry / New Mexican Privet	Native
Hordeum jubatum L.	HOJU	Foxtail barley	Native
Medicago sativa L.	MESA	Alfalfa	Non-native
Rhus trilobata Nutt.	RHTR	Skunkbush sumac	Native
Ribes aureum Pursh	RIAU	Golden currant	Native
Rosa woodsia Lindl.	ROWO	Wood's rose / Rose woods	Native
Sarcobatus vermiculatus (Hook.) Torr.	SAVE4	Greasewood	Native
Schizachyrium littorale (Nash) E.P. Bicknell	SCLI11	Shore little bluestem	Native
Sphaeralcea coccinea (Nutt.) Rydb.	SPCO	Scarlet globemallow	Native

Table S2-2.1. Trait abbreviations for TRY data sources table S2-2.2.

Abbreviation	**Trait name**
SLA	Specific Leaf Area

Seed_weight	Weight of 1000 seeds
HT_matur	Average height at maturity
Anae_tol	Anaerobic tolerance
Drgt_Tol	Drought tolerance
Fire_tol	Fire tolerance
Mois_use	Moisture use
Salin_tol	Salinity tolerance
Shade_tol	Shade tolerance
Growth_R	Growth rate
Lifespan	Lifespan
Sex_repr	Ability to reproduce sexually
Veg_repr	Ability to reproduce vegetatively
Spread_rt	Spread rate
Resprout	Resprout ability
Actual_bloom	Bloom period

Table S2-2.2. TRY data sources. This table details the datasets and reference information for each TRY dataset accessed and used in our trait analysis. The dataset ID used to reference data in the TRY database, species and trait information and reference information are included. If unpublished, the submitting author is listed. Species are listed as their USDA code and traits are listed as the trait ID used by the TRY database (Kattge et al., 2020). References are listed as they are listed in the TRY database.

Dataset ID	**USDA CODE (trait abb.)**	**Reference**
3	AMPS (Fire_tol), COAR4 (Resprout)	unpublished. Ross Bradstock. Australian Fire Ecology Database.

4	AMRE (Actual_bloom), COAR4 (Veg_repr, Acutal_bloom), COSE16 (Veg_repr), DAST (Actual_bloom, Veg_repr), LEDE (Veg_repr, Actual_bloom), LEDR (Vegr_repr, Actual_bloom), LEPE2 (Veg_repr, Actual_bloom), PECR2 (Veg_repr, Spread_rt, Actual_bloom), PHCA5 (Veg_repr, Actual_bloom), SAKA (Veg_repr, Acutal_bloom), SOPA10 (Actual_bloom), VETH (Veg_repr, Spread, rt), URDI (Veg_repr, Actual_bloom)	Kühn, I., W. Durka, and S. Klotz. 2004. BiolFlor - a new plant-trait database as a tool for plant invasion ecology. Diversity and Distribution 10:363-365.
20	MOAL (SLA), SANI (SLA)	Wright, I. J., P. B. Reich, M. Westoby, et al. 2004. The worldwide leaf economics spectrum. Nature 428:821-827.
25	AGGI2 (SLA), AMRE (SLA, HT_matur), ATPA4 (SLA, HT_matur), BRAR5 (SLA), CANU4 (SLA, HT_matur), CHAL7 (HT_matur), CIAR4 (SLA, HT_matur), CIVU (SLA, HT_matur), COAR4 (SLA), DAST (SLA), KOSCT (SLA), LEDE (HT_matur), LEDR (SLA, HT_matur), LEPE2 (HT_matur), PECR2 (HT-matur), PHAR3 (SLA), SAKA (SLA), SIAL2 (SLA, HT_matur), SOPA10 (SLA, HT_matur), URDI (SLA)	Kleyer, M., R. M. Bekker, I. C. Knevel, et al. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. Journal of Ecology 96:1266-1274.
27	CIAR4 (Resprout), CIVU (Resprout), COAR4 (Fire_tol), LEDR (Resprout)	Paula, S., M. Arianoutsou, D. Kazanis, et al. 2009. Fire-related traits for plant species of the Mediterranean Basin. Ecology 90:1420.
50	ACMI2 (RGR), BOCU (RGR), CIIN (RGR), PAVI2 (RGR), PHAR3 (RGR), RUCR (RGR, Growth_R), SOCA6 (RGR), SONU2 (RGR), SPPE (RGR), TYAN (RGR), VETH (RGR)),	Shipley B., 2002. Trade-offs between net assimilation rate and specific leaf area in determining relative growth rate: relationship with daily irradiance. Functional Ecology 16: 682-689.

	URDI (RGR)	
63	SAKA (HT_matur)	Fonseca, C. R., J. M. Overton, B. Collins, and M. Westoby. 2000. Shifts in trait-combinations along rainfall and phosphorus gradients. Journal of Ecology 88:964-977.
68	BEOC2 (SLA), FRAXI (SLA), MOAL (HT_matur)	Wirth, C. and J. W. Lichstein. 2009. The imprint of species turnover on old-growth forest carbon balances - Insights from a trait-based model of forest dynamics. Pages 81-113 in C. Wirth, G. Gleixner, and M. Heimann, editors. Old-Growth Forests: Function, Fate and Value. Springer, New York, Berlin, Heidelberg.
92	CIIN (rt_dpt_max), CLLI2 (rt_dpt_max), FOPU2 (HT_matur, Anae_tol, Fire_tol, Mois_use, Salin_tol, Shade_tol, Growth_R, Resprout, Seed_period)	Green, W. 2009. USDA PLANTS Compilation, version 1, 09-02-02. (http://bricol.net/downloads/data/PLANTSdatabase/) NRCS: The PLANTS Database (http://plants.usda.gov, 1 Feb 2009). National Plant Data Center: Baton Rouge, LA 70874-74490 USA.
102	EQAR (SLA)	Blonder, Benjamin (Unpublished). Photosynthesis and Leaf Characteristics Database
108	AGGI2 (RGR), ATPA4 (RGR), CHAL7 (RGR)	Fry, E.L., Power, S.A. Manning, P. 2014 Trait based classification and manipulation of functional groups in biodiversity-ecosystem function experiments. Journal of Vegetation Science 25:248-261.
159	GUMI (RGR)	Butterfield, B.J. and J.M. Briggs. 2011. Regeneration niche differentiates functional strategies of desert woody plant species. Oecologia 165:477-487.

163	BOCU (SLA), CHBE4 (SLA), GRSQS2 (RGR)	Craine J.M., J.B. Nippert, E.G. Towne et al. 2011. Functional consequences of climate-change induced plant species loss in a tallgrass prairie. Oecologia 165:1109-1117.
164	CHTE2 (HT_matur), SONI (HT_matur)	Bragazza, L. 2009. Conservation priority of Italian alpine habitats: a floristic approach based on potential distribution of vascular plant species. Biodiversity and Conservation 18:2823–2835.
173	ATLE (max salinity), ATPA4 (max salinity)	Flowers, T.J., H.K. Galal and L. Bromham. 2010. Evolution of halophytes: multiple origins of salt tolerance in land plants. Functional Plant Biology. 37:604–612.
174	ARMI2 (rt_dpt_max, Drgt_tol, Shade_tol), ASOF (Shade_tol), ATPA4 (Shade_tol, Salin_tol), CANU4 (rt_dpt_max, Shade_tol), CHAL7 (Shade_tol), CIAR4 (Shade_tol), CIVU (rt_dpt_max, Shade_tol), COAR4 (Drgt_tol, Shade_tol), DAST (rt_dpt_max, Shade_tol), LEDR (Shade_tol), RUCR (Shade_tol), SOAR2 (Salin_tol, Shade_tol, Actual_bloom), SOPA10 (Salin_tol, Shade_tol), VETH (rt_dpt_max, Actual_bloom), URDI (Salin_tol, Shade_tol)	Fitter, A. H. and H. J. Peat. 1994. The Ecological Flora Database. Journal of Ecology 82:415-425.
193	CHFR3 (SLA, HT_matur), CHFR3 (SLA, HT_matur), COAR4 (HT_matur), ERDI4 (SLA, HT_matur), IPAG (SLA), LEDE (SLA), ROWO (SLA), TRDU (SLA)	Laughlin, D.C., P.Z. Fulé, D.W. Huffman, J. Crouse, and E. Laliberté. 2011. Climatic constraints on trait-based forest assembly. Journal of Ecology 99:1489-1499.

221	PAVI2 (SLA)	Wright J.P., Sutton-Grier A. 2012. Does the leaf economic spectrum hold within local species pools across varying environmental conditions? Functional Ecology doi: 10.1111/1365-2435.12001
226	AGCR (SLA), PRVI (SLA)	Blonder, B., B. Buzzard, L. Sloat, et al. 2012. The shrinkage effect biases estimates of paleoclimate. American Journal of Botany.
327	SOCA6 (HT_matur)	Siefert, A., J.D. Fridley, and M.E. Ritchie. 2014. Community functional responses to soil and climate at multiple spatial scales: when does intraspecific variation matter? PLOS ONE 9: e111189
339	CAREX (rt_dpt_max)	Iversen CM, McCormack ML, Powell AS, et al. (2017) A global Fine-Root Ecology Database to address belowground challenges in plant ecology. New Phytologist. doi:10.1111/nph.14486.
342	ACMI2 (SLA), CIIN (SLA), RHTR (SLA)	Maire V., I.J. Wright, I.C. Prentice, et al. 2015. Data from: Global effects of soil and climate on leaf photosynthetic traits and rates. Dryad Digital Repository. http://dx.doi.org/10.5061/dryad.j42m7
378	SCTA2 (SLA), SOAR2 (SLA)	Lhotsky B., A. Csecserits, B. Kovács, Z. Botta-Dukát: New plant trait records of the Hungarian flora.
309	SONU2 (SLA), SPCO (SLA)	La Pierre, KJ and M.D. Smith. 2015. Functional trait expression of grassland species shift with short- and long-term nutrient additions. Plant Ecology 216: 307 doi:10.1007/s11258-014-0438-4

236	ULPU (SLA)	Prentice, I.C., T. Meng, H. Wang, S.P. Harrison, J. Ni, G. Wang. 2011. Evidence for a universal scaling relationship of leaf CO2 drawdown along a moisture gradient. New Phytologist 190:169–180

Table S2-3. Literature search sources. This table provides detailed citation information for each paper used as a source for trait data. The Species name, USDA code (https://plants.sc.egov.usda.gov/), trait found in the paper and reference information are included.

