



Invasive tree cover covaries with environmental factors to explain the functional composition of riparian plant communities

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Received: 24 January 2021 / Accepted: 11 July 2021

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Abstract

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 and 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* 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 growth form, height, seed weight, specific leaf area, drought and anaerobic tolerance. Guild abundance 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, lowest *Tamarix* cover sites as well as in the driest, most stable, highest *Tamarix* cover sites. These guilds can be used to anticipate plant community response to restoration efforts and in selecting appropriate species for revegetation.

Keywords Riparian guilds · Invasive species · *Tamarix* · Plant community · Trait-based approaches

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 (Vilà et al. 2011; Foxcroft et al. 2017; Alahuhta et al. 2019). 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). This is especially relevant in riparian ecosystems, which 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 (Naiman et al. 2005; Mortenson and Weisberg 2010). As a consequence, many riparian corridors are increasingly dominated by not typically riparian, upland and non-native species (Mortenson and Weisberg 2010; Catford et al. 2011, 2014). Understanding the relationships among abiotic conditions, invasive species and community functional composition are, therefore, of particular importance in riparian systems.

Functional diversity is an important aspect of a plant community, influencing the resilience and stability of that community in response to shifting abiotic conditions and disturbances (Díaz and Cabido 2001; Laureto et al. 2015). A wide range of trait values reflects varied co-existing strategies in response to the abiotic environment, whereas low

Communicated by Edith B. Allen.

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functional diversity reflects a high degree of specialization in the community. Specialized communities may be more vulnerable to altered disturbance regime or resource availability (Lozanovska et al. 2018; Scott and Merritt 2020). In arid and semi-arid riparian ecosystems, flood disturbance and water stress can act, in turn, on the same plant community (Stromberg et al. 2007). Expanding on the intermediate disturbance hypothesis (IDH) which predicts highest levels of diversity at moderate intensity and frequency of disturbance (Huston 1979), intermediate levels of both stress and disturbance may produce the highest levels of species and functional diversity. Previous research has shown the IDH to apply to species and functional diversity of riparian vegetation in flood disturbed environments (Crandall et al. 2003; Biswas and Mallik 2010). Understanding the relationship between invasive species and functional diversity in flood disturbance adapted systems would provide insight into the validity of the IDH in this context.

Another way to understand the functional composition of a community is to identify groups of species that share similar traits (morpho-physio-phenological characteristics of organisms) specifically related to responses to environmental filters (Díaz et al. 2007). These groups are referred to as functional response guilds (Merritt et al. 2010; Stromberg and Merritt 2015; Diehl et al. 2017). Compared to taxonomic approaches, trait-based approaches to studying plant communities can provide a more mechanistic understanding of responses to environmental change, such as invasive species dominance or removal (Drenovsky et al. 2012; Díaz et al. 2016).

Over the past decade, trait-based approaches have been increasingly applied to riparian ecosystems and riparian plant communities in particular (Stromberg and Merritt 2015; Diehl et al. 2017; Bejarano et al. 2018; Lozanovska et al. 2018; Scott and Merritt 2020). A primary objective of riparian trait studies has been to identify plant community responses to hydrogeomorphic conditions (Stromberg and Merritt 2015; Diehl et al. 2017; Bejarano et al. 2018; Lozanovska et al. 2018; Scott and Merritt 2020). 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 (Stromberg and Merritt 2015; Aguiar et al. 2018). Less frequently flooded terraces have been characterized by resource conservative strategies and drought tolerance (e.g. low specific leaf area and fewer, heavier seeds; Stromberg and Merritt 2015; Aguiar et al. 2018).

To date, however, no riparian trait-based study has explicitly incorporated the influence of woody invasive species that so often dominate riparian ecosystems and have a high likelihood of altering functional composition. Additionally,

despite several studies employing a trait-based 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 (but see Butterfield et al. 2020; Scott and Merritt 2020). 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). In this study, we examine the functional response of plant communities to varied levels of a dominant invasive species, including herbaceous species in our analysis.

