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Functional stability of vegetation following biocontrol of an invasive riparian shrub

A. L. Henry · E. González-Sargas ·
P. B. Shafroth · A. R. B. Goetz · A. A. Sher

Abstract Understanding plant community response to environmental change is a crucial aspect of biological conservation and restoration, but species-based approaches are limited in that they do not reveal the underlying mechanisms driving vegetation dynamics. An understanding of trait-environment relationships is particularly important in the case of invasive species which may alter abiotic conditions and available resources. This study is the first to measure the functional response of riparian plant communities to biocontrol of an invasive species. We focused on an invasive shrub, *Tamarix* (saltcedar), that is defoliated by a beetle that was released by the US Department of Agriculture along the Upper Colorado River (southwestern United States). We calculated community weighted means and functional dispersion of individual traits, multivariate functional dispersion and species diversity. We used linear mixed effect models (LME) to compare these metrics at paired vegetation patches dominated and not dominated by *Tamarix* during cycles of defoliation and refoliation over eight years. We found that community-weighted average trait values, species diversity and functional dispersion changed little in response to defoliation, and instead seemed to be responding to fluctuations in yearly precipitation. Average height and seed weight were greater in *Tamarix*-dominated patches relative to control patches. Functional dispersion followed a similar trajectory to species diversity, but was a more sensitive indicator of plant community change. We showed that riparian vegetation can be resilient to *Tamarix* biocontrol, and that defoliation might not necessarily always lead to substantial changes in ecosystem function.

A. L. Henry (✉) · A. R. B. Goetz · A. A. Sher
Department of Biological Sciences, University of Denver, F. W. Olin Hall, 2190 E Iliff Ave, Denver, CO 80210, USA
e-mail: annie.henry@du.edu

E. González-Sargas
Department of Biology, Colorado State University, 251 W Pitkin St, Fort Collins, CO 80521, USA

E. González-Sargas · P. B. Shafroth
 Fort Collins Science Center, U.S. Geological Survey, 2150 Centre Avenue, Building C, Fort Collins, CO 80526, USA

Introduction

The species-based metrics that are commonly used to assess ecosystem change do not adequately reveal the underlying mechanisms driving plant community dynamics (Funk et al. 2017; Mcgill et al. 2006). This is because species are not a direct measure of

response to environmental conditions, rather their presence is a consequence of the traits they possess (Keddy 1992). A trait-based approach provides a direct link to understanding which properties of the environment are acting as filters to drive community assembly. The trajectories of species diversity and functional diversity are dependent on these environmental filters, such as resource availability and primary sources of stress (Mayfield et al. 2010). As such, trait-based approaches are increasingly used to assess community response to ecosystem change globally (Jeliazkov et al. 2020). Among recent studies that use both species and functional approaches, some have found that functional metrics respond more strongly to ecosystem change than species-based approaches (e.g., Woodcock et al. 2011), while some studies have found that species diversity measures respond more strongly (e.g., Pilotto et al. 2019). 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).

Restoration efforts such as invasive species control alter both the biotic and abiotic environment, providing natural experiments through which we can test trait-environment relationships. Most control techniques change the abiotic environment both through direct disturbances (such as from machinery or pesticides), as well as indirect alterations that follow control of a dominant species, such as an increase in resource availability. Despite the importance of these potential environmental filters, there are still very few studies that examine the impact of invasive species control on community function (but see McNeish et al. 2017; Modiba et al. 2017; O'Leary et al. 2018). Rather, species-based measures are generally used in monitoring the impact of invasive species management on the broader plant community (González et al. 2015; Kettenring and Adams 2011; Wortley et al. 2013). Understanding the underlying mechanisms driving plant community change facilitates effective management following invasive species control.

One control method in particular—biological control (biocontrol)—presents a unique opportunity to study functional relationships in response to environmental filters. This is because, unlike either mechanical or chemical control, effective biocontrol typically creates few additional disturbances beyond

the reduction of the target. Furthermore, biocontrol can create gradients of impact over time and space that facilitate our ability to identify trajectories of response. Despite this potential, however, to our knowledge a trait-based approach has never been used to study the response of plant communities to biocontrol.