DA code	**Trait found**	**Authors**	**Year**	**Title**	**Journal**	**Vol/Iss**
ACMI2	Seed weight	Fenner, M.	1983	Relationships between seed weight, ash content and seedling growth in twenty-four species of compositae	The New Phytologist	95/4
ACMI2	Maximum salinity tolerated	Niu, G. et al.	2007	Growth and landscape performance of ten herbaceous species in response to saline water irrigation	Journal of Environmental Horticulture	25/4
ACHY	Relative growth rate, Specific leaf area	Defalco, L.	2003	Physiological ecology of the invasive annual grass, *Bromus madritensis* ssp. *rubens*, and its interaction with native Mojave Desert species	University of Nevada, Reno Unpublished Dissertation	N/A
ACRE3	Shade tolerance	Alder, C.	2012	Evaluating integrated weed management: Russian knapweed control with goat grazing and aminopyralid	Utah State University Unpublished Thesis	N/A
ACRE3	Ability to reproduce sexually, Ability to reproduce vegetatively	Beck, K.G.	1994	Russian Knapweed Biology and Management	Colorado State University: University Cooperative Extension	N/A

ACRE3	Growth rate	Goslee, S. et al.	2001	Modeling invasive weeds in grasslands: the role of allelopathy in Acroptilon repens invasion	Ecological Modeling	139/1
ACRE3	Fire tolerance, Resprout ability, Spread rate,	Meyers, K.	2012	Phenology of the gall midge *Jaapiella ivannikovi fedotova* (Diptera: Cecidomyiidae), a biological control agent of Russian knapweed *Rhaponticum repens* (Asteraceae) in Wyoming	University of Wyoming Unpublished Dissertation	N/A
ACRE3	Anaerobic tolerance, Drought tolerance, Maximum salinity tolerate, Moisture use	Stannard, M.	1993	Overview of the basic biology, distribution and vegetative suppression of four knapweed species in Washington	Plant Materials Program	Technical Note #25
AGCR	Maximum salinity tolerated	Bischoff, J. and Werner, H.	1999	Salt salinity tolerance of common agricultural crops in South Dakota: Forages and grasses/grains and field crops	South Dakota State University Extension Unpublished Fact Sheet	903/5
AGCR	Maximum root depth	Eckert, R. et al.	1961	Responses of *Agropyron cristatum*, *A. Desertorum*, and other range grasses to three different sites in eastern Nevada	Ecology	42/4
ALMA12	Moisture use	NV Dept. of Agriculture	accessed June 2018	Camelthorn (*Alhagi maurorum*) - http://agri.nv.gov/Plant/Noxious_Weeds/WeedList/Camelthorn_(Alhagi_maurorum)/	N/A	N/A
ALMA12	Spread rate	DiTomaso et al.	2013	Weed Control in Natural Areas in the Western United States - https://wric.ucdavis.edu/information/natural%20areas/wr_A/Alhagi.pdf	Weed Research and Information Center	N/A
ALMA12	Growth rate, Anaerobic tolerance, Resprout ability	USDA	2014	Field Guide for Managing Camelthorn in the Southwest	N/A	N/A

AMAL	Seed weight	Cheplick, G.	2002	Size and architectural traits as ontogenetic determinants of fitness in a phenotypically plastic annual weed (*Amaranthus albus*)	Plant Species Biology	17/1
AMAL	Ability to reproduce vegetatively, Spread rate	Costea, M. and Tardif F.J.	2003	The Biology of Canadian weeds. 126. *Amaranthus albus* L., *A. blitoides* S. Watson and *A. blitum* L.	Canadian Journal of Plant Science	126
AMAL	Drought tolerance	Fenesi, A. et al.	2014	Can transgenerational plasticity contribute to the invasion success of annual plant species?	Oecologia	176/1
AMAL	Average height at maturity, Growth rate, Relative growth rate, Specific leaf area	Horak, M. and Loughin, T.	2000	Growth analysis of four *Amaranthus* species	Weed Science	48/1
AMAL	Shade tolerance	Stoller, E. and Meyers, R.	1989	Response of soybeans (*Glycine max*) and four broadleaf weeds to reduced irradiance	Weed Science	37/4
AMAL	Resprout ability	Sunderman, S.	2009	Fire patterns and post-fire vegetation response in a Mojave Desert spring ecosystem	U of NV, Reno Unpublished Dissertation	N/A
AMRE	Maximum salinity tolerated	Costea Mihai et al.	2004	The biology of Canadian weeds. 130. *Amaranthus retroflexus* L., *A. powellii* S. Watson and *A. hybridus* L.	Canadian Journal of Plant Science	84/2
AMRE	Fire tolerance, Resprout ability	Fornwalt, P.	2009	Disturbance impacts on understory plant communities of the Colorado Front Range	Colorado State University Dissertations	N/A
AMRE	Growth rate, Relative growth rate	Horak, M. and Loughin, T.	2000	Growth analysis of four *Amaranthus* species	Weed Science	48/2
AMRE	Shade tolerance	Mchlachlan, S. et al.	1993	Effect of corn-induced shading on dry matter accumulation, distribution, and architecture of redroot pigweed	Weed Science	41/4

AMRE	Seed weight	McWilliams E.L. et al.	1968	Variation in seed weight and germination in populations of *Amaranthus retroflexus* L.	Ecology	49/2
AMRE	Ability to reproduce vegetatively, Maximum root depth, Moisture use	University of AK, Anchorage	2011	redroot pigweed *Amaranthus retroflexus* L.	N/A	N/A
AMRE	Drought tolerance	Valerio et al.	2011	Quantifying the effect of drought on carbon dioxide-induced changes in competition between a C3 crop (tomato) and a C4 weed (*Amaranthus retroflexus*)	Weed Research	51/6
AMPS	Ability to reproduce sexually, Ability to reproduce vegetatively, Spread rate	Bassett, I.J. and Crompton, C.W.	1975	The Biology of Canadian Weeds. 11. *Ambrosia artemisiifolia* L. and *A. psilostachya* DC.	Canadian Journal of Plant Science	55
AMPS	Anaerobic tolerance, Drought tolerance, Moisture use, Resprout ability	Grimm, E.C.	2001	Trends and palaeoecological problems in the vegetation and climate history of the Northern Great Plains, U.S.A.	Biology and Environment: Proceedings of the Royal Irish Academy	101B/1/2
AMPS	Bloom period, Maximum salinity tolerated	Salzman, A. and Matthew P.	1985	Neighbors ameliorate local salinity stress for a rhizomatous plant in a heterogeneous environment	Oecologia	65/2
ARMI2	Specific leaf area	Almeida-Cortez, J.S. et al.	2004	Growth and chemical defense in relation to resource availability: tradeoffs or common responses to environmental stress?	Brazilian Journal of Ecology	64/2
ARMI2	Average height at maturity	Gross, R. et al.	1980	The Biology of Canadian Weeds. 38. *Arctium minus* (Hill) Bernh. and *A. lappa* L.	Canadian Journal of Plant Science	60

ARDR4	Maximum salinity tolerated	Sharif, F.E.	2012	In vitro NaCl tolerances of Artemisia dracunculus	Int. J. Med. Arom. Plants	2/4
ARDR4	Spread rate	University of AZ, Extension	2007	Growing Herbs	N/A	Bulletin #5
ARDR4	Moisture use	Utah State University Extension	2009	French Tarragon in the Garden	N/A	N/A
ASOF	Average height at maturity	Blasberg, C.	1932	Phases of the anatomy of Asparagus officinalis	Botanical Gazette	94/1
ASOF	Drought tolerance	Liddycoat, S. et al.	2009	The effect of plant growth-promoting rhizobacteria on asparagus seedlings and germinating seeds subjected to water stress under greenhouse conditions	Canadian Journal of Microbiology	55
ASOF	Maximum salinity tolerated	Shannon, M.C. and Grieve, C.M.	1998	Tolerance of vegetable crops to salinity	Scientia Horticulture	78/1-4
ATLE	Specific leaf area, Relative growth rate	Ishikawa, S.	2008	Growth and photosynthetic responses of one C3 and two C4 Chenopodiaceae plants to three CO2 concentration conditions.	Journal of Ecology and Field Biology	31/4
ATPA4	Anaerobic tolerance, Drought tolerance	Maganti, M. et al.	2005	Responses of spreading orach *(Atriplex patula)* and common lambsquarters (*Chenopodium album*) to soil compaction, drought, and waterlogging	Weed Science	53/1
ATPA4	Seed weight	Stevens, O.A.	1932	The number and weight of seeds produced by weeds	American Journal of Botany	19/9

BAEM	Ability to reproduce vegetatively, Anaerobic tolerance, Drought tolerance, Resprout ability Seed period, Shade tolerance	Mortenson, S.	2009	Plant community invasibility in riparian landscapes: Role of disturbance, geomorphology, and life history traits	U of NV, Reno Unpublished Dissertation	N/A
BAEM	Fire tolerance	Sunderman, S.	2009	Fire patterns and post-fire vegetation response in a Mojave Desert spring ecosystem	U of NV, Reno Unpublished Dissertation	N/A
BASA	Growth rate	Dreeson, D. et al.	N/A	Southwest riparian restoration considerations: New stock types, planting methods and site limitations	NRCS, USDA	N/A
BASA	Ability to reproduce sexually, Ability to reproduce vegetatively, Average height at maturity, Bloom period, Fire tolerance, Resprout ability, Seed period	Holmes, M.	1998	Management and ecology of willow baccharis in the Texas rolling plains	Texas Tech University Unpublished Master's Thesis	N/A
BASA	Maximum salinity tolerated, Moisture use	Munoz, A.	2007	Consumption of saltcedar and willow baccharis by Boer-cross goats	Angelo State University Unpublished Dissertation	N/A
BOBA2	Maximum salinity tolerated	Beauchamp, V. and Shafroth, P.	2011	Floristic composition, beta diversity, and nestedness of reference sites for restoration of xeroriparian areas	Ecological Applications	21/2
BOBA2	Seed period	Mehlhop, P.	1983	Temporal patterns of seed use and availability in a guild of desert ants	Ecological Entomology	8/1

BRTO	Spread rate	Alfaro, B. and Marshall, D.L.	2019	Phenotypic variation of life-history traits in native, invasive, and landrace populations of *Brassica tournefortii*	Ecology and Evolution	9
BRTO	Ability to reproduce vegetatively	Winkler, et al.	2019	Multiple introductions and population structure during the rapid expansion of the invasive Sahara mustard (*Brassica tournefortii*)	Ecology and Evolution	9
BRAR5	Seed period	Baskin, J.M. and Baskin, C.C.	1981	Ecology of germination and flowering in the weedy winter annual grass *Bromus japonicus*	Journal of Range Management	34/5
BRTE	Moisture use	Cline, J.F. et al.	1977	Comparison of soil water used by a sagebrush-bunchgrass and a cheatgrass community	Journal of Range Management	30/3
CANU4	Bloom period, Fire tolerance	CO Dept. of Agriculture	2016	Musk Thistle Identification and Management	N/A	N/A
CANU4	Ability to reproduce vegetatively	Desrochers, A.M. et al.	1988	The Biology of Canadian Weeds: 89. *Carduus nutans* L. and *Carduus acanthoides* L.	Canadian Journal of Plant Science	68
CANU4	Growth rate	Ervin, G. et al.	2007	Nodding Plumeless Thistle	Mississippi State University	N/A
CANU4	Drought tolerance	Han, J. and Young, S.	2016	Invasion during extreme weather: Success and failure in a temperate perennial grassland	Great Plains Research	68/1
CANU4	Resprout ability	Hull, A.C. and Evans, J.O.	1973	Musk thistle (*Carduus nutans*): An undesirable range plant	Rangeland Ecology and Management	26/5