Plant communities with varying abundances of invasive non-native shrubs in the *Tamarix* genus (tamarisk, salt cedar) 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. Due to their ecological similarity and to the difficulty of distinguishing species, *Tamarix* refers to the two most common species in the U.S. and their hybrids—*T. ramosissima* and *T. chinensis* (Gaskin 2013). 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 (Merritt and Shafroth 2012; Ohrtman et al. 2012; Auerbach et al. 2013; Bateman and Merritt 2020). 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; Sher et al. 2018).

Regionally, *Tamarix* cover is more dominant in drier areas with less precipitation (Nagler et al. 2011; Hultine and Dudley 2013; González et al. 2017). 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; Nagler et al. 2011) where its control is commonly the objective of riparian management (Shafroth et al. 2005; Sher 2013; González et al. 2015, 2017). 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 presence of the biocontrol agent *Diorhabda* provides a gradient of *Tamarix* cover without the confounding factors of additional disturbances that other removal methods create (Nagler et al. 2018).

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, 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.

Methods

Study area

We selected 98 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 Colorado, and two of the main tributaries: Dolores and Green rivers, as well as in small order streams in the Colorado catchment (Online Resource 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. The other 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. 2017). Sites used in the current study were exposed to *Diorhabda* biological control for 5 to 9 years at the time of sampling, with no other mechanical or chemical removal methods used. 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; González et al. 2020).

Native vegetation in the study area is primarily made up of riparian and upland riparian shrubs (e.g. *Forestiera neomexicana* and *Ericameria nauseosa*), forbs (*Solidago occidentalis*) and graminoids (e.g. *Achnatherum hymenoides* and *Distichlis spicata*). “Desirable reference sites” are characterized by a higher cover of hydrophytic species such as *Salix exigua* and *Carex* spp. if regularly flooded or by native xeroriparian (sensu Beauchamp and Shafroth 2011) species if hydrologically disconnected. Thirty-three percent of these desirable reference sites have some presence of *Populus* spp.

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 (Online Resource 2). 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 19 traits related to resource acquisition, stress tolerance and reproductive strategy using online databases and literature searches (Table 1). We chose these traits based on previous studies that have shown them to be relevant for defining riparian plant guilds (Stromberg and Merritt 2015; Diehl et al. 2017; McCoy-Sulentich et al. 2017; Scott and Merritt 2020).

We collected continuous and categorical trait data primarily using plant trait values from Palmquist et al. (2017), the TRY database (Kattge et al. 2020; Online Resource 3), 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

Table 1 Traits 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

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 eFlora (Tela Botanica 2020). 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 (Online Resource 4). 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 Quedstedt 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 (Online Resource 2) across 95 sites ultimately included in our analysis.

Environmental variables

We compiled climatic and hydrogeomorphic data from González et al. (2017) and summarized this information for our study sites (Table 2; Online Resource 5). Variables were checked for multicollinearity with a correlation matrix (Online Resource 6). 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 Data ranges, mean and standard deviation for environmental variable included in the RDA and regression models

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 electrical conductivity (EC)	µS/cm	Local	30	25,280	2519.1 ± 4280.4
Elevation above river water channel	cm	Local	12	450	212.5 ± 109.0
Absolute <i>Tamarix</i> cover	Percent cover	Local	0	100	13.0 ± 17.1
Relative <i>Tamarix</i> cover	<i>Tamarix</i> cover/total overstory cover	Local	0	1	0.3 ± 0.3

Correlation coefficients can be found in Online Resource 6. Elevation above river water level was not used in the regression models because of a large number of missing values

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 the 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 (Online Resource 7).

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” (Beauchamp and Stromberg 2008; González et al. 2017). 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 of the guilds we created (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). Variables were standardized 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 the six river regions. We further examined two of the guilds most strongly correlated with the RDA axes using generalized linear mixed effects models with maximum likelihood estimation. We used log-transformed guild cover as the response variable and the same set of explanatory variables as stated above as fixed factors, using river 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. For all mixed effects models, we report marginal R^2 (R^2_m)—the variance explained by fixed effects

only, as well as conditional R^2 (R^2_c)—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 function

“dbFD” in the package “FD” (Laliberté and Legendre 2010). The defaulted generic function “scale” was used to standardize the variables.