The environmental alterations we expect from the biocontrol of a dominant invasive shrub include increased resource availability (light and nutrients) and shifts in environmental stressors (e.g., increased temperature, reduced soil moisture). Provided enough elapsed time, these changes alter the filters that select for specific traits and subsequently are expected to impact the functional composition of the community (Keddy 1992). However, how the species and functional community composition changes are context-dependent. In a species-poor environment, the release of competitive pressure caused by the control 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 control of a dominant invasive species through biocontrol may shift the community from shade-tolerant species to stress-tolerant species that can cope with a hot, dry environment, altering both the identity and number of species, and functional diversity (Suding and Goldberg 2001). Ultimately, species diversity may be similar, but the trait values may have changed drastically. Additionally, invasive species control occurs in the context of abiotic conditions and disturbance regimes, such as precipitation, fire and flooding, whose fluctuations also impact species and trait composition.

We examined plant community traits in a system subjected to biocontrol defoliation of non-native, invasive *Tamarix* spp., a Eurasian shrub that has successfully invaded North American riparian systems (Nagler et al. 2011). Because they are difficult to distinguish and ecologically similar, *Tamarix* here refers to the two most common species in the United States Southwest (*T. ramosissima* and *T. chinensis*) and their hybrids (Gaskin 2013). 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)). *Diorhabda* spp. are gregarious beetles and a swarm can defoliate an entire stand of *Tamarix*. However, multiple defoliation events are generally required to cause shrub or branch mortality (Bean 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; Henry et al. 2018; Kennard et al. 2016; Sher et al. 2018). Previous research has shown a highly varied response of plant communities to *Tamarix* defoliation (González et al. 2020a, b, 2017; Henry et al. 2018; Kennard et al. 2016; Sher et al. 2018).

The immediate effects of biocontrol can seem drastic, while 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 since beginning of defoliation; González et al. 2020a, b). González et al. (2020a) reported plant community response to a first cycle of *Tamarix* biocontrol along the Virgin River in Arizona and found that *Tamarix* was largely replaced with the native shrub *Pluchea sericea* and that there was a temporary increase in opportunistic understory species. In this river, the effects of biocontrol on vegetation were shown to be strongly affected by the local flooding regime, which is a key driver of vegetation in riparian systems. Along the Colorado River near Moab UT, González et al. (2020b) examined the plant community response to a second cycle of defoliation (i.e., a new defoliation event after a first cycle of defoliation and subsequent recovery of *Tamarix* canopy, typical of plant-insect interactions) and reported an increase in the cover of the native shrub *Salix exigua* and some fluctuations in herbaceous species cover, but overall, 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 if community-weighted averages and ranges of key individual response traits as well as multivariate measures of functional diversity changed (A) over time, (B) following the cycle of biocontrol defoliation and recovery, and (C) whether they differed between vegetation patches where *Tamarix* was present and where *Tamarix* was absent. Henry et al. (2021) showed that *Tamarix*-dominated communities across the Upper Colorado basin tend to be more specialized in terms of reproductive strategies and phenological and morphological traits. We therefore hypothesized that those differences would exist between *Tamarix* and control patches, and 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 had stabilized following the first cycle of defoliation as González et al. (2020b) suggested, and functional and taxonomic diversity followed similar trajectories, we would expect little functional change specifically in response to the second defoliation event.

Methods

Study area

This study included 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; Fig. 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

Fig. 1 Map of study area. Cisco Wash/Dry Gulch contains sites A–B, with a total of 20 transects. Gold Bar contains sites C–J, with a total of 28 transects (black dots represent sites). Gray shading represents the Upper Colorado river basin. Red dots represent the two study reaches. Red star represents Moab, Utah
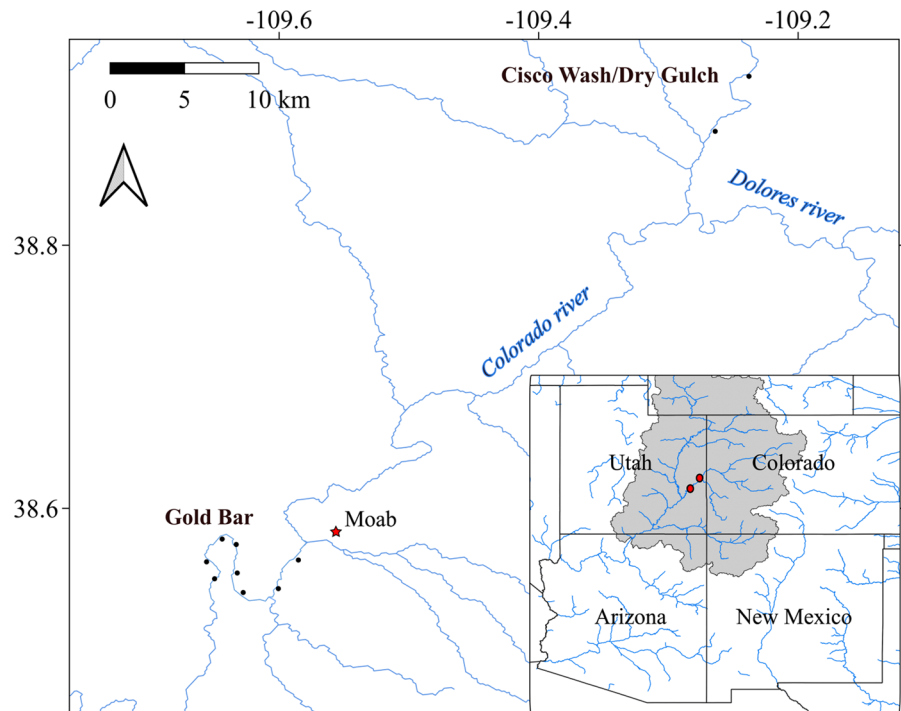
"Gold Bar" which extends through a sandstone-walled canyon and consists of two large meander bends. The Gold Bar reach has eight sites.