CANU4	Maximum salinity tolerated	Kaya, G. et al.	2009	Comparative analysis for germination and seedling growth of wheat with some competitive weeds under salinity	Journal of Food, Agriculture & Environment	7/3&4
CAMI12	Fire tolerance	McLean, A.	1969	Fire resistance of forest species as influenced by root systems	Journal of Range Management	22/2
CAMI12	Bloom period	Mosquin, T.	1971	Competition for pollinators as a stimulus for the evolution of flowering time	Oikos	22/3
CAMI12	Seed period	Mulvey, R.L. and Hansen, E.M.	2011	*Castilleja* and *Pedicularis* confirmed as telial hosts for *Cronartium ribicola* in whitebark pine ecosystems of Oregon and Washington	Forest Pathology	41
CHAL7	Maximum salinity tolerated	Al-Oudat, M. and Quadir, M.	2011	The Halophytic Flora of Syria	International Center for Agricultural Research in the Dry Areas	N/A
CHAL7	Ability to reproduce sexually, Ability to reproduce vegetatively, Bloom period, Seed weight, Spread rate, Average height at maturity	Bassett, I.J. and Crompton, C.W.	1978	The Biology of Canadian Weeds: 32. *Chenopodium album* L	Canadian Journal of Plant Science	58
CHAL7	Growth rate, Moisture use	Curran, B. et al.	no date available	Biology and Management of Common Lambsquarters	The Glyphosate, Weeds, and Crops Series: Purdue University Extension	11
CHAL7	Specific leaf area	Kropff, M.J. and Spitters, C.J.T.	1992	An eco-physiological model for interspecific competition, applied to the influence of *Chenopodium album* L. on sugar beet. I. Model description and parameterization	Weed Research	32
CHAL7	Anaerobic tolerance, Drought tolerance	Maganti, M. et al.	2005	Responses of spreading orach (*Atriplex patula*) and common lambsquarters (*Chenopodium album*) to soil compaction, drought, and waterlogging	Weed Science	53/1

CHFR3	Shade tolerance	Butterwick, M. et al.	1992	Vascular Plants of the Northern Hualapai Mountains, Arizona	Journal of the Arizona-Nevada Academy of Science	24-25
CHFR3	Fire tolerance	Fornwalt, P. and Kaufmann, M.	2006	Short-term effects of fire and postfire rehabilitation on the forest understory: A case study from the Colorado Front Range	Newsletter of the Colorado Native Plant Society	30/1
CHFR3	Ability to reproduce vegetatively	Hamrick, J.L.	1979	Relationships between life history characteristics and electrophoretically detectable genetic variation in plants	Annual Review of Ecology and Systematics	10
CHFR3	Drought tolerance, Maximum salinity tolerated	Weber, D.J. and Hanks, J.	2008	Salt tolerant plants from the Great Basin region of the United States	CH5 in Ecophysiology of High Salinity Tolerant Plants	N/A
CHFR3	Anaerobic tolerance	Wolden, L.G. et al.	1995	Flora and vegetation of the Hassayampa River Preserve, Maricopa County, Arizona	Journal of the Arizona-Nevada Academy of Science	28/1-2
CHTE2	Specific leaf area	Ahrendsen, D.L.	2014	Biodiversity assessment using next-generation sequencing: A rosid comparison of phylogenetic and functional diversity between Nebraska grasslands	U of NE Omaha Unpublished Dissertation	N/A
CHTE2	Ability to reproduce vegetatively	Donaldson, S. and Mazet, W.	2011	A Northern Nevada homeowner’s guide to identifying and managing blue mustard	U of NV Extension Fact Sheet	N/A
CHTE2	Anaerobic tolerance	Downard, R. et al.	2017	Wetland plants of Great Salt Lake: A guide to identification, communities, & bird habitat	Utah State University Extension	N/A

CHTE2	Growth rate	Virtue, J. and Thomas, P.	1999	Field screening techniques to assess new crop weeds	Twelfth Australian Weed Conference	N/A
CHTE2	Ability to reproduce sexually, Bloom period	Vorndam, M.	2016	Wicked Weeds: Purple mustard, *Chorispora tenella*	From the Ground Up (CSU extension)	7/1
CHTE2	Shade tolerance	Yin, L.C. et al.	2012	Effects of phosphorus and light intensity on the growth and competition of the two weed species, *Veronica persica* and *Chorispora tenella*	Weed Biology and Management	12
CIAR4	Fire tolerance	Kraushar, M. et al.	2012	Control of Canada thistle in CRP and other non-crop acreage	Purdue University Extension	N/A
CIAR4	Ability to reproduce sexually, Ability to reproduce vegetatively, Maximum root depth, Moisture use	Moore, R.J.	1975	The Biology of Canadian Weeds. 13. *Cirsium arvense* (L.) Scop	Canadian Journal of Plant Science	55
CIAR4	Maximum salinity tolerated	Unknown	2007	Pest management – Invasive plant control Canada thistle (*Cirsium arvense*)	NRCS - Conservation Practice Job Sheet	N/A
CIAR4	Anaerobic tolerance	Tiley, G.	2010	Biological flora of the British Isles: *Cirsium arvense* (L.) Scop.	Journal of Ecology	98/4
CIAR4	Growth rate	WA State Noxious Weed Control Board	NR	Canada thistle *Cirsium arvense*	Clark County Public Works Vegetation Management Program	N/A

CIAR4	Drought tolerance	Wilson, Jr., R.G.	1979	Germination and seedling development of Canada thistle (*Cirsium arvense*)	Weed Science	27/2
CIVU	Drought tolerance	Klinkhamer, P. and de Jong, T.	1993	*Cirsium vulgare* (Savi) Ten.	Journal of Ecology	81/1
COUM	Seed period	Barnes, C. et al.	2005	Spatial and temporal dynamics of *Puccinia andropogonis* on *Comandra umbellata* and *Andropogon gerardii* in a native prairie	Canadian Journal of Botany	83
COUM	Bloom period	Dunnell, K. and Travers, S.	2011	Shifts in the flowering phenology of the northern Great Plains: Patterns over 100 years	American Journal of Botany	98/6
COUM	Average height at maturity	Fisk, J.R. and Hoover, E.	2015	Wild fruits of Minnesota: a field guide	N/A	N/A
COUM	Drought tolerance	Newton, R.	2008	A floristic inventory of selected Bureau of Land Management wetlands in Wyoming	University of Wyoming, Unpublished Thesis	N/A
COUM	Ability to reproduce vegetatively	Reynolds, H. et al.	2007	No effect of varying soil resource heterogeneity on plant species richness in a low fertility grassland	Journal of Ecology	95/4
COAR4	Spread rate	Frazier, J.	1943	Nature and rate of development of root system of *Convolvulus arvensis*	Botanical Gazette	104/3
COAR4	Maximum salinity tolerated	Mostafavi, K. and Farid G.	2012	Effects of salt and drought stresses on germination and seedling growth of bindweed (*Convolvulus arvensis* L.)	Research Journal of Applied Sciences, Engineering and Technology	4/21
COAR4	Anaerobic tolerance	Scott, J.	2008	Bidding farewell to the dreaded bindweed	Oregon State University Extension: Gardening	N/A

COSE16	Average height at maturity, Growth rate	Pijut, P.	2004	*Cornus sericea* L.	Forest Service, USDA	N/A
DACA7	Average height at maturity	Iwaasa, A.D. et al.	2014	Forage and nutritional benefits of grazing purple prairie clover and white prairie clover on western Canadian grasslands	Proceedings of the 10th Prairie Conservation and Endangered Species Conference	N/A
DACA7	Shade tolerance	Leidolf, A. and McDaniel, S.	1998	A floristic study of Black Prairie plant communities at Sixteen Section Prairie, Oktibbeha County, Mississippi	Southern Appalachian Botanical Society	63/1
DACA7	Specific leaf area	Mischkolz, J. et al.	2016	Assembling productive communities of native grass and legume species: Finding the right mix	Applied Vegetation Science	19/1
DACA7	Bloom period	Rafferty, N. and Ives, A.	2011	Effects of experimental shifts in flowering phenology on plant-pollinator interactions	Ecology Letters	14/1
DACA7	Fire tolerance	Towne, E.G. and Knapp, A.K.	1996	Biomass and density responses in tallgrass prairie legumes to annual fire and topographic position	American Journal of Botany	83/2
DAST	Ability to reproduce sexually, Ability to reproduce vegetatively, Spread rate	Weaver, S.E. and Warwick, S.I.	1984	*Datura stramonium* L.	The Biology of Canadian Weeds	64
DEPI	Maximum salinity tolerated	Orsini, F. et al.	2010	A comparative study of salt tolerance parameters in 11 wild relatives of *Arabidopsis thaliana*	The Journal of experimental Botany	61/13
FOAN	Specific leaf area	Maiti et al.	2014	Variability in leaf traits of 14 native woody species in semiarid regions of northeastern Mexico	International Journal of Bio-resource and Stress Management	5/4

FOAN	Average height at maturity	Ramirez-Lozano, R.G. et al.	2013	Composition and diversity of the vegetation in four sites of Mexico's Northeast	Madera y Bosques	19/2
FOAN	Drought tolerance	Gonzalez-Rodriguez, H. et al.	2016	Seasonal water relations in four co-existing native shrub species from northeastern Mexico	Arid Land Research and Management	30/4
GAPA6	Bloom period, Growth rate, Seed period	Chenault, T.P.	1940	The phenology of some bob-white food and cover plants in Brazos County, Texas	The Journal of Wildlife Management	4/4
GAPA6	Drought tolerance	Huang, P. et al.	2011	Physiological responses of exotic weeds *Gaura parviflora* to drought stress.	Journal of Northeast Agricultural University	42/4
GAPA6	Seed weight	Stevens, O.A.	1957	Weights of seeds and numbers per plant	Weeds	5/1
GUMI	Moisture use	Ralphs, M. and McDaniel, K.	2011	Broom snakeweed (*Gutierrezia sarothrae*): Toxicology, ecology, control, and management	Invasive Plant Science and Management	4/1
HAGL	Seed weight	Ahmed, M.Z. and Ajmal, K.	2010	Tolerance and recovery responses of playa halophytes to light, salinity and temperature stresses during seed germination	Flora	205/11
HAGL	Growth rate	Cronin, E.	1965	Ecological and physiological factors influencing chemical control of *Halogeton glomeratus*	U.S. Dept. of Agriculture	1325
HAGL	Maximum salinity tolerated	Khan, A. et al.	2001	Seed germination characteristics of *Halogeton glomeratus*	Canadian Journal of Botany	79/10
HAGL	Fire tolerance	St Clair, S. et al.	2016	Biotic resistance and disturbance: Rodent consumers regulate post-fire plant invasions and increase plant community diversity	Ecology	97/7