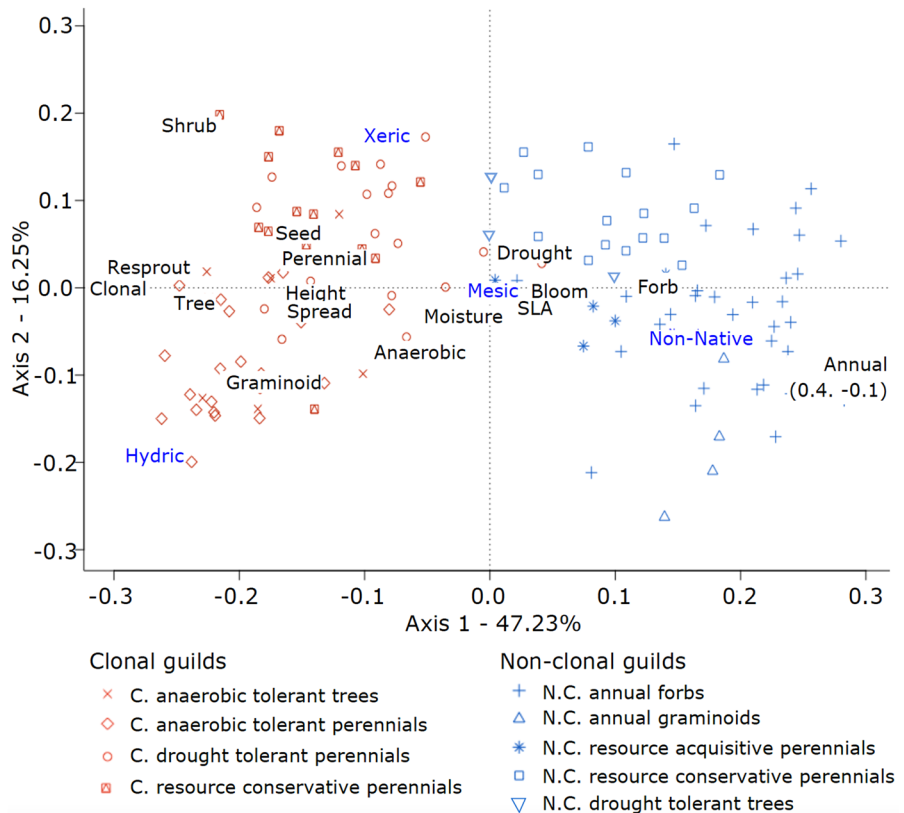
Results

Defining guilds

From the 125 species included in the complete linkage clustering, we identified nine riparian plant guilds (Online Resource 7). These guilds were defined based on their placement on the PCoA axes as well as average trait values for each guild (Fig. 1; Online Resource 7). 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 growth form, 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 (Fig. 1, Online Resource 7) contained plant species that cannot reproduce vegetatively and were differentiated from each other primarily by duration, growth

Fig. 1 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 averages or centroids of the top 12 most important traits in defining the axes are included. All weighted averages and centroids were multiplied by two to better visualize the relationship. While the attributes “hydric”, “mesic”, “xeric” and native vs. non-native (in blue text) were not included in the cluster analysis, they are plotted to aid in the interpretation of the guilds. *Clonal* Ability to reproduce vegetatively, *Resprout* Ability to resprout following disturbance, *Seed* Seed mass, *Spread* Vegetative spread rate, *Anaerobic* Anaerobic tolerance, *Drought* Drought tolerance, *Moisture* Moisture tolerance, *Bloom* Total bloom period, *SLA* Specific leaf area



form and 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, relative to other guilds. Two of the non-clonal guilds were made up of perennials and were differentiated from each other primarily by specific leaf area. 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 and 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 shows the trait profiles of each guild.

When *Tamarix* is included in the guild analysis, the guilds change 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 (Online Resource 2).