The biocontrol beetle (*Diorhabda* spp.) was released at eight locations along the same segment of the Colorado River as our study area between 2004 and 2006 (Henry et al. 2018). 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; Fig. 2a). The percent cover of dead *Tamarix* followed an approximately inverse pattern (Fig. 2b). Therefore, this study captures plant community response to the 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, and a notable increase of *Salix exigua* from the beginning to the end of the

study, but otherwise there was little change in species diversity.

Data collection

Field surveys/vegetation

Within the study area, sites were selected by González et al. (2020b) to represent a range of vegetated landforms ranging from near channel bars and banks, adjacent floodplains, and higher terraces within both meander bends and straighter sections of the river. While a single site was defined as having a homogeneous origin (i.e., occupied either the right or left river margin along an entire alluvial deposit), each site typically included multiple landforms. At each study site, 1 to 10 transects were established depending on the size, shape and heterogeneity of the site (20 transects in Cisco, 40 transects in Gold Bar). Transects were oriented perpendicular to the channel and extended from the transition between the uplands and the riparian corridor to the edge of the river water or the top of the riverbank if too steep to sample safely. Transects were sampled in the fall of 2010, 2012, 2013, 2015 and 2017. Only transects that had no *Tamarix* control other than biocontrol for the
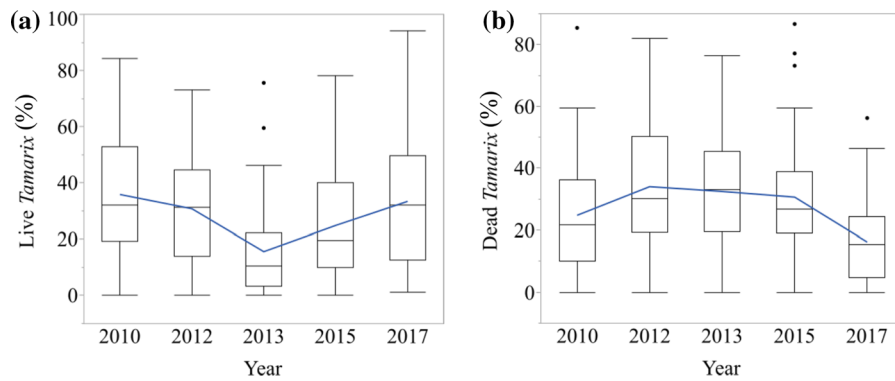
Fig. 2 *Tamarix* cover at all sites. Included here to show the defoliation cycle from 2010 to 2013 and refoliation from 2013 to 2017 (González et al. 2020b; Nagler et al. 2018). The horizontal line within the box represents the median cover value; the top and bottom edges of the box represent the first and third quartiles. The whiskers extend to the outermost datapoint that falls within the first or third quartile ± 1.5*(interquartile range). Outliers exceed the 1.5*interquartile range and are indicated with filled circles. The blue line connects the mean cover from one year to the next. A pinpoint was considered dead if a twig or a branch that showed no sign of life that season (i.e., no evidence of new leaves in that sampling year) was hit, irrespective of whether it was attached to a larger live branch. We assumed brown leaves indicated desiccation of live vegetation caused by beetle herbivory during that sampling year and therefore were counted as live points

entire sampling period were used in the study, resulting in 20 transects in Cisco and 28 transects in Gold Bar. We used vegetation data described in González et al. (2020b) and published in Shafroth et al. (2020). The point-intercept method with pinpoints spaced 50 cm or 1 m depending on transect characteristics was used to sample vegetation (understory and overstory), including live and dead *Tamarix*, along each transect (Bonham 1989). Dead *Tamarix* in this area was assumed to be due to biocontrol rather than the effects of other factors such as drought stress or competition, which tend to be minor (González et al. 2020b). The presence of the most common ground cover constituents was also registered at the pinpoint level: bare ground, coarse litter (> 0.75 cm diameter) and fine litter (< 0.75 cm diameter).