HAGL	Drought tolerance	Wang, J. et al.	2015	Transcriptomic profiling of the salt-stress response in the halophyte *Halogeton glomeratus*	BMC Genomics	16/169
HAGL	Average height at maturity	Zappettini, G.	1953	The taxonomy of *Halogeton glomeratus*	The American Midland Naturalist	50/1
HEAN3	Specific leaf area	Rosenthal et al.	2002	Phenotypic differentiation between three ancient hybrid taxa and their parental species	International Journal of Plant Sciences	8/3
HEPE	Maximum salinity tolerated	Bush, J.K. and Van Auken, O.W.	2004	Relative competitive ability of *Helianthus paradoxus* and its progenitors, *H. annuus* and *H. petiolaris* (Asteraceae), in varying soil salinities	International Journal of Plant Sciences	165/2
HEPE	Bloom period	Gross, B. et al.	2004	Reconstructing the origin of *Helianthus deserticola*: Survival and selection on the desert floor	The American Naturalist	164/2
HEPE	Specific leaf area	Rosenthal, D. et al.	2002	Phenotypic differentiation between three ancient hybrid taxa and their parental species	International Journal of Plant Sciences	163/3
HEPE	Drought tolerance	Sobrado, M.A. and Turner, N.	1983	A comparison of the water relations characteristics of *Helianthus annuus* and *Helianthus petiolaris* when subjected to water deficits	Oecologia	58/3
IPAG	Growth rate, Resprout ability	Belsky, A.J. et al.	1993	Overcompensation by plants: Herbivore optimization or red herring?	Evolutionary Ecology	7/1
IPAG	Maximum salinity tolerated	Borden, R. and Black, R,	2005	Volunteer revegetation of waste rock surfaces at the Bingham Canyon Mine, Utah	Journal of Environmental Quality	34/6
IPAG	Fire tolerance	Paige, K.	1992	The effects of fire on scarlet gilia: An alternative selection pressure to herbivory?	Oecologia	92/2
KOSCT	Average height at maturity	Dodd, R. and Randall, P.	2002	Eradication of kochia (*Bassia scoparia* (L.) A.J. Scott, Chenopdiaceae) in western Australia	Proceedings of the 13th Australian Weeds Conference	

LEDE	Maximum salinity tolerated	Orsini, F. et al.	2010	A comparative study of salt tolerance parameters in 11 wild relatives of *Arabidopsis thaliana*	The Journal of experimental Botany	61/13
OEVI	Shade tolerance	Cochrane, T. and Iltis, H.	2000	Atlas of the Wisconsin Prairie and Savanna Flora	N/A	N/A
OEVI	Drought tolerance	Gilbert, E. and Licher, M.	2005	Flora and vegetation of the West Fork of Oak Creek Canyon, Coconino County, Arizona	Desert Plants	21/1
OEVI	Fire tolerance	Morgan, P. et al.	2015	Vegetation response to burn severity, native grass seeding, and salvage logging	Fire Ecology	11/2
OEVI	Maximum salinity tolerated	Rolfsmeier, S.	1993	The saline wetland-meadow vegetation and flora of the North Platte River Valley in the Nebraska Panhandle	Transactions of the Nebraska Academy of Sciences and Affiliated Societies	N/A
OPPH	Fire tolerance	McLaughlin, S. and Bowers, J.	1982	Effects of wildfire on a Sonoran Desert plant community	Ecology	63/1
OPPH	Bloom period	Osborn, M.M. et al.	1988	Pollination biology of *Opuntia polycantha* and *Opunia phaeacanth* (Cactaceae) in southern Colorado	Plant Systematics and Evolution	159/1
PECR2	Drought tolerance	Kleinwachter, M. et al.	2014	Moderate drought and signal transducer induced biosynthesis of relevant secondary metabolites in thyme (*Thymus vulgaris*), greater celandine (*Chelidonium majus*) and parsley (*Petroselinum crispum*)	Industrial Crops and Products	64/1
PECR2	Maximum salinity tolerated	McFarland, M. et al.	2014	An index of salinity and boron tolerance of common native and introduced plant species in Texas	Texas A&M Agrilife Extension	N/A
PECR2	Specific leaf area	Pokhrel, B. et al.	2017	Processing methods of organic liquid fertilizers affect nutrient availability and yield of greenhouse grown parsley	Renewable Agriculture and Food Systems	19/1
PHCA5	Shade tolerance	Falck, M. and Garske, S.	2003	Invasive non-native plant management during 2002	Great Lakes Indian Fish and Wildlife Commission	N/A

PHCA5	Average height at maturity	Sangster, A.G. et al.	1983	A developmental study of silicification in the trichomes and associated epidermal structures of the inflorescence bracts of the grass, *Phalaris canariensis* L.	Annals of Botany	52/2
RUCR	Fire tolerance	Contreras, T. et al.	2011	Fire regimen and spread of plants naturalized in central Chile	Revista Chilena de Historia Natural	84/3
RUCR	Resprout ability	Hatcher, P.	1996	The effect of insect-fungus interactions on the autumn growth and over-wintering of *Rumex crispus* and *R. obtusifolius* seedlings	Journal of Ecology	84/1
SCPR4	Average height at maturity	Brink, G.E. et al.	2013	Residual sward height effects on growth and nutritive value of grazed temperate perennial grasses	Crop Science	53/5
SCPR4	Specific leaf area	Siefert, A., Fridley, J.D., Ritchie, M.E.	2014	Community functional responses to soil and climate at multiple spatial scales: When does intraspecific variation matter?	PlosOne	9/10
SCPR4	Seed weight	Wali, P.R. et al.	2008	Endophyte infection, nutrient status of the soil and duration of snow cover influence the performance of meadow fescue in sub-arctic conditions	Grass and Forage Science	63/3
SCPR4	Moisture use	Watkins, E. et al.	2011	Low-input turfgrass species for the North Central United States	Applied Turfgrass Science	8/1
SCLI11	Average height at maturity	Lonard, R. and Judd, F.	2010	The biological flora of coastal dunes and wetlands: *Schizachyrium littorale* (G. Nash) E. Bicknell	Journal of Coastal Research	264
SCLI11	Anaerobic tolerance	Maricle, B.R. et al.	2014	Effect of ethanol toxicity on enzyme activity in anaerobic respiration in plants	Transactions of the Kansas Academy of Science	117/3-4
BOMA7	Growth rate	Blanch, S. et al.	1999	Growth and resource allocation in response to flooding in the emergent sedge *Bolboschoenus medianus*	Aquatic Botany	63/2
BOMA7	Shade tolerance	Caton, B. P. et al.	2010	A Practical Field Guide to Weeds of Rice in Asia	N/A	N/A

BOMA7	Specific leaf area	Clevering, O. and Hundscheid, M.	1998	Plastic and non-plastic variation in growth of newly established clones of *Scirpus* (*Bolboschoenus*) *maritimus* L. grown at different water depths	Aquatic Botany	62/1
BOMA7	Maximum salinity tolerated	Santos, M. et al.	2015	Phytoremediation of cadmium by the facultative halophyte plant *Bolboschoenus maritimus* (L.) Palla, at different salinities	Environmental Science and Pollution Research	22/20
SONI	Specific leaf area	Kremer, E. and Kropff, M.J.	1999	Comparative growth of triazine-susceptible and -resistant biotypes of *Solanum nigrum* at different light levels.	Annals of Botany	83/6
SOPA10	Drought tolerance	Staley, J.T. et al.	2007	Drought impacts on above-belowground interactions: Do effects differ between annual and perennial host species?	Basic and Applied Ecology	9/6
SOAR2	Fire tolerance	Ahlgren, C.E.	1960	Some effects of fire on reproduction and growth of vegetation in northeastern Minnesota	Ecology	41/3
SOAR2	Average height at maturity, Growth rate	Lemna, W. and Messersmith C.	1990	The biology of Canadian weeds. 94. *Sonchus arvensis* L.	Revue canadienne de la science du sol	70/2
SOAR2	Anaerobic tolerance	Mallik, A. et al.	2001	Vegetation zonation among the microhabitats in a lacustrine environment: Analysis and application of belowground species trait patterns	Ecological Engineering	18/2
SOAR2	Drought tolerance	van Tooren, B.F. et al.	1983	Succession and fluctuation in the vegetation of a Dutch beach plain	Vegetation	53/3
SPPE	Specific leaf area	Henschke et al.	2018	Effect of salinity on selected physiological and morphological characteristics of *Spartina pectinata* (Link.) 'Aureomarginata'	Acta Sci. Pol. Hortorum Cultus	17/6
SUMO	Seed period	Felger, R.S. et al.	2015	Ajo Peak to Tinajas Atlas: A flora of southwestern Arizona, Part 9. Eudicots: *Convolvulaceae* - morning glory family	Phytoneuron	2
SUMO	Drought tolerance	Limon, S.M. et al.	2014	Leaf, stem and root content of proline in *Atriplex canescens* and *Suaeda nigra*	International Journal of Bio-resource and Stress Management	5/1

SYER	Average height at maturity, Anaerobic tolerance, Moisture use, Salinity tolerance, Shade tolerance, Growth rate, Ability to reproduce vegetatively, Resprout, Bloom period	Chmielewski, J.G. and Semple, J.C.	2003	The biology of Canadian weeds. 125. *Symphyotrichum ericoides* (L.) Nesom (*Aster ericoides* L.) and *S. novae-angliae* (L.) Nesom (*A. novae-angliae* L.)	Canadian Journal of Plant Science	83/4
SYER	Fire tolerance	Towne, E.G. and Kemp, K.E.	2003	Vegetation dynamics from annually burning tallgrass prairie in different seasons	Journal of Range Management	56/2
TACH	Moisture use	Cleverly, J.R. et al.	1997	Invasive capacity of *Tamarix ramosissima* in a Mojave Desert floodplain: The role of drought	Oecologia	111/1
TACH	Specific leaf area	Nagler, P.L. et al.	2009	Wide-area estimates of saltcedar (*Tamarix* spp.) evapotranspiration on the lower Colorado River measured by heat balance and remote sensing methods	Ecohydrology	2/1
THIN	Bloom period	Al-Shehbaz, I.A.	1972	The biosystematics of the genus *Thelypodium* (Cruciferae)	Contributions from the Gray Herbarium of Harvard University	no. 204
THIN	Ability to reproduce sexually, Average height at maturity	Welsh, S.L. and Reveal, J.L.	1977	Utah flora: Brassicaceae (Cruciferae)	The Great Basin Naturalist	37/3
THIN6	Seed weight, Specific leaf area	Larson, J.E. et al.	2015	Do key dimensions of seed and seedling functional trait variation capture variation in recruitment probability?	Oecologia	181/1

TORY	Seed period	Brown, D.	2016	Identifying poison ivy isn't always easy to do	Michigan State University	n/a
TORY	Growth rate	French, J.	1977	Growth relationships of leaves and internodes in viny angiosperms with different modes of attachment	American Journal of Botany	64/3
TORY	Specific leaf area	Jelesko, J. et al.	2017	Differential responses to light and nutrient availability by geographically isolated poison ivy accessions	Northeastern Naturalist	24/2
TORY	Anaerobic tolerance	Karty, R.	2006	The influence of urbanization on structure and function of riparian forest fragments in New Haven County, Connecticut	Yale University	N/A
TYAN	Specific leaf area	Farnsworth, E.J. and Meyerson, L.A.	2003	Comparative ecophysiology of four wetland plant species along a continuum of invasiveness	Wetlands	23/4
ULPU	Ability to reproduce vegetatively	Duansuram et al.	2009	Performance of Siberian elm (*Ulmus pumila*) on steppe slopes of the northern Mongolian mountain taiga: Drought stress and herbivory in mature trees	Environmental and Experimental Botany	66/1
URDI	Fire tolerance, Resprout ability, Resprout ability	Fornwalt, P.J.	2009	Disturbance impacts on understory plant communities of the Colorado Front Range	Colorado State University Dissertations	N/A
URDI	Anaerobic tolerance, Drought tolerance, Moisture use, Seed weight, Spread rate	Taylor, K.	2009	Biological flora of the British Isles: *Urtica dioica* L.	Journal of Ecology	97/6
VETH	Average height at maturity, Drought tolerance, Moisture use	Gross, K.L. and Werner, P.A.	1978	The biology of Canadian weeds. 28. *Verbascum thapsus* L. and *V. blattaria* L.	Canadian Journal of Plant Science	58/1

VETH	Fire tolerance	Parker, I. et al.	2003	An evolutionary approach to understanding the biology of invasions: Local adaptation and general-purpose genotypes in the weed *Verbascum thapsus*	Conservation Biology	17/1
XAST	Seed period	James, T. K. et al.	2016	Seed germination characteristics and control options for Noogoora bur (*Xanthium strumarium*) in commercial maize production	New Zealand Plant Protection	69
XAST	Moisture use	Jones, R.E. Jr. and Walker, R.H.	1993	Effect of interspecific interference, light intensity, and soil moisture on soybean (*Glycine max*), common cocklebur (*Xanthium strumarium*), and sicklepod (*Cassia obtusifolia*) water uptake	Weed Science	41/4

Table S2-4. Abbreviations for environmental variables. Abbreviated variable labels are used in supplemental Figure S2-1. This table provides definitions for those variables and notes whether they were included in the study and if not, why.