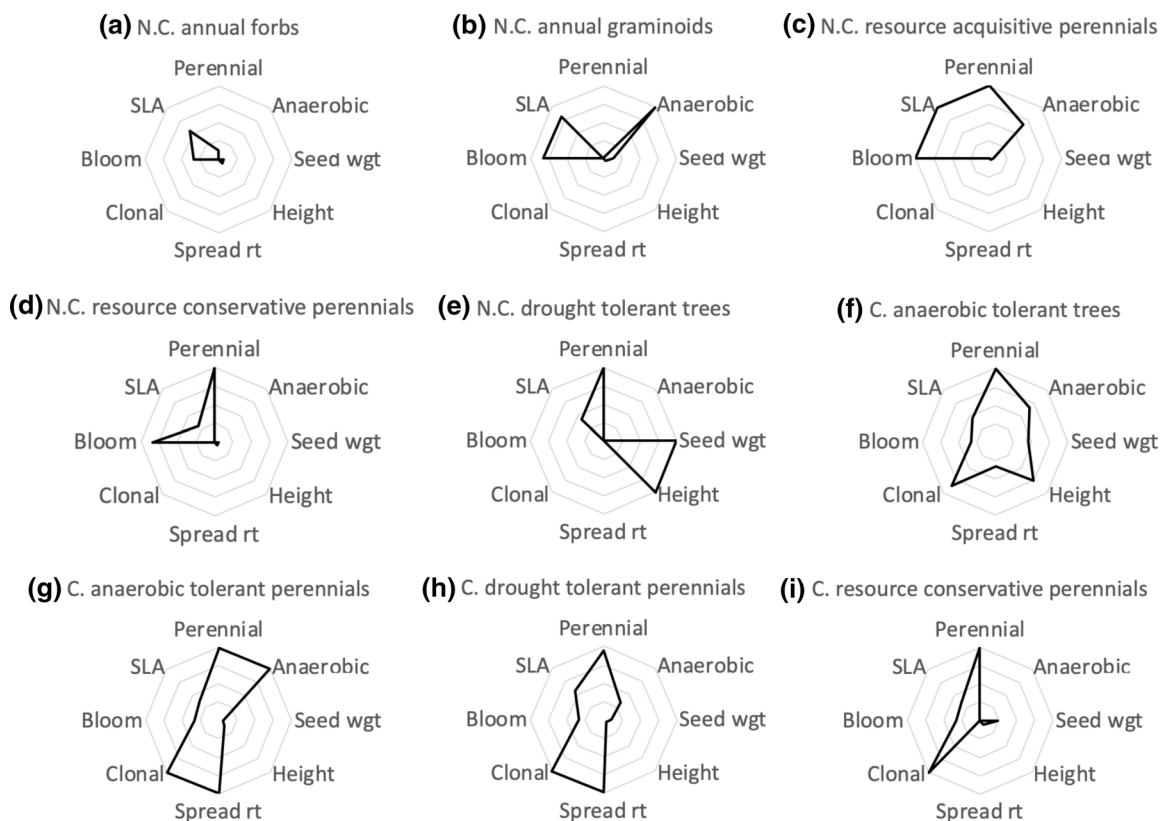


Fig. 2 Radar plots showing the trait profiles for each guild. For guild names, *N.C.* Non-clonal, *C.* Clonal, *Perennial* Perennial vs. Annual, *Anaerobic* Anaerobic tolerance, *Seed* Seed mass, *Height* Height at maturity, *Spread rt* Spread rate, *Clonal* Ability to reproduce vegeta-

tively, *Bloom* Total bloom period, *SLA* Specific leaf area. The grid lines represent continuous and ordinal values scaled to 0–100. For categorical variables—*Perennial* (0=annual, 100=perennial); *Clonal* (0=no, 100=yes)

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 (RDA1, 23%, Fig. 3). At low values of RDA1, sites tended to be higher in elevation above sea level (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”, “Non-clonal resource conservative perennials” and “Non-clonal annual graminoids” increased with increasing RDA1 values. These three guilds had the highest proportion of non-native taxa. 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 associated, although weakly, with increasing distance to water. At lower values of RDA1 there was a greater abundance of “Clonal anaerobic tolerant perennials”. 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” and “Clonal anaerobic 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 (Online Resource 8).

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 but ANOSIM values were not exceptionally low, which was consistent with some degree of overlap in guild composition (ANOSIM; Online Resource 9). These differences were driven primarily by lower cover of clonal guilds—both resource conservative and anaerobic tolerant perennials and higher cover of “Non-clonal annual forbs” and “Non-clonal annual graminoids” along the Colorado river (in Utah and in Colorado). The opposite pattern was seen along the Dolores River, above and below the San Miguel which had higher cover of “Clonal resource conservative perennials” and “Clonal anaerobic tolerant perennials” (ANOVAs, Online Resource 10).