Because we were particularly interested in the effects of biocontrol, we divided the observations collected across the transects into two subsets. The first subset ("*Tamarix*" hereafter) represented *Tamarix* patches and included the sections of the transects that had consecutive pinpoints with counts of either *Tamarix* live or dead over the entire study period, with intervals of less than 2 m with no *Tamarix* record also included. The second subset ("Control") included the pinpoints in "gaps" between *Tamarix* patches equal to or larger than 2 m, and other non-*Tamarix* pinpoints along the transect, which were mostly located at the upland end. Because the length of each transect could differ across years as the river water's edge fluctuated with water levels, only pinpoints that were present in all years were included. Transects with five or fewer pinpoints in the Control patches were also excluded from the Control subset, rendering the number of transects with control data to 19 in Cisco and 10 in Gold Bar. The point data for plant species and ground cover constituents were transformed to percent cover per transect by dividing the number of points with each species or ground cover constituent present by the total number of transect points in the corresponding subset. All analyses were conducted using the transect-year combination as the study unit.

From the original 119 taxa identified by González et al. (2020b), we considered 112 taxa. The seven excluded taxa were only present at the transect sections that were discarded when creating the two *Tamarix* and Control subsets. 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. This reduced the taxa list for trait data searches to 103. For simplicity we will refer to all taxa as "species".

Trait data

We collected data on eight reproductive, phenological and morphological traits identified as important in riparian plant communities generally (Stromberg and Merritt 2015) as well as specifically in the reaches of the Upper Colorado River where this study was conducted (Table 1; Henry et al. 2021). We collected trait data primarily using online databases (see associated data release), following the methods outlined in Henry et al. (2021) (e.g., TRY—Kattge et al. (2020) and Palmquist et al. (2017; Table S2)). When trait values could not be found, we conducted literature searches using Web of Science and Google Scholar (Table S3). These traits characterize resource acquisition, stress tolerance and reproductive strategies of the plants included in this study.

Of the eight traits for which we collected data, we examined specific leaf area (SLA), height at maturity and seed mass as individual traits. These represent the three axes of the Leaf–Height–Seed (L–H–S) scheme 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 a conservative resource use 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 (Aguiar et al. 2018; Bejarano et al. 2017; 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 data subset and transect. Seed mass and height were both log-transformed prior to calculating functional metrics to improve 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 and represents 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 1). 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 data subset and transect in the study area.

Statistical analysis

From the filtered list of 103 species, we included those with at least half of the eight trait values in our analysis. While this led to the removal of eight additional species, at least 80% vegetation cover was still accounted for at all transects (i.e., the combination of the *Tamarix* and Control subsets). Subsequent analyses were carried out using the remaining 95 species

Table 1 Traits used 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 bloom period	Total number of months blooming	Ordinal

(Table S1). We did not include *Tamarix* in our calculation of functional metrics because it was used as the main factor to create the *Tamarix* and Control subsets, and as an explanatory variable in subsequent analyses.

To identify changes over time and the influence of *Tamarix* cover on individual traits, we ran linear mixed effects (LME) models using CWM and FDis of each L–H–S trait, the multivariate FDis metric, and Shannon's diversity as response variables, and the interaction of year and subset type (*Tamarix* vs. Control) as fixed factors. Random variables were transect nested within site, and site nested within reach. Tukey post-hoc tests were conducted ($P < 0.05$). We also conducted a second set of LME models with *Tamarix* and Control subsets separately to identify potential drivers of functional diversity within each type of vegetation. In these models, we used the same response variables as above and the cover of the three ground cover constituents (bare, coarse litter, and fine litter) for the Control subset, plus the cover of live, dead *Tamarix*, and the proportion of dead *Tamarix* (dead/(dead + live)*100) for the *Tamarix* subset as fixed factors. We used a backward selection procedure and the same random structure as above. All mixed effects models were fitted using the maximum likelihood method. 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 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 FDis using Pearson's correlation coefficient.

