

# Patterns of herbivory-induced mortality of a dominant non-native tree/shrub (*Tamarix* spp.) in a southwestern US watershed

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**Abstract** The capacity for plant species or populations to cope with herbivory depends in large part on the complex interactions between resource availability, life history and adaptive strategies to maximize defense and/or tolerance to herbivory. Given these complex interactions, the impacts of repeated herbivory on plant stress and subsequent mortality is often difficult to predict. To better understand relationships between herbivory and environmental condition, we studied the relationship between the non-native shrub/tree tamarisk (*Tamarix* spp.) and a specialist herbivore, the northern tamarisk leaf beetle (*Diorhabda carinulata*) released as a biological control agent of *Tamarix* in the Virgin River watershed in the southwestern United States. The beetle feeds exclusively on *Tamarix* foliage resulting in complete stand foliage

desiccation (i.e. defoliation) that lasts several weeks. Approximately 900 *Tamarix* plants were surveyed over three consecutive growing seasons for canopy dieback and mortality across 10 sites varying in the number of defoliation events, tree height, soil salinity, soil texture and bulk leaf carbon isotope ratios ( $\delta^{13}\text{C}$ ). Canopy dieback increased from 27 % by volume in the spring of 2012 to 41 % and 54 % in 2013 and 2014, respectively. Tree mortality increased from 0 % in 2012 to 6 % and 10 % in 2013 and 2014, respectively. Surprisingly, percent canopy dieback was not related to the number of defoliation events that ranged from 2 to 7 across the 10 sites prior to the 2013 growing season. On the other hand, canopy dieback increased with soil salinity in both 2013 ( $R^2 = 0.39$ ,  $F = 5.07$ ,  $P = 0.055$ ) and 2014 ( $R^2 = 0.56$ ,  $F = 10.26$ ,  $P = 0.015$ ). Canopy dieback in 2013 increased with bulk leaf  $\delta^{13}\text{C}$  ( $R^2 = 0.38$ ,  $F = 4.08$ ,  $P = 0.078$ ), although  $\delta^{13}\text{C}$  also decreased with the number of defoliation events ( $R^2 = 0.64$ ,  $F = 14.17$ ,  $P = 0.0055$ ), suggesting that photosynthetic rate or drought stress (as indicated by leaf  $\delta^{13}\text{C}$ ) may serve as a poor predictor for *Tamarix* canopy dieback in response to defoliation. Percent canopy dieback was correlated with shifts in NDVI measured from annual MODIS imagery ( $R^2 = 0.61$ ,  $F = 12.32$ ,  $P = 0.008$ ), demonstrating that the tree surveys reflect site-scale changes in canopy cover. Results show that patterns of *Tamarix* canopy dieback and subsequent mortality following episodic defoliation by *D. carinulata* are likely to vary across broad gradients in soil salinity and other abiotic

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and biotic factors. Documented impacts of this biocontrol agent reported here will aid management efforts aimed at preserving riparian habitat in the short-term with conservation efforts targeting the removal and control of *Tamarix* over the long term.

**Keywords** Plant mortality · *Tamarix* · *Diorhabda carinulata* ·  $\delta^{13}\text{C}$  · MODIS · Riparian ecosystems

## Introduction

On average, herbivores consume more than 10 percent of the planet's annual net primary productivity in non-cultivated ecosystems (Coley et al. 1985). Consequently, the impact of herbivory on individual plants, populations and communities can be profound. A potential consequence of herbivory is plant mortality, which may be enhanced when herbivory outbreaks coincide with other stress mechanisms such as drought. In contrast to additive effects, stress factors often interact so that their combined effects on plant mortality may operate synergistically (Lichtenthaler 1998). Intense herbivory can, therefore, result in significant shifts in vegetation cover, community structure and ecosystem function at large spatial scales.