Mixed models showed that “Clonal anaerobic tolerant perennials” increased with decreasing relative *Tamarix* cover and distance to water (Table 3). 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

Fig. 3 RDA of a Hellinger-transformed matrix of guild abundance (scaling = 2) with 31.5% of total variability explained ($df=8$, $F=6.41$, $p=0.001$). Symbols represent the position of the nine guilds in the bidimensional space determined by the first two axes of constrained variability and were multiplied by 0.8 for visual clarity. 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)

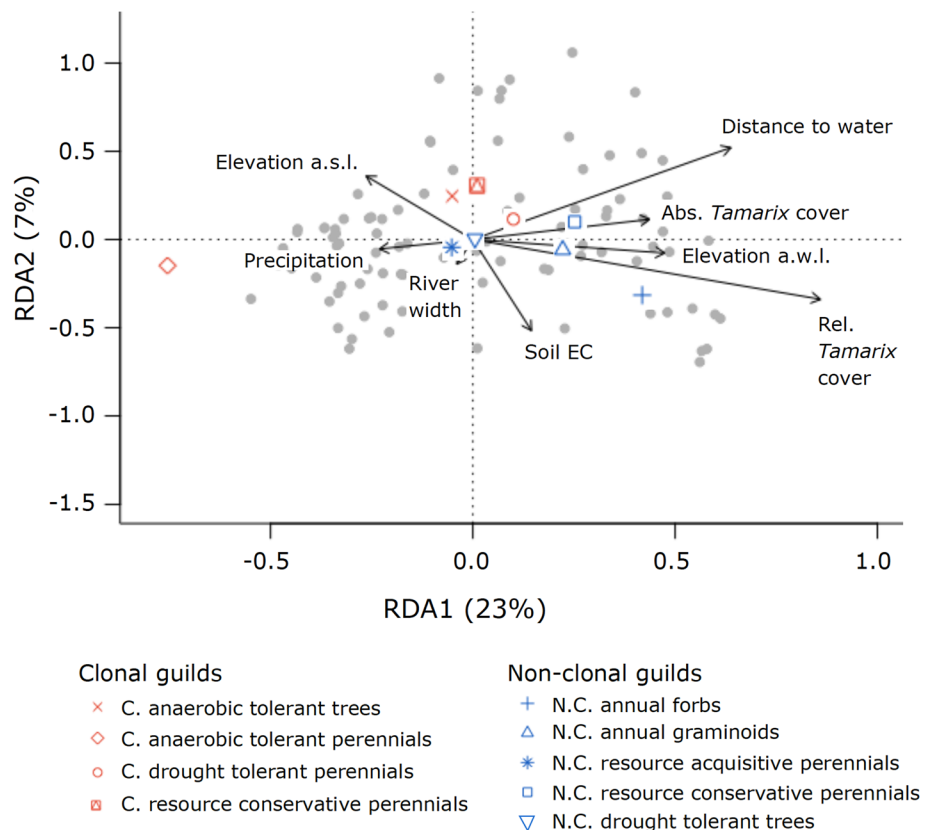


Table 3 General linear mixed models with either “Clonal anaerobic tolerant perennials” or “Non-clonal annual forbs” as dependent variables and abiotic condition and *Tamarix* cover as independent variables, selected by backward selection using the Akaike information criteria

	Value	S.E	d.f	<i>T</i>	<i>p</i>	<i>R</i> ² _m	<i>R</i> ² _c
Clonal anaerobic tolerant perennials							
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 <i>Tamarix</i> cover	− 0.822	0.137	87	− 6.009	0.00		
Non-clonal annual forbs							
Intercept	2.000	0.118	85	16.877	0.00	0.15	0.15
Distance to water*	− 0.227	0.127	85	− 1.794	0.08		
Soil EC*	0.210	0.135	85	1.560	0.12		
Relative <i>Tamarix</i> cover	0.409	0.130	85	3.141	0.00		
Soil EC*:Rel. <i>Tamarix</i> cover	− 0.204	0.122	85	− 1.670	0.10		

Guild cover of both models was log transformed, as were explanatory variables marked with an asterisk* to improve model residuals