All analyses were done in RStudio (1.4.1564 on MacOS 10.15.7) 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). LME models were conducted using the function "lmer" of package "lme4" (Bates et al. 2015) and "lme" of the package "nlme" (Pinheiro et al. 2019). Backward selection was conducted with the function "stepAIC" of the package "MASS" (Venables and Ripley 2002). Pearson's correlation coefficient was calculated using the function "pairs.panels" of the package "psych" (Revelle 2019). Model diagnostics were run with the functions "r.squaredGLMM"

of "MuMIn" (Bartoń 2019) and "testDispersion", "testOutliers", and "testUniformity" of "DHARMa" (Hartig 2021). Tukey tests were done with the function "lsmeans" of the package "lsmeans" (Lenth 2016).

Results

Changes in L–H–S traits over time and in response to biocontrol

Overall, there were slight, statistically significant fluctuations in height and SLA community weighted means (CWM) and functional dispersion (FDis) over time, but none of the indicators changed in accordance with the 2010–2013 *Tamarix* cover decline and 2013–2017 recovery caused by biocontrol (Fig. 3 with observed values, Suppl. Material Figure S1 with predicted values by LME). Rather, SLA mean and heterogeneity decreased between 2010 and 2012 and then returned to 2010 levels by the end of the study in 2017, independent of the type of dominant vegetation (Figs. 3, S1). The community had taller plants in 2012 and 2017, particularly in the *Tamarix* subset, with a narrower range as shown by lower diversity. The amount of variability explained by time and subset type was low in all cases (adj R^2 m < 10%, Fig. 3, Suppl. Material Table S4).

The *Tamarix* and Control subsets consistently differed only in the case of seed weight CWM with the *Tamarix* subset having heavier seeds than the Control subset. Within each subset, the observed patterns in L–H–S traits were poorly explained by ground and/or *Tamarix* cover (the latter only in the *Tamarix* subset; all models explained < 7% of the variability; adj R^2 m, Suppl. Material Table S5).

Species diversity and multivariate functional dispersion

Shannon diversity and functional dispersion (using all traits included in the study) had a Pearson's correlation coefficient of 0.70. Both Shannon diversity and multivariate functional dispersion decreased from 2010 to 2012, recovered in 2013, and then declined in 2017, but the pattern was more marked (Figs. 3 and S1), and distinctive (i.e., better explained by the LME model) for functional diversity (adj R^2 m of 3.3 vs.
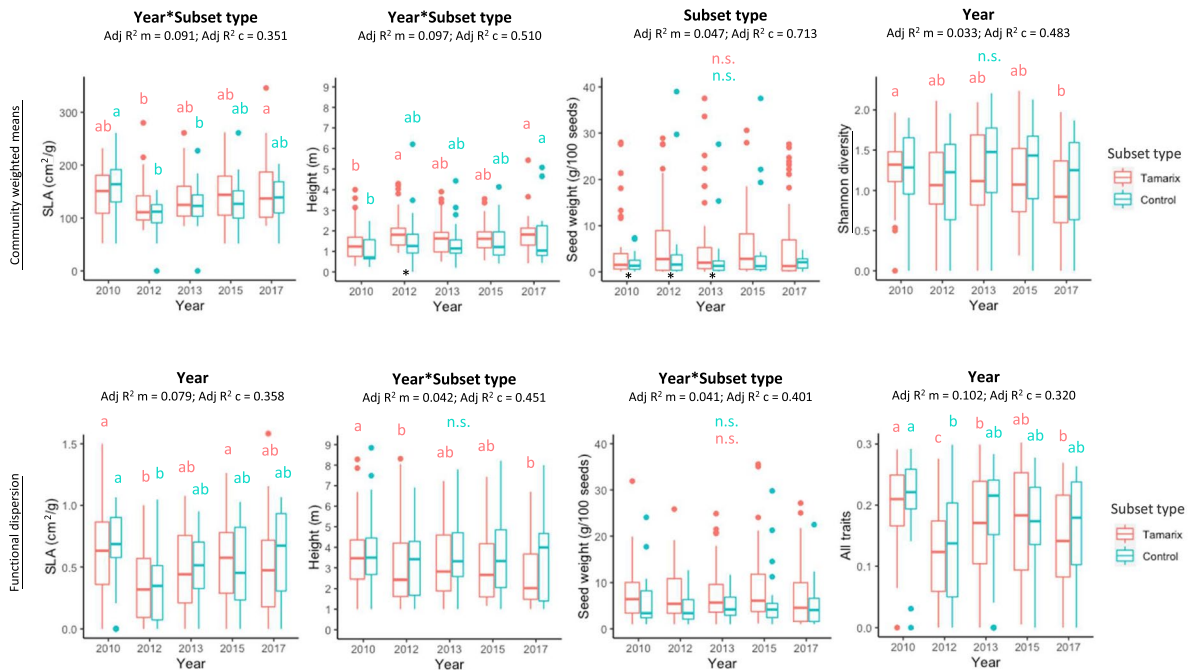
Fig. 3 Observed values for community weighted means and dispersion of individual traits, Shannon diversity and multivariate functional dispersion from eight traits of Table 1 at the *Tamarix* and Control subsets. Each boxplot represents the values of all transects with the *Tamarix* or Control subset for each year. The horizontal line within the box represents the median cover value; the top and bottom edges of the box represent the first and third quartiles. The whiskers extend to the outermost datapoint that falls within the first or third quartile ± 1.5*(interquartile range). Outliers exceed the 1.5*interquartile range and are indicated with filled circles. The width of the boxplots is proportional to the number of transects. Letters indicate homogeneous years within *Tamarix* bands if red and within Control bands if blue, after Tukey tests ($P < 0.05$). n.s., non-significant differences between years. Black asterisks indicate differences between *Tamarix* and Control subsets, after Tukey tests ($P < 0.05$). On top of each panel, best LME selected from a stepAIC procedure of the MASS package, with the interaction of year and subset type as fixed factor, and transect nested within site, site nested within river reach as random structure. Adj R^2 m, adjusted marginal R^2; Adj R^2 c, adjusted conditional R^2. SLA—Specific leaf area. See model diagnostics coefficients and predicted values of LMEs in Supplementary Material (Table S4). Three values were excluded from the plot of seed mass CWM because they skewed the axis too far to be legible. Note that the three upper left panels are for CWM and the three lower left panels for individual (one trait) FDis. Lower right panel is the multivariate FDis, analogous to the Shannon diversity above it