Abbreviation	**Full variable name**	**Units**	**Notes**
Riv_width	River width	meters	Included in study
Elev_asl	Elevation above sea level	meters	Included in study
relelev	Relative elevation	centimeters	Included in RDA, not included in mixed models due to missing values (43 blanks out of 95)
Dist_water	Distance to nearest water source (river water's edge)	meters	Included in study
EC	Soil electroconductivity	µS/cm	Included in study

pptnorm	Precipitation 30-year average	centimeters	Not included due to high correlation with elevation above sea level
tmaxnorm	Max temperature 30-year average	Celsius	Not included due to high correlation with elevation above sea level
tminnorm	Min temperature 30-year average	Celsius	Not included due to high correlation with elevation above sea level
pptyear	Precipitation year of sampling	centimeters	Included in study
tminyear	Min temperature year of sampling	Celsius	Not included due to high correlation with elevation above sea level
TACH	*Tamarix* percent cover		Included in study
Rel_Tach	*Tamarix* cover relative to total overstory		Included in study

Table S2-5. Average and standard deviation of each trait calculated from all species included in each guild, as well as a description of the guild and representative species. n equals the number of species found in each guild. Categorical variables are broken down by the number of species for each level in each group.

Trait/Attribute	**Non-clonal annual forbs (n=34)**	**Non-clonal annual graminoids (n=4)**	**Non-clonal resource acquisitive perennials (n=5)**	**Non-clonal resource conservative perennials (n=16)**	**Non-clonal drought tolerant trees (n=3)**

Specific leaf area	198.64 ± 76.85	310.83 ± 74.93	292.50 ± 179.14	111.87 ± 66.34	141.80 ± 9.61
Seed weight	4.55 ± 11.18	1.78 ± 1.34	1.41 ± 1.78	1.22 ± 1.70	12.89 ± 8.32
Height at maturity	0.88 ± 0.60	0.435 ± 0.18	0.55 ± 0.40	0.68 ± 0.36	12.11 ± 2.93
Anaerobic tolerance	1.72 ± 0.94	3.25 ± 0.96	2.60 ± 0.55	1.33 ± 0.65	1.33 ± 0.58
Drought tolerance	3.03 ± 0.95	2.75 ± 0.96	3 ± 0	3.81 ± 0.40	3 ± 0
Fire tolerance	2.70 ± 1.17	2.50 ± 1.29	2.5 ± 1.29	2.67 ± 0.98	2 ± 1
Moisture use	2.96 ± 0.71	3.25 ± 0.50	3.2 ± 0.45	2.28 ± 0.47	2.33 ± 0.58
Salinity tolerance	2.33 ± 1.18	2.25 ± 1.50	2.4 ± 0.89	2.87 ± 0.92	1.67 ± 1.155
Shade tolerance	1.21 ± 0.49	1 ± 0	2.6 ± 0.55	1.07 ± 0.27	1.33 ± 0.58
Growth rate	2.76 ± 0.66	3 ± 0	2.25 ± 0.50	2 ± 0.71	2 ± 0
Spread rate	1.04 ± 0.20	1 ± 0	1.2 ± 0.45	1.07 ± 0.27	1 ± 0
Bloom period - median	7.45 ± 1.55	7 ± 1.08	7 ± 1.50	7.59 ± 1.36	4.5 ± 0.5
Bloom period - total	4.00 ± 1.77	5 ± 2.16	5.2 ± 2.49	4.94 ± 1.53	2.33 ± 0.58
Seed period - median	8.20 ± 2.91	4.25 ± 4.60	7.83 ± 1.61	8.62 ± 1.40	8 ± 1.73
Seed period - total	4.20 ± 1.54	4.5 ± 2.12	7 ± 1.73	5.23 ± 1.88	6 ± 0
Vegetative reproduction					
Yes	0	0	0	0	0
No	34	4	5	15	3
Resprout ability					
Yes	4	0	1	3	1
No	23	4	3	10	2
Lifeform					

Forb/Herb	34	0	4	9	0
Graminoid	0	4	1	4	0
Shrub	0	0	0	3	0
Tree	0	0	0	0	3
Wetland affinity status					
Hydro	2	2	0	1	0
Mesic	19	1	4	2	1
Xeric	0	0	0	2	0
Unknown	13	1	1	11	2
Duration					
Annual	30	4	0	0	0
Perennial	4	0	5	16	3
Nativity					
Native	12	0	3	16	2
Non-native	22	4	2	0	1
Description	Non-clonal forbs with a wide range of SLA values and anaerobic/drought tolerances. Slow spreading annuals with midweight seeds. Some are able to resprout.	Non-clonal graminoids with a high SLA and a range of drought/anaerobic tolerances. All are slow spreading annuals with light seeds and long bloom period.	Non-clonal forbs and graminoids with a high SLA. All are slow spreading, perennials with light seeds and long bloom period. Some are able to resprout.	Non-clonal forbs, graminoids and shrubs with a low SLA. All are slow spreading, perennials with light seeds and long bloom period. Some are able to resprout.	Non-clonal trees, many of which can resprout following disturbance. Drought tolerant with midweight seeds and low SLA.

Representative species	*Salsola tragus (Russian thistle); Kochia scoparia (Common kochia); Lactuca serriola (Prickly lettuce)*	*Echinochloa crus-galli (Barnyard grass); Bromus japonicus (Field brome); Bromus tectorum (Cheatgrass)*	*Taraxacum officinale (Common dandelion); Plantago lanceolata (Narrowleaf plantain); Elymus canadensis (Canadian wildrye)*	*Ericameria nauseosa (Rubber rabbitbrush); Sporobolus airoides (Alkali sacaton); Gutierrezia sarothrae (Broom snakeweed)*	*Morus alba (White mulberry); Malus spp. (Crab apple)*
Trait/Attribute (cont.)	**Clonal anaerobic tolerant trees (n=7)**	**Clonal anaerobic tolerant perennials (n=21)**	**Clonal drought tolerant perennials (n=21)**	**Clonal resource conservative perennials (n=14)**	
SLA	159.81 ± 42.51	144.35 ± 68.22	207.42 ± 86.11	126.40 ± 71.11	
Seed weight	21.56 ± 29.97	2.05 ± 3.75	9.46 ± 24.53	7.60 ± 10.63	
Height at maturity	11.69 ± 7.03	1.41 ± 1.02	0.79 ± 0.57	1.12 ± 0.65	
Anaerobic tolerance	2.83 ± 0.98	3.65 ± 0.59	2.13 ± 0.99	1.54 ± 0.88	
Drought tolerance	3 ± 0.82	2.1 ± 0.81	3.10 ± 0.88	3.29 ± 0.73	
Fire tolerance	2.86 ± 1.21	3.55 ± 0.94	3.59 ± 0.80	2.7 ± 1.11	
Moisture use	3.57 ± 0.53	3.67 ± 0.48	2.68 ± 0.67	2.64 ± 0.74	
Salinity tolerance	2.86 ± 0.90	2.48 ± 0.98	2.68 ± 1.34	2.78 ± 1.12	
Shade tolerance	1.43 ± 0.53	1.40 ± 0.68	1.15 ± 0.49	1.54 ± 0.78	
Growth rate	3 ± 0	2.43 ± 0.68	2.54 ± 0.82	2.25 ± 0.75	
Spread rate	2 ± 0.89	3.20 ± 0.95	3.12 ± 0.96	2 ± 1.18	
Bloom period - median	0.85 ± 2.86	6.50 ± 1.50	7.74 ± 1.32	5.93 ± 1.62	
Bloom period - total	2.86 ± 0.90	3 ± 1.12	3.10 ± 0.89	2.86 ± 1.17	

Seed period - median	7.33 ± 3.36	7.67 ± 1.99	8.58 ± 2.32	8.23 ± 1.27	
Seed period - total	4 ± 1.55	5.11 ± 2.14	4.38 ± 1.71	4.77 ± 1.83	
Vegetative reproduction					
Yes	6	21	20	14	
No	1	0	0	0	
Resprout ability					
Yes	7	19	14	13	
No	0	0	0	0	
Lifeform					
Forb/Herb	0	5	21	2	
Graminoid	0	14	0	6	
Shrub	0	2	0	6	
Tree	7	0	0	0	
Wetland affinity status					
Hydro	3	13	1	1	
Mesic	2	7	10	7	
Xeric	1	0	2	1	
Unknown	1	1	8	5	
Duration					
Annual	0	0	1	0	
Perennial	7	21	20	14	
Nativity					
Native	6	19	11	12	
Non-native	1	2	10	2	

Description	Clonal, resprouting trees. Moderately anaerobic tolerant with midweight seeds and medium SLA.	Clonal, resprouting forbs, graminoids and shrubs. All are fast spreading perennials with high moisture use, light seeds, a wide range of SLA values and high anaerobic tolerance.	Clonal, resprouting drought tolerant forbs. Fast spreading perennials with midweight seeds and medium SLA.	Clonal, resprouting drought tolerant forbs, graminoids and shrubs. Slow spreading with midweight seeds and low SLA.
Representative species	*Prunus virginiana (Chokecherry); Acer negundo (Boxelder); Betula occidentalis (Water birch)*	*Phragmites australis (Common reed); Glycyrrhiza lepidota (Wild licorice); Salix exigua (Coyote willow)*	*Acroptilon repens (Rusian knapweed); Cirsium arvense (Canada thistle); Convolvulus arvensis (Field bindweed)*	*Sarcobatus vermiculatus (Greasewood); Agropyron cristatum (Crested wheatgrass); Atriplex canescens (Fourwing saltbush)*

Table S2-6. Details of RDAs used to calculate individual and overlapping portions of explained variation presented in figure 4 of the main manuscript. This figure includes details for the RDA with all environmental variables and *Tamarix*, as well as details for the RDA with only environmental variables and the RDA with only *Tamarix* and relative *Tamarix* cover.