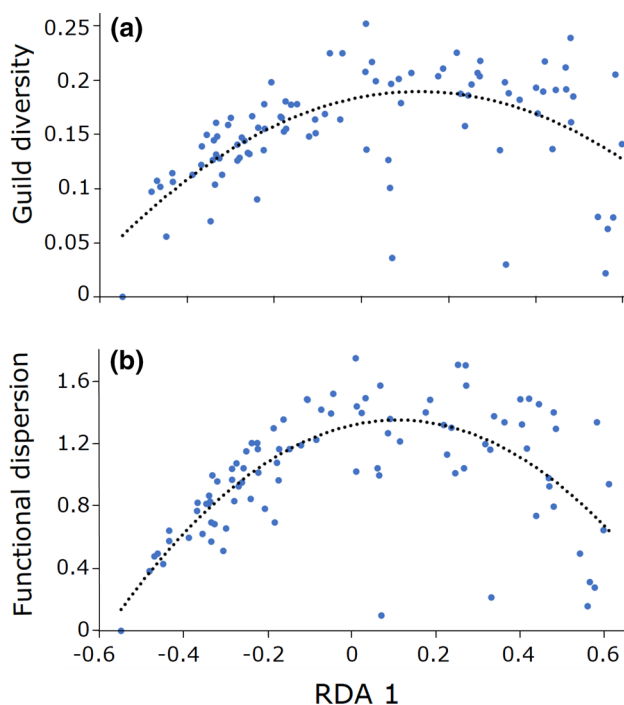


Fig. 4 RDA1 vs. guild diversity and functional dispersion (calculated using all traits). A quadratic mixed effects model fit by maximum likelihood was used to determine how RDA1 influenced guild diversity ($R^2_{\text{m}}=0.43$, $R^2_{\text{c}}=0.62$, $df=87$, $t=13.40$, $p<0.0001$) and functional dispersion ($R^2_{\text{m}}=0.35$, $R^2_{\text{c}}=0.38$, $df=87$, $t=22.17$, $p<0.0001$)

was explained by both relative *Tamarix* cover and distance to water (Online Resource 11). Cover of “Non-clonal annual forbs” was significantly positively correlated to relative *Tamarix* cover, and no other variables (Table 3).

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 (Fig. 4). At the highest elevation and precipitation values, where *Tamarix* tends to be lower (negative RDA values), both measures of diversity are at their lowest. At the highest levels of *Tamarix*, distance to water, elevation above water and EC (positive RDA values), 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).

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. 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). However, Merritt et al. (2010) proposed that selection for annual life cycle and sexual reproduction would be stronger in river systems experiencing frequent, channel-forming fluvial disturbances. That in the present study plant communities closer to water, both in horizontal and vertical distance, were characterized by asexual reproduction and perennial growth suggests that fluvial disturbances in our study area do not likely scour the riverbanks enough to discourage clonal and perennial growth. 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 reproduction by seed as compared to vegetative reproduction.

Within each of these types of reproductive strategies, 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).

***Tamarix* cover encourages either resource conservative or shade tolerant strategies**

With decreasing elevation above sea level (and so decreasing precipitation and increasing temperature), increasing 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 short species (Westoby 1998). The more native-dominated guild associated with these low resource environments are “Non-clonal resource conservative perennials” (e.g. *Ericameria nauseosa* and *Gutierrezia sarothrae*) whose woody species do not tend to form high, dense canopies. We can therefore interpret the mid to high SLA of the two understory guilds most strongly associated with higher RDA1 values (and so, higher *Tamarix* cover) 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, particularly in the context of biocontrol defoliation, 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 higher temperature and lower precipitation), farther from water, with higher soil salinity and *Tamarix* cover.