10.2%, Table S4, Fig. 3). No differences were found between the *Tamarix* and Control subsets. While there was higher functional trait diversity associated with lower *Tamarix* cover and with higher bare ground, fine, and coarse litter cover, *Tamarix* and ground cover generally explained very little of the patterns within each subset (adj R^2 m < 5%, Suppl. Material Table S5).

Discussion

This study is the first to examine the functional response of the underlying plant community to biocontrol of an invasive species. We found that functional dispersion is more sensitive to community dynamics than species diversity. While decreased *Tamarix* cover was associated with higher functional trait diversity, there was little fluctuation in individual functional traits in response to the second cycle of biocontrol defoliation. There was also little difference in the functional responses of the plant community between patches of vegetation with and without *Tamarix* present. 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 being affected, obscured responses in more heavily impacted sites, or that *Tamarix* cover was too low in our study sites to affect the plant community substantially. This highlights the importance and need for a better understanding the underlying drivers of biocontrol impact (Bean and Dudley 2018; Henry et al. 2018; Hultine et al. 2015).

Plant community functional dynamics may depend on abiotic conditions such as precipitation more strongly than on invasive species presence and removal

The main shifts in community weighted mean and dispersion of individual traits and diversity measures occurred in 2012, a year before peak defoliation, suggesting stronger drivers underlying plant community change than biocontrol defoliation. These changes in community weighted trait values and range are likely due to precipitation patterns in the study area (Fig. 4). A dry 2012 may have caused an overall reduction in herbaceous species, which tend to be shorter than other growth forms, and presumably with higher SLA, between these sampling periods. Further, lower SLA species are likely to dominate in drought stress scenarios (Wright et al. 2004). This would result in the observed increase in mean height and decrease in mean SLA. Another

possibility is that a large flood in June 2011 may have scoured and/or buried some herbaceous vegetation, but we believe this is unlikely as only some transects were partially flooded (field observations) and the plant community composition along the study transects only changed slightly across topographic gradients (elevation above river water and distance to water's edge) that theoretically determine the effects of flooding (González et al. 2020b). Additionally, the trait values of 2017 were overall similar to those of 2012, and coincidentally, 2017 was the second driest year of the five analyzed (Fig. 4).