	FULL RDA		**Environment only RDA**		***Tamarix* only RDA**	
Inertia Proportion						
Total	0.381	1.000	0.381	1.000	0.381	1.000
Constrained	0.142	0.374	0.105	0.276	0.076	0.198
Unconstrained	0.238	0.627	0.276	0.724	0.305	0.802
Importance of components:						
	RDA1	RDA2	RDA1	RDA2	RDA1	RDA2
Eigenvalue	0.086	0.028	0.066	0.017	0.068	0.007
Proportion explained	0.227	0.073	0.173	0.044	0.179	0.020
Cumulative proportion	0.227	0.300	0.173	0.217	0.179	0.198
Adjusted R2	0.315		0.227		0.181	

Table S2-7. ANOSIM for regions plotted as ellipses in Figure 4 and as random effects in mixed effect models. Significant p values indicate that similarity within groups is greater than between groups. Higher values of the test statistic - *R* - indicate greater similarity within groups as compared to between groups. 0 - total similarity, 1 - total dissimilarity

	Colorado river in Colorado	Colorado river in Utah	Dolores river above San Miguel	Dolores river below San Miguel	Green river - North	Green river - South
Colorado river in Colorado						
Colorado river in Utah	0.1899 **p=0.0273**					
Dolores river above San Miguel	0.1817 **p=0.0507**	**0**.3673 **p=0.00001**				
Dolores river below San Miguel	0.2472 **p=0.0265**	0.3225 **p=0.00000**	0.004936 p=0.3387			
Green river - North	0.2209 **p=0.0476**	0.4585 **p=0.0012**	0.3384 **p=0.013**	0.3196 **p=0.0238**		
Green river - South	0.4871 **p=0.0033**	0.2225 p=0.122	0.7421 **p=0.0000**	0.6504 **p=0.0000**	0.2956 **p=0.0543**	

Table S2-8. Details of mixed models used to calculate individual and overlapping portions of explained variation in cover of “Clonal anaerobic perennials”. The environmental model uses only environmental variables, the *Tamarix* model uses only relative *Tamarix* cover, the full model uses both sets of variables as fixed effects. Region is used as the random effect in all models. Forward and backward stepwise selection was used to select the best model in all cases where more than one fixed effect was used. Variables with an asterisk next to their name were log transformed to improve model fit.

Full	**Value**	**Standard error**	**DF**	**t-value**	**p-value**	**R2m**	**R2c**
(Intercept)	2.608	0.203	87	12.860	0.000	0.49	0.53
Distance to water*	-0.636	0.133	87	-4.780	0.000		
Relative *Tamarix cover*	-0.822	0.137	87	-6.010	0.000		
Environment only							
(Intercept)	2.322	0.377	87	6.165	0.000	0.26	0.46
River width*	0.331	0.154	87	2.148	0.035		
Distance to water*	-0.915	0.143	87	-6.400	0.000		
Relative *Tamarix* only							
(Intercept)	2.591	0.212	88	12.218	0.000	0.38	0.42
Relative *Tamarix* cover	-1.056	0.143	88	-7.410	0.000		

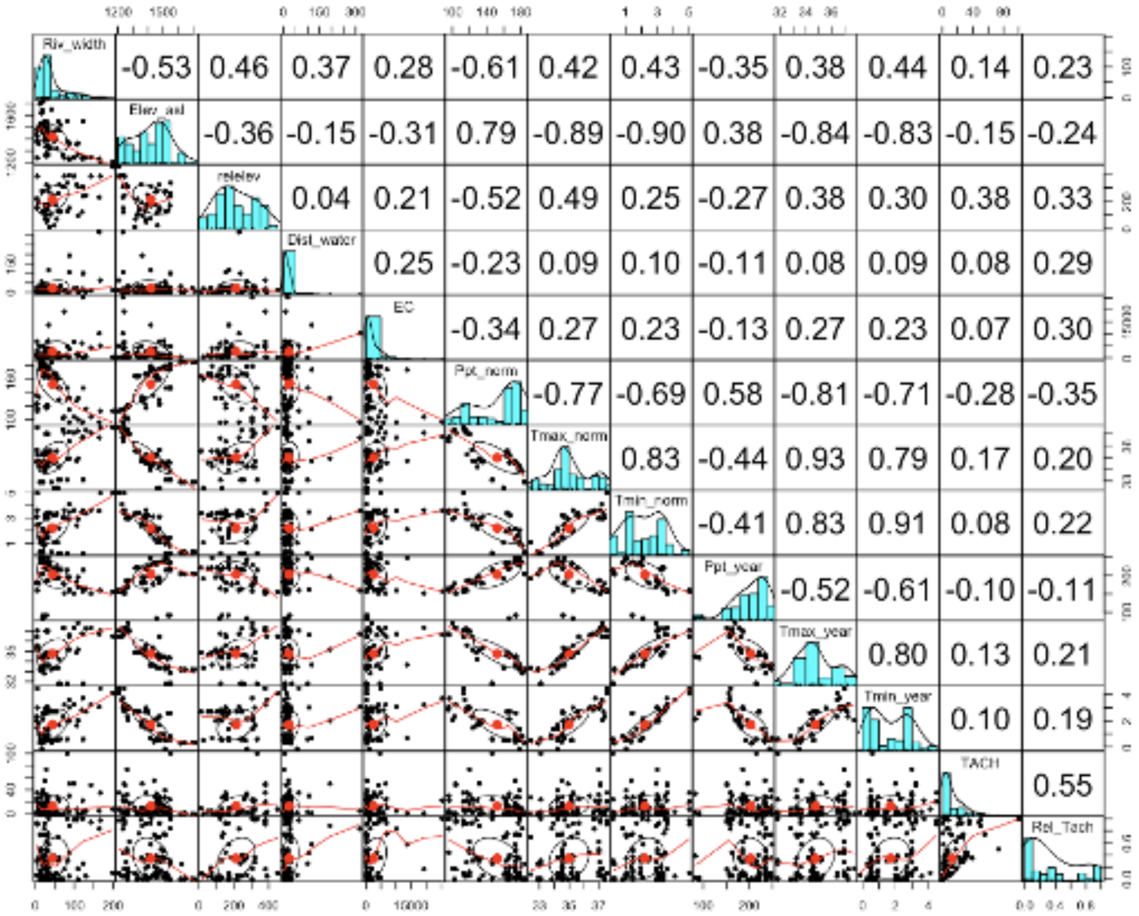


Figure S2-1. Pearson correlations for environmental variables and *Tamarix* cover using R function pairs.panels of package "psych" (Revell, 2019). Abbreviations are explained in Table S2-2.1.

Literature Cited: Revelle, W. (2019) psych: Procedures for personality and psychological research, Northwestern University, Evanston, Illinois, USA, https://CRAN.R-project.org/package=psych, Version = 1.9.12. (Figure S2-1)

Table S3-1: All species included in the study, listed alphabetically. Refer to González et al. 2020 for a full list of all species in the study area.

Species	**USDA code**	**Common name**	**Nativity**
Acer negundo L.	ACNE2	Boxelder	Native
Achnatherum hymenoides (Roem. & Schult.) Barkworth	ACHY	Indian ricegrass	Native
Acroptilon repens (L.) DC.	ACRE3	Hardheads / Russian knapweed	Non-native
Aegilops cylindrica Host	AECY	Jointed goatgass	Non-native
Agrostis stolonifera L.	AGST2	Creeping bentgrass	Non-native
Amaranthus retroflexus L.	AMRE	Redroot amaranth	Native
Apocynum cannabinum L.	APCA	Indian hemp / Dogbane	Native
Aristida purpurea Nutt.	ARPU9	Purple threeawn / Threeawn	Native
Artemisia campestris L.	ARCA12	field sagewort	Native
Artemisia dracunculus L.	ARDR4	Tarragon	Native
Artemisia ludoviciana Nutt.	ARLU	White sagebrush	Native
Artemisia tridentata Nutt.	ARTR2	Big sagebrush	Native
Asclepias asperula (Decne.) Woodson	ASAS	Spider milkweed	Native
Asclepias subverticillata (A.Gray) Vail	ASSU2	Horsetail milkweed	Native
Atriplex canescens (Pursh) Nutt.	ATCA2	Fourwing saltbush	Native
Atriplex confertifolia (Torr. & Frém.) S. Watson	ATCO	Shadscale saltbush	Native
Bassia americana (S. Watson) A.J. Scott	BAAM4	Green molly	Native

Bassia hyssopifolia (Pall.) Kuntz	BAHY	Fivehorn smotherweed	Non-native
Bassia scoparia (L.) A.J. Scott	KOSCT	Common kochia	Non-native
Bouteloua barbata Lag.	BOBA2	Sixweeks grama	Native
Bouteloua gracilis (Willd. ex Kunth) Lag. Ex Griffiths	BOGR2	Blue grama	Native
Bromus tectorum L.	BRTE	Cheatgrass	Non-native
Carex spp.	CAREX	Sedge	Native
Celtis laevigata Willd. Var. reticulata (Torr.) L.D. Benson	CERE2	Netleaf hackberry	Native
Cenchrus longispinus (Hack.) Fernald	CELO3	Mat sandbur	Native
Chenopodium album L.	CHAL7	Lambsquarters	Non-native
Chenopodium fremontii S. Watson	CHFR3	Fremont's goosefoot	Native
Chenopodium incanum (S. Watson) A. Heller	CHIN2	Mealy goosefoot	Native
Chenopodium leptophyllum (Moq.) Nutt. ex S. Watson	CHLE4	Narrowleaf goosefoot	Native
Chenopodium rubrum L. red goosefoot	CHRU	Red goosefoot	Native
Chrysothamnus linifolius Greene	CHLI3	Spearleaf rabbitbrush	Native
Cirsium vulgare (Savi) Ten.	CIVU	Bull thistle	Non-native
Cleome lutea Hook.	CLLU2	Yellow spiderflower	Native
Conyza canadensis (L.) Cronquist	COCA5	Canadian horseweed	Native
Cortaderia Stapf	CORTA	Pampas grass	Non-native
Corydalis aurea Willd.	COAU2	Scrambled eggs	Native
Cyperus erythrorhizos Muhl.	CYER2	Redroot flatsedge	Native
Datura wrightii Regel	DAWR2	Sacred thorn-apple	Native

Descurainia pinnata (Walter) Britton	DEPI	Western tansy mustard	Native
Distichlis spicata (L.) Greene	DISP	Saltgrass / Inland saltgrass	Native
Echinochloa crus-galli (L.) P. Beauv	ECCR	Barnyardgrass	Non-native
Eleagnus angustifolia L.	ELAN	Russian olive	Non-native
Eleocharis palustris (L.) Roem. & Schult.	ELPA3	Common spikerush	Native
Eleocharis parishii Britton	ELPA4	Parish's spikerush	Native
Elymus elymoides (Raf.) Sweezey	ELEL5	Squirreltail	Native
Elymus repens (L.) Gould	ELRE4	Quackgrass	Non-native
Elymus trachycaulus (Link) Gould ex Shinners	ELTR7	Slender wheatgrass	Native
Equisetum arvense L.	EQAR	Field horsetail	Native
Eragrostis hypnoides (Lam.) Britton, Sterns & Poggenb.	ERHY	Teal lovegrass	Native
Ericameria nauseosa (Pall. ex Pursh) Britton	CHNA2	Rubber rabbitbrush / Rabbitbrush	Native
Erodium cicutarium (L.) L'Hér. ex Aiton	ERCI6	Redstem stork's bill	Non-native
Forestiera pubescens Nutt.	FOPU2	Stretchberry / New Mexican Privet	Native
Glycyrrhiza lepidota Pursh	GLLE3	American licorice / Wild licorice	Native
Grindelia squarrosa (Pursh) Dunal	GRSQS2	Curlycup gumweed	Native
Gutierrezia sarothrae (Pursh) Britton & Rusby	GUSA2	Broom snakeweed / Snake weed	Native
Halogeton glomeratus (M. Bieb.) C.A. Mey.	HAGL	Saltlover	Non-native
Hesperostipa comata (Trin. & Rupr.) Barkworth	HECO26	Needle and thread	Native