Our result that cover of “Clonal anaerobic tolerant perennials” was negatively correlated to distance to water is in agreement with previous studies that showed obligate riparian guilds decreased with decreasing water availability (Aguiar et al. 2018). However, our finding that this guild is also negatively correlated to *Tamarix* cover (independent of abiotic conditions) provides new insight into the influence of *Tamarix* on the functional composition of plant communities. Although *Tamarix* is generally associated with sites

farther from water, when it does grow directly along riverbanks *Tamarix* changes the functional nature of these riparian plant communities. While historically, cottonwoods may have created densely shaded areas, current riparian areas are cottonwood-depauperate due to less frequent flooding (Merritt and Poff 2010). Follow-up analyses showed no relationship between other riparian trees and “Clonal anaerobic tolerant perennials”. Some of the ecosystem engineer effects of *Tamarix* are also likely in play here, for example –altering the litter mat which may interfere with seed germination in the context of reduced flooding and increasing soil salinity (Ohrman et al. 2012; González et al. 2020). The pattern described here highlights the role of *Tamarix* as both a passenger and driver of ecological change (Sher 2013). *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 (Sher 2013). Once established, *Tamarix* also creates an environment that is different from areas where it is not present.

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 (Huston 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. This finding supports previous studies that have similarly found the highest level of functional diversity at intermediate levels of flood disturbance (Biswas and Mallik 2010).

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 in choosing 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* by active methods and/or biological control, 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 also 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 dracuncululus*, *Solidago occidentalis*) to mitigate potential secondary invasions.

While guilds responded to *Tamarix* cover specifically, they also varied along abiotic conditions independent of *Tamarix* cover. Our result that increasing distance to water was associated with a decreased cover of “Clonal anaerobic tolerant perennials” reiterates the importance of considering the current or anticipated abiotic environment when planning for restoration. Climate change is manifesting in these areas as an increase in temperature and a decrease in precipitation, thus being able to easily identify replacement species with adaptive functional traits is an important application of these findings (Garfin et al. 2013).

Conclusion

This is the first time that the response of plant communities to the largest plant invasion in North American riparian ecosystems has been 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 dry, low-resource areas that would otherwise have little canopy. While large trees such as native cottonwoods may have historically shaded some riparian plant communities, their current populations are not dense enough to form closed canopies the way *Tamarix* now does. 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. Given the spatial extent of the study, it was not feasible to collect field measurements for traits. This represents a potential limitation of the study in regard to traits that may vary within a species based on environmental conditions. Specific leaf area is such a trait and so we have likely underestimated its importance in defining the response of plant communities to abiotic conditions. Ongoing efforts to collect field measurements for traits across a range of environmental conditions will increase our understanding of plant community response to environmental change. 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 (González et al. 2020; Henry et al. 2018; Nagler et al. 2018). Of the 13 sites for which we had multiple years of observations, nine sites had less than 10% change in absolute *Tamarix* cover across three years, while four sites had from 18 to 40% change in cover. These changes included both increases and decreases in cover. 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. The approach we present in this study can be applied to any system with a dominant, woody invasive species. It could be used, for example, to understand the mechanisms underlying plant community response to the removal of *Acacia* (Ruwanza and Tshililo 2019), *Elaeagnus* (Katz et al. 2020) and *Eucalyptus* (Hirsch et al. 2020) where they are invasive. 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.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00442-021-04990-z>.

Acknowledgements We acknowledge the National Science Foundation Dynamics of Coupled Natural and Human Systems award (project number 1617463) and the University of Denver for providing A.L.H. with salary funding, and the U.S. Geological Survey Invasive Species Program that partially funded E.G. collaboration. We thank Emily Palmquist for advising on trait data collection, Lindsay Reynolds for contributing some trait data and Pat Shafroth for advising on plant traits and guild definitions. Thanks also to the authors of González et al. 2017, Ecological Applications and González et al. 2017, Biological Conservation for providing plant species and environmental data, as well as to Alex Goetz, Kayleigh Kearnan, Kyla Reiner and James Sheinbaum for assistance in trait data collection. This study complies with the current laws of the country in which it was performed.

Author contribution statement ALH, EG and AAS conceived the ideas. ALH collected and analyzed the data with the advice of all authors. BB contributed to scripts for analysis. All authors discussed and interpreted the results. ALH led the writing and all authors contributed to the manuscripts revisions and intellectual content and gave approval for publication.

Funding We acknowledge the National Science Foundation Dynamics of Coupled Natural and Human Systems award (project number

1617463) and the University of Denver for providing A.L.H. with salary funding, and the U.S. Geological Survey Invasive Species Program that partially funded E.G. collaboration.

Availability of data and material Data are available in the Zenodo Digital Repository; <https://doi.org/10.5281/zenodo.5047316>

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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