Overall, the only consistent difference between *Tamarix* and control patches was in mean seed weight; *Tamarix* patches had heavier seeds. Plants with higher seed mass tend to be more stress-tolerant (Westoby 1998). This suggests that in our study area, *Tamarix* patches may have had more stressful conditions; there is extensive documentation of various sources of stress due to *Tamarix* dominance, including elevated soil salinity, lower light penetrance, altered soil microbiome, and altered fire regimes (Sher and Quigley 2013). Nevertheless, the overall lack of differences between *Tamarix* and control patches in the rest of functional parameters explored provides further evidence that *Tamarix* and its fluctuations were not strong drivers of community functional composition in the study area.
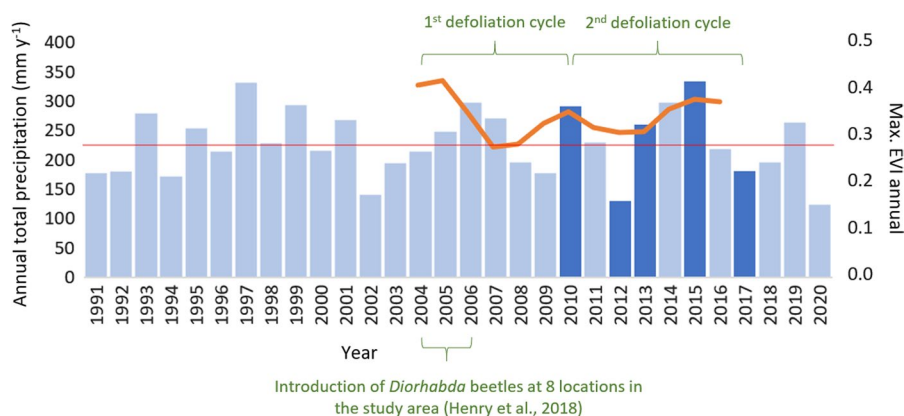

Fig. 4 Annual total precipitation for the period 1991–2020, in columns, as registered in the weather station of Moab, UT (#425,733, Western Regional Climate Center 2022). Darker columns denote years of survey. The red line indicates the normal (median 1991–2020 = 233.9 mm yr^{-1}). The orange line indicates the maximum Enhanced Vegetation Index value recorded by year in the study area (Matheson Wetland Preserve), as reported by Nagler et al. (2018), and is a proxy of vegetation greenness that helped us to identify the *Tamarix* defoliation cycles

Functional diversity was more sensitive than species diversity to community dynamics

Our finding that functional dispersion changed over time more distinctively than species diversity demonstrates the importance of incorporating functional measures of diversity in the study of plant communities. Given that there were no differences between control groups and *Tamarix* groups for these models, the drop in functional dispersion in 2012 is more likely a result of decreased precipitation that occurred in this time period. That the reduction in functional diversity happened before peak defoliation (2013) further suggests that this was a response to moisture availability rather than *Tamarix* biocontrol. Several previous studies have also found that while species and functional diversity are often closely linked, functional diversity provides information that species diversity alone does not (Bejarano et al. 2017; Biswas and Mallik 2010; England and Wilkes 2018; Tabacchi et al. 2019). For example, strong selective pressures can reduce functional diversity by filtering for a narrow range of strategies, even while species diversity is maintained (Mayfield et al. 2010). Biswas and Mallik (2010) found that in highly disturbed riparian habitats, species richness and diversity increased as functional diversity decreased, likely due to the selective pressures of high disturbance intensity. In the present study, functional and species diversity patterns were more similar, but we think that the slightly larger and more distinctive decrease in functional dispersion suggests that selective pressures have filtered out diverse plant strategies in larger proportion than species were reduced.

Weak evidence of influence of invasive *Tamarix* and biocontrol on the range of trait values and community averages

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). Recently, trait-based studies have shown that invasive species tend to reduce plant community functional diversity as well as taxonomic diversity (Henry et al. 2021; Sodhi et al. 2019; Tordoni et al. 2019). However, we found weak, or at least mixed evidence to support these findings in our study area. We found few differences in community traits between areas with no *Tamarix* present and areas with fluctuating *Tamarix* cover. Additionally, models containing only *Tamarix* areas showed only very weak responses of functional diversity indicators to fluctuations in *Tamarix* cover. This provides evidence that, in this case study, plant communities were not only taxonomically but also functionally resilient to biocontrol, and that abiotic factors influenced the plant community more strongly than invasive species cover. It is also possible that *Tamarix* cover was too low in our study sites (ca. 35% in the highest yearly median cover, Fig. 2) to have a significant effect on the plant community. This also highlights the need to assess biocontrol effects on a case-by-case basis (González et al. 2020b).