Heterotheca villosa (Pursh) Shinners	HEVI4	Hairy false goldenaster	Native
Juncus bufonius L.	JUBU	Toad rush	Native
Lactuca serriola L.	LASE	Prickly lettuce	Non-native
Lepidium montanum Nutt.	LEMO2	Mountain pepperweed / Whitetop	Native
Leymus cinereus (Scribn. & Merr.) Á, Löve	LECI4	Basin wildrye	Native
Machaeranthera canescens (Pursh) A. Gray	MACA2	Hoary tansyaster	Native
Mahonia fremontii (Torr.) Fedde	MAFR3	Fremont's mahonia	Native
Melilotus alba (L.) Lam.	MEAL12	Sweet clover	Non-native
Morus alba L.	MOAL	White mulberry	Non-native
Muhlenbergia asperifolia (Nees & Meyen ex Trin.) Parodi	MUAS	Scratchgrass	Native
Oenothera villosa Thunb.	OEVI	Hairy evening primrose	Native
Panicum obtusum Kunth	PAOB	Vine mesquite	Native
Phragmites australis (Cav.) Trin. ex Steud.	PHAU7	Common reed	Native
Physalis longifolia Nutt.	PHLO4	Longleaf groundcherry	Native
Plantago patagonica Jacq.	PLPA2	Woolly plantain	Native
Pleuraphis jamesii Torr.	PLJA	James' galleta	Native
Populus fremontii S. Watson	POFR2	Fremont cottonwood	Native
Quercus gambelii Nutt.	QUGA	Gambel oak	Native
Rhus trilobata Nutt.	RHTR	Skunkbush sumac	Native
Rosa woodsia Lindl.	ROWO	Wood's rose / Rose woods	Native
Salix exigua Nutt.	SAEX	Coyote willow / Narrowleaf willow	Native
Salsola kali L.	SAKA	Russian thistle / Tumbleweed	Non-native
Sarcobatus vermiculatus (Hook.) Torr.	SAVE4	Greasewood	Native

Schkuhria multiflora Hook. & Arn.	SCMU6	Manyflower false threadleaf	Native
Senecio spartioides Torr. & A. Gray	SESP3	Broom-like ragwort	Native
Solanum dulcamara L.	SODU	Climbing nightshade	Non-native
Solidago occidentalis (Nutt.) Torr. & A. Gray	SOOC4	Western goldentop	Native
Solidago speciosa Nutt.	SOSP2	Showy goldenrod	Native
Sonchus asper (L.) Hill	SOAS	Spiny sowthistle / Sow thistle	Non-native
Sphaeralcea ambigua A. Gray	SPAM2	Desert globemallow	Native
Sphaeralcea parvifolia A. Nelson	SPPA2	Small-leaf globemallow	Native
Sporobolus airoides (Torr.) Torr.	SPAI	Alkali sacaton	Native
Stanleya pinnata (Pursh) Britton	STPI	Desert prince's-plume / Prince's plume	Native
Streptanthella longirostris (S. Watson) Rydb.	STLO4	Longbeak streptanthella	Native
Suaeda moquinii (Torr.) Greene	SUMO	Mojave seablite / Bush seepweed	Native
Symphyotrichum ascendens (Lindl.) G.L Nesom	SYAS3	Western aster	Native
Taraxacum officinale F.H. Wigg.	TAOF	Common dandelion	Native
Toxicodendron rydbergii (Small ex Rydb.) Greene	TORY	Western poison ivy	Native
Tribulus terrestris L.	TRTE	Puncturevine	Non-native
Typha latifolia L.	TYLA	Broadleaf cattail	Native
Ulmus pumila L.	ULPU	Siberian elm / Chinese elm	Non-native
Verbena bracteata Cav. ex Lag. & Rodr.	VEBR	Bigbract verbena	Native
Xanthium strumarium L.	XAST	Rough cocklebur / Cocklebur	Native

González, E., Shafroth, P.B., Lee, S.R., Reed, S.C., Belnap, J., 2020. Riparian plant communities remain stable in response to a second cycle of *Tamarix* biocontrol defoliation. Wetlands. https://doi.org/10.1007/s13157-020-01381-7

Table S3-2: TRY data sources. This table details the datasets and reference information for each TRY dataset accessed and used in the trait analysis of this study. The Dataset ID used to reference data in the TRY database, species, trait and reference information are included. If unpublished, the submitting author is listed. Species are listed as their USDA code. Trait abbreviations are as follows: Bloom – bloom period, HT_matur – average height at maturity, Resprout – ability to resprout following above ground biomass removal, SLA – specific leaf area, Veg_repr – ability to reproduce clonally. References are listed as they are listed in the TRY database (https://www.try-db.org/TryWeb/Home.php).

Dataset ID	**USDA code (trait abb.)**	**Reference**
4	AMRE (Bloom); ARCA12 (Bloom); SAKA (Veg_repr, Bloom); SODU (Bloom)	Kühn, I., W. Durka, and S. Klotz. 2004. BiolFlor - a new plant-trait database as a tool for plant invasion ecology. Diversity and Distribution 10:363-365.
20	MOAL (SLA)	Wright, I. J., P. B. Reich, M. Westoby, et al. 2004. The worldwide leaf economics spectrum. Nature 428:821-827.
25	AMRE (SLA, HT_matur); KOSCT (SLA); CHAL7 (HT_matur); CHRU (SLA); CIVU (SLA, HT_matur); JUBU (SLA); SAKA (SLA)	Kleyer, M., R. M. Bekker, I. C. Knevel, et al. 2008. The LEDA Traitbase: a database of life-history traits of the Northwest European flora. Journal of Ecology 96:1266-1274.

27	CIVU (Resprout)	Paula, S., M. Arianoutsou, D. Kazanis, et al. 2009. Fire-related traits for plant species of the Mediterranean Basin. Ecology 90:1420.
28	CHLE4 (HT_matur)	Moles, A. T., D. S. Falster, M. R. Leishman, and M. Westoby. 2004. Small-seeded species produce more seeds per square metre of canopy per year, but not per individual per lifetime. Journal of Ecology 92:384-396.
37	SODU (SLA, HT_matur)	Cornelissen, J. H. C. 1996. An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. Journal of Ecology 84:573-582.
50	AECY (SLA); ELRE4 (SLA)	Shipley B., 2002. Trade-offs between net assimilation rate and specific leaf area in determining relative growth rate: relationship with daily irradiance. Functional Ecology 16: 682-689.
63	SAKA (HT_matur)	Fonseca, C. R., J. M. Overton, B. Collins, and M. Westoby. 2000. Shifts in trait-combinations along rainfall and phosphorus gradients. Journal of Ecology 88:964-977.
68	MOAL (HT_matur)	Wirth, C. and J. W. Lichstein. 2009. The imprint of species turnover on old-growth forest carbon balances - Insights from a trait-based model of forest dynamics. Pages 81-113 in C. Wirth, G. Gleixner, and M. Heimann, editors. Old-Growth Forests: Function, Fate and Value. Springer, New York, Berlin, Heidelberg.
92	FOPU2 (HT_matur, Resprout)	Green, W. 2009. USDA PLANTS Compilation, version 1, 09-02-02. (http://bricol.net/downloads/data/PLANTSdatabase/) NRCS: The PLANTS Database (http://plants.usda.gov, 1 Feb 2009). National Plant Data Center: Baton Rouge, LA 70874-74490 USA.
102	EQAR (SLA)	Blonder, B. (Unpublished). Photosynthesis and Leaf Characteristics Database.
159	SPAM2 (SLA)	Butterfield, B.J. and J.M. Briggs. 2011. Regeneration niche differentiates functional strategies of desert woody plant species. Oecologia 165:477-487.

163	AECY (Bloom); CELO3 (Bloom)	Craine J.M., J.B. Nippert, E.G. Towne et al. 2011. Functional consequences of climate-change induced plant species loss in a tallgrass prairie. Oecologia 165:1109-1117.
174	ARCA12 (Veg_repr); SODU (Veg_repr)	Fitter, A. H. and H. J. Peat. 1994. The Ecological Flora Database. Journal of Ecology 82:415-425.
175	AECY (HT_matur)	Gachet, S., E. Vèla, T. Tatoni. 2005. BASECO: a floristic and ecological database of Mediterranean French flora. Biodiversity and Conservation 14(4):1023-1034.
193	ARCA12 (SLA, HT_matur); CHFR3 (SLA, HT_matur); QUGA (SLA); ROWO (SLA); SYAS3 (SLA, HT_matur)	Laughlin, D.C., P.Z. Fulé, D.W. Huffman, J. Crouse, and E. Laliberté. 2011. Climatic constraints on trait-based forest assembly. Journal of Ecology 99:1489-1499.
205	DAWR2 (SLA)	Price, C.A. and B.J. Enquist. 2007. Scaling of mass and morphology in Dicotyledonous leaves: an extension of the WBE model. Ecology 88(5):1132-1141.
236	ULPU (SLA)	Prentice, I.C., T. Meng, H. Wang, et al. 2011. Evidence for a universal scaling relationship of leaf CO2 drawdown along a moisture gradient. New Phytologist 190:169–180.
251	ASSU2 (HT_matur); COAU2 (HT_matur); MAFR3 (HT_matur)	Schweingruber, F.H. and W. Landolt. 2005. The Xylem Database. Swiss Federal Research Institute WSL.
296	CHLE4 (SLA)	Blumenthal, D. (Unpublished).
342	RHTR (SLA)	Maire V., I.J. Wright, I.C. Prentice, et al. 2015. Data from: Global effects of soil and climate on leaf photosynthetic traits and rates. Dryad Digital Repository. http://dx.doi.org/10.5061/dryad.j42m7
412	CELO3 (SLA); DISP (SLA); PAOB (SLA); SPAI (SLA); STLO4 (SLA)	Serge Sheremetev, S. (Unpublished).
443	HAGL (SLA)	Wang, H., S. P. Harrison, I. C. Prentice, et al. 2017. The China Plant Trait Database. PANGAEA. https://doi.org/10.1594/PANGAEA.871819

Table S3-3: Literature search sources. This table provides detailed citation information for each paper used as a source for trait data. The Species name, USDA code (https://plants.sc.egov.usda.gov/), trait found in the paper and reference information are included. N/A - Not available