Herbivory can function as a physical disturbance agent that removes or damages plant biomass, just as do abiotic factors (Cooke et al. 2007). The capacity of a plant to resist or tolerate episodic disturbance is often a function of its access to resources. Plants that occur under poor edaphic conditions are often exposed to a low availability of resources such as sunlight, water and mineral nutrients, or they occur in locations where access to resources is inhibited by abiotic conditions such as high soil salinity. Chronic resource limitation often triggers a “mortality spiral” where the combination of a long-term stressor from poor edaphic conditions and a short-term stressor such as drought or episodic herbivory results in a spiraling set of resource deficiencies that ultimately leads to plant mortality (Manion 1991). A classic example for the mortality spiral concept has been the recent landscape-level conifer tree die offs in the western United States caused by a combination of inter-annual drought and pine beetle outbreaks throughout the region (Breshears et al. 2005, 2009; Van Mantgem et al. 2009; Adams et al. 2009; Allen et al. 2010). Although the exact

causes of mortality in these forests have been widely debated (i.e. drought induced mortality vs. carbon starvation), there is clear evidence that trees growing in less favorable habitats were generally more likely to succumb to the effects of drought and herbivory than trees growing in more favorable locations (Koeppke et al. 2010; Looney et al. 2012).

Independent of resource availability, some plant genotypes or populations may be better suited to tolerate stress or disturbance than others across various edaphic conditions. This is because adaptive traits arise from the complex tradeoffs plants often face in maximizing fitness (Ruel and Whitham 2002; Stultz et al. 2009). These tradeoffs require plants to balance the allocation of resources such as photosynthates and mineral nutrients to growth, reproduction, defense (i.e. secondary metabolites) and internal storage (Bloom et al. 1985; Chapin et al. 1990; Ayres 1993). If all else is equal, plants that allocate a larger proportion of resources to growth must do so at the expense of allocating fewer resources to other areas such as storage (Hultine et al. 2013). Therefore, plants that are well adapted to episodic disturbance often ‘bank’ internal resources within complex storage organs, while plants well-adapted for more rapid growth rates are more likely to allocate a larger proportion of labile storage pools for tissue construction and growth respiration. Because allocation strategies within and among populations can be highly diverse (Hoch et al. 2003; Sala et al. 2012), patterns of mortality following disturbance may or may not match edaphic gradients in resource availability and stress.

Riparian woodlands in arid regions of North America are highly productive ecosystems with disproportionately greater plant and animal diversity compared to surrounding landscapes. These ecosystems have experienced a dramatic shift in vegetation cover over the last several decades from native riparian forests to shrublands dominated by the Eurasian tree/shrub tamarisk (*Tamarix* spp.). Several *Tamarix* species, also known as saltcedar, were introduced to North America in the early to mid nineteenth century, and two species, *T. chinensis* Lour. and *T. ramosissima* Ledeb. and their hybrid forms, have become widely established throughout much of the western United States and northern Mexico (Gaskin and Schaal 2002; Friedman et al. 2005).

*Tamarix* has been a target for management in many regions because of its documented and speculated

negative impacts to biodiversity, water resources and ecosystem functions in arid and semi-arid riparian ecosystems (Shafroth et al. 2005). The northern tamarisk leaf beetle, *Diorhabda carinulata* (Chrysomelidae), was initially released in 2000–2001 in the US for the biological control of *Tamarix* (DeLoach et al. 2003). The beetle feeds exclusively on *Tamarix* foliage, resulting in periods of complete stand defoliation that lasts for several weeks (Fig. 1; Dudley 2005; Hultine et al. 2010). Specifically, the beetles scrape leaf waxes and the cuticle before attacking the mesophyll and the vascular system resulting in leaf desiccation and subsequent leaf drop (Dudley 2005). It was anticipated that herbivory by this specialist herbivore would reduce the cover and ultimately lead to mortality of at least some target plants. The actual rate of mortality, however, appears to be highly variable across the landscape. Repeated years of



**Fig. 1** Photographs showing a *Tamarix* stand approximately 4 km upstream from Site 3 near the town of Scenic, AZ before (June 2009) and after (July 2009) defoliation by *Diorhabda carinulata*. Photo credit: Mike Kuehn