In U.S. western riparian systems, measuring functional diversity following various *Tamarix* removal methods including follow-up control treatments would add to our general understanding of plant community recovery, resilience and stability. Previous research encompassing several major watersheds and multiple study sites has found that control methods have significantly different effects on both the change in *Tamarix* cover and the resulting plant community, and that the effects of mechanical, chemical and burning methods are generally stronger than biocontrol (González et al. 2017; Sher et al. 2018).

Implications for effective management and ecosystem functioning

Biocontrol alone is unlikely to permanently reduce *Tamarix* cover or allow for the recovery of a diverse understory community in our study area. As biocontrol has been shown to reduce *Tamarix* less reliably and at lower magnitude than active methods and natural disturbance (González et al. 2017; Sher et al. 2018; González et al. 2020a, b), additional management actions (e.g., other control approaches, restoration actions) may need to be implemented to cause lasting change in *Tamarix* dominance (provided that is the main management goal). However, biocontrol of an invasive species can be implemented over a much larger area whereas other, more active methods are limited by cost and labor and thus tend to be implemented at smaller scales. In this study, we have provided evidence that as *Tamarix* dominance fluctuates, taxonomic and functional diversity are affected, but not necessarily as substantially as initially

anticipated when the biocontrol program was put in place. Within *Tamarix* patches, functional diversity tends to be higher with low *Tamarix* cover (Table S5, see also Henry et al. 2021). Given that low *Tamarix* cover alone is not necessarily associated with higher functional diversity (Henry et al. 2021), invasive species removal should be combined with active revegetation to accelerate the return of a diverse plant community and mitigate the loss of some ecosystem services provided by the dominant invasive species (Shafroth et al. 2008). When *Tamarix* cover is low, planting a broad range of life forms with different life strategies is more likely to be successful and increase functional diversity than *Tamarix* removal alone.

Abiotic conditions must be considered when anticipating plant community response to invasive species control. The changes in *Tamarix* cover that affect vegetation occur in the context of the abiotic environment and disturbance regime of riparian ecosystems (González et al. 2020a, b; Henry et al. 2021). For this reason, recovery of functionally diverse plant communities following *Tamarix* control may be limited to the extent that river-flow regulation and climate change have altered the abiotic environment. Previous studies have shown functional diversity in riparian plant communities is strongly linked to the frequency and duration of peak flows, and that the loss of those peak flows leads to a loss of functional diversity (Aguiar et al. 2018; Bejarano et al. 2017; Bruno et al. 2016). When revegetation occurs in the context of historic flood regimes it results in some functional recovery of the plant community (Engst et al. 2016; Fournier et al. 2015).

The recovery of functional diversity has important implications for ecosystem functioning and ecosystem services. In the present study, bloom period and ability to reproduce vegetatively are two traits that contributed to our measure of functional dispersion. A greater range in length of bloom periods can influence several ecosystem functions, such as synchrony with pollinators and synchrony with flood regimes to ensure continued germination (Bartomeus et al. 2013; Stella et al. 2006). Similarly, variation in the ability to reproduce vegetatively may have consequences for ecosystem function. Previous studies have shown that *Tamarix*-dominated communities are associated with more species that are not able to reproduce vegetatively (Henry et al. 2021). Species that reproduce vegetatively invest more in below ground biomass

and so contribute to substrate stability and soil fertility (de Bello et al. 2010). Additionally, higher functional diversity may confer resistance to further species invasion, buffer against the impacts of extreme climate events and provide wildlife habitat (de la Riva et al. 2016; Funk et al. 2008; Raynor et al. 2017).

Conclusion

We found that measures of species diversity and functional diversity generally followed similar patterns within a context of a second cycle of biocontrol defoliation, and overall showed high stability of plant communities. However, functional measures were slightly more variable over time, as well as likely more sensitive to environmental factors such as precipitation. We found that, in a regulated river where a biocontrol agent has been present for more than 10 years, defoliation-related dieback of an invasive species (*Tamarix*), and its cover generally, has little influence on the taxonomic or functional diversity of plant communities. However, when *Tamarix* does have an influence, it is to make plant communities more functionally specialized. The plant community response to peak defoliation and refoliation was minor and, apparently, was a smaller response than to yearly precipitation. This may suggest an overall resistance of the plant community to fluctuations in *Tamarix* cover, that plant communities have gained stability as a result of the first defoliation cycle, or both. 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 to formally test the effects of yearly precipitation on plant community traits. 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 sometimes used for nesting.

descriptive purposes only and does not imply endorsement by the U.S. Government.

Declaration

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