USDA code	**Trait**	**Authors**	**Year**	**Title**	**Publisher**	**Vol/Iss**
ACHY	SLA	Defalco, L.	2003	Physiological ecology of the invasive annual grass, *Bromus madritensis* ssp. *rubens*, and its interaction with native Mojave Desert species	University of Nevada, Reno Unpublished Dissertation	N/A
AMRE	Seed weight	McWilliams, E.L. et al.	1968	Variation in seed weight and germination in populations of *Amaranthus retroflexus* L.	Ecology	49/2
AMRE	Vegetative reproduction; Spread rate	University of AK, Anchorage	2011	Redroot pigweed *Amaranthus retroflexus* L.	N/A	N/A
AMRE	Reprout	Fornwalt, P.	2009	Disturbance impacts on understory plant communities of the Colorado Front Range	Colorado State University Dissertations	N/A
ARDR4	Spread rate	University of AZ, Extension	2007	Growing Herbs	N/A	Bulletin #54
KOSCT	Height; Spread rate	Dodd, R. and Randall, P.	2002	Eradication of kochia (*Bassia scoparia* (L.) A.J. Scott, Chenopodiaceae) in western Australia	Proceedings of the 13th Australian Weeds Conference	
BOGR2; LECI4; PLJA	SLA	Balazs, K and Butterfield, B.	2018	A trait assessment of commonly used species in restoration on the Colorado Plateau	Colorado Plateau Native Plant Program 2018 Annual Meeting	
CAREX	Reprout	Murphy, C.	2002	CEGL001176 *Salix* (*boothii, geyeriana*)/*Carex acquatilis* wet shrubland	https://www1.usgs.gov/csas/nvcs/nvcsGetUnitDetails?elementGlobalId=687862	N/A

ACRE 3	SLA	Bordini, A.T.	2017	Changes in leaf area and nurtient content of *Celtis* spp. across a precipitation gradient in Texas	Texas State University, Thesis	N/A
CERE 6	Vegetative reproduction	Beck, K.G.	1994	Russian Knapweed Biology and Management	Colorado State University: University Cooperative Extension	N/A
CERE 6	Spread rate; Resprout	Meyers, K.	2012	Phenology of the gall midge *Jaapiella ivannikovi fedotova* (Diptera: Cecidomyiidae), a biological control agent of Russian knapweed *Rhaponticum repens* (Asteraceae) in Wyoming	University of Wyoming Unpublished Dissertation	N/A
CHAL 7	SLA	Kropff, M.J. and Spitters, C.J.T.	1992	An eco-physiological model for interspecific competition, applied to the influence of *Chenopodium album* L. on sugar beet. I. Model description and parameterization	Weed Research	32
CHAL 7	Vegetative reproduction; Spread rate; Bloom period	Bassett, I.J. and Crompton, C.W.	1978	The Biology of Canadian Weeds: 32. *Chenopodium album* L	Canadian Journal of Plant Science	58
CHFR 3	Vegetative reproduction; Spread rate	Hamrick, J.L.	1979	Relationships between life history characteristics and electrophoretically detectable genetic variation in plants	Annual Review of Ecology and Systematics	10
CHFR 3	Reprout	Fornwalt, P. and Kaufmann, M.	2006	Short-term effects of fire and postfire rehabilitation on the forest understory: A case study from the Colorado Front Range	Newsletter of the Colorado Native Plant Society	30/1
CHFR 3	Bloom period	Wolden, L.G. et al.	1995	Flora and vegetation of the Hassayampa River Preserve, Maricopa County, Arizona	Journal of the Arizona-Nevada Academy of Science	28/1-2
COAU 2	Vegetative reproduction	Hanzawa, M. et al.	1988	Demographic analysis of an ant-seed mutualism	The American Naturalist	131/1

CORTA	SLA	Vourlistis, G.L. and Kroon, J.L.	2013	Growth and resource use of the invasive grass, pampasgrass (*Cortaderia solloana*), in response to nitrogen and water availability	Weed Science	61/1
DISP	Reprout	Munnecke, M.	2020	Ecological site R020XI118CA marine terraces 21-34" p.z.	Natural Resource Conservation Service	N/A
HAGL	Seed weight	Ahmed, M.Z. and Ajmal, K.	2010	Tolerance and recovery responses of playa halophytes to light, salinity and temperature stresses during seed germination	Flora	205/11
HAGL	Height; Spread rate	Zappettini, G.	1953	The taxonomy of *Halogeton glomeratus*	The American Midland Naturalist	50/1
HAGL	Bloom period	Cronin, E.	1965	Ecological and physiological factors influencing chemical control of *Halogeton glomeratus*	U.S. Dept. of Agriculture	1325
HEVI4	SLA	Zeldin, J. et al.	2020	Intraspecific functional trait structure of restoration-relevant species: Implications for restoration seed sourcing	Journal of Applied Ecology	57
OEVI	Reprout	Morgan, P. et al.	2015	Vegetation response to burn severity, native grass seeding, and salvage logging	Fire Ecology	11/2
PHAU7	Reprout	Saltinstal, K. and Meyerson, L.	2010	Genetics and reproduction of common (*Phragmites australis*) and giant reed (*Arundo donax*)	Invasive Plant Science and Management	3
SESP3	Height; Bloom period; Vegetative reproduction	Nellessen, J.E.	2004	*Senecio spartioides* Torr. & Gray in "Wildland shrubs of the United States and its territories: Thamnic descriptions"	USDA: Forest Service	1

SPPA2	Height; Vegetative reproduction; Spread rate; Bloom period	Gucker, C.L. and Shaw, N.L.	2018	Western forbs: Biology, ecology, and use in restoration	Great Basin Fire Science Exchange	N/A
TORY	SLA	Jelesko, J. et al.	2017	Differential responses to light and nutrient availability by geographically isolated poison ivy accessions	Northeastern Naturalist	24/2
ULPU	Vegetative reproduction	Duansuram et al.	2009	Performance of Siberian elm (*Ulmus pumila*) on steppe slopes of the northern Mongolian mountain taiga: Drought stress and herbivory in mature trees	Environmental and Experimental Botany	66/1

Table S3-4: Details of mixed models for community weighted means and functional dispersion of average height at maturity (Height), specific leaf area (SLA) and seed weight as response variables. Each model includes year, live and dead *Tamarix* cover as fixed explanatory effects and transect nested within site, site nested within reach, and reach as random effects. Backward stepwise selection was used to select the best model. The significance of each model was checked by comparing the full model to a null model using only random effects. For each model we report the marginal adjusted R^2 (R^2m; variation explained by fixed effects only) as well as the conditional adjusted R^2 (R^2c; variation explained by fixed and random effects).

Response variable	**Explanatory variable**	**Coefficient**	**Stnd error**	**DF**	**t-value**	**p-value**	**R^2m**	**R^2c**
Height - cwm	(Intercept)	0.024	0.028	186	0.876	0.38	0.14	0.73
	2012	0.173	0.022	186	7.813	<0.0001		
	2013	0.142	0.024	186	5.829	<0.0001		

	2015	0.127	0.022	186	5.637	<0.0001		
	2017	0.177	0.022	186	7.971	<0.0001		
	live *Tamarix*	0.044	0.012	186	3.58	<0.0001		
	dead *Tamari*x	0.021	0.011	186	1.982	0.05		
Height - dispersion	(Intercept)	0.619	0.04	183	15.626	0	0.14	0.49
	live *Tamarix*	-0.021	0.029	183	-0.728	0.47		
	2012	-0.138	0.037	183	-3.698	<0.0001		
	2013	-0.135	0.045	183	-3.018	<0.0001		
	2015	-0.139	0.038	183	-3.675	<0.0001		
	2017	-0.115	0.038	183	-3.071	<0.0001		
	Tamarix:2012	-0.057	0.039	183	-1.472	0.14		
	Tamarix:2013	-0.014	0.044	183	-0.319	0.75		
	Tamarix:2015	-0.022	0.039	183	-0.569	0.57		
	Tamarix:2017	-0.107	0.037	183	-2.9	<0.0001		
SLA - cwm	(Intercept)	154.761	6.682	179	23.16	0	0.11	0.46
	live *Tamarix*	-5.935	4.717	179	-1.258	0.21		
	2012	-32.161	6.149	179	-5.23	<0.0001		
	2013	-21.553	7.267	179	-2.966	<0.0001		
	2015	-11.001	6.199	179	-1.775	0.08		
	2017	-7.782	6.271	179	-1.241	0.22		
	Tamarix:2012	1.847	6.464	179	0.286	0.78		
	Tamarix:2013	11.782	7.236	179	1.628	0.11		
	Tamarix:2015	10.752	6.404	179	1.679	0.09		
	Tamarix:2017	-3.238	6.045	179	-0.536	0.59		
SLA - dispersion	(Intercept)	0.727	0.067	184	10.796	<0.0001	0.11	0.41
	2012	-0.304	0.048	184	-6.282	<0.0001		
	2013	-0.216	0.048	184	-4.489	<0.0001		
	2015	-0.134	0.048	184	-2.782	0.01		
	2017	-0.138	0.049	184	-2.818	0.01		
Seed weight - cwm	(Intercept)	0.073	0.158	183	0.461	0.65	0.05	0.81
	live *Tamarix*	0.08	0.053	183	1.508	0.13		
	2012	0.103	0.065	183	1.576	0.12		
	2013	0.072	0.08	183	0.9	0.37		
	2015	0.078	0.067	183	1.176	0.24		
	2017	-0.004	0.066	183	-0.068	0.95		

	Tamarix:2012	-0.187	0.068	183	-2.754	0.01		
	Tamarix:2013	-0.098	0.079	183	-1.24	0.22		
	Tamarix:2015	-0.137	0.07	183	-1.959	0.05		
	Tamarix:2017	-0.35	0.065	183	-5.391	<0.0001		
Seed weight - dispersion	N.S.							

Table S3-5: Details of mixed models for Shannon diversity and multivariate functional dispersion as response variables. Each model includes year, live and dead *Tamarix* cover as fixed explanatory effects and transect nested within site, site nested within reach, and reach as random effects. Backward stepwise selection was used to select the best model. The significance of each model was checked by comparing the full model to a null model using only random effects. For each model we report the marginal adjusted R^2 (R^2m; variation explained by fixed effects only) as well as the conditional adjusted R^2 (R^2c; variation explained by fixed and random effects).

Response variable	**Explanatory variable**	**Coefficient**	**Stnd error**	**DF**	**t-value**	**p-value**	**R^2m**	**R^2c**

Shannon diversity	(Intercept)	1.54	0.161	186	9.54	0	0.08	0.62
	2012	-0.161	0.065	186	-2.49	0.01		
	2013	-0.153	0.071	186	-2.14	0.03		
	2015	-0.183	0.066	186	-2.78	0.01		
	2017	-0.384	0.065	186	-5.91	0		
	live *Tamarix*	-0.076	0.036	186	-2.12	0.04		
	dead *Tamarix*	-0.055	0.03	186	-1.82	0.07		
Functional dispersion	(Intercept)	0.215	0.011	183	19.12	0	0.22	0.47
	2012	-0.081	0.011	183	-7.28	0		
	2013	-0.054	0.013	183	-4.04	0		
	2015	-0.029	0.011	183	-2.54	0.01		
	2017	-0.052	0.011	183	-4.58	0		
	live *Tamarix*	0	0.009	183	-0.05	0.96		
	*Tamarix:*2012	0	0.012	183	0.04	0.97		
	*Tamarix:*2013	-0.027	0.013	183	-1.99	0.05		
	*Tamarix:*2015	0.006	0.012	183	0.47	0.64		
	*Tamarix:*2017	-0.032	0.011	183	-2.94	0		