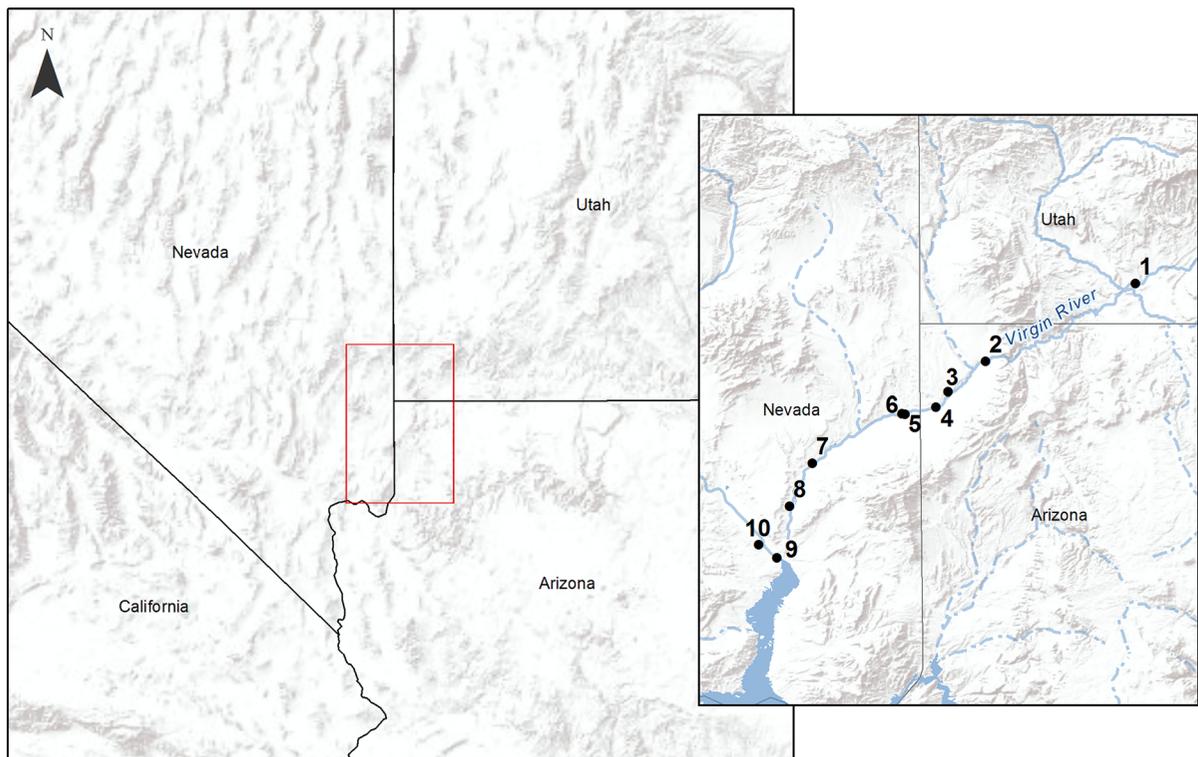
defoliation can result from anywhere between 0 and 100 % stand-level mortality (Hultine personal observation), with mortality ranging from 20 to 40 % being common after 3–5 years (Dudley and Bean 2012). Evidence from annual growth rings suggests that patterns of mortality may be related to contrasting patterns in resource allocation whereby faster growing *Tamarix* trees may be more likely to succumb to repeated defoliation than slower growing trees (Hultine et al. 2013). The authors speculated that the inverse relationship between growth and survival was linked to adaptive tradeoffs in allocation of non-structural carbohydrates (i.e. free sugars and starch) and nutrients for growth versus storage. If so, adaptive tradeoffs associated with resource allocation may partially decouple the capacity for *Tamarix* plants to cope with episodic disturbance from edaphic conditions.

In 2006, *D. carinulata* beetles were released in the upper Virgin River watershed in SW Utah, and within 2 years, beetles had established and dispersed downstream into Arizona and Nevada, reaching Lake Mead and the lower Colorado River by 2012 (Dudley and Bean 2012). We monitored canopy dieback and rates of mortality in approximately 900 *Tamarix* trees across 10 sites along a ca. 140 km reach of the Virgin River from St. George, Utah to Lake Mead near Overton, Nevada. Our objective was to evaluate whether impacts of the leaf beetle on *Tamarix* can be predicted by environmental and biological gradients related to plant stress. We evaluated stress from measurements of soil salinity, soil silt and clay content, number of defoliation events and leaf carbon isotope ratios (a proxy for plant water balance). Results from this study provide insight into the abiotic and biotic factors that can be associated with the impacts of herbivory on this widely distributed invasive plant, and shed new light on the complex interactions between plants and herbivores.

## Materials and methods

### Site description and analysis of tree condition

Ten sites were selected for study in the Virgin River Watershed in May of 2012 (Fig. 2). The sites were selected based on having reliable data for the number of *Tamarix* defoliation events by *D. carinulata*, distance from the original release site, site access and stand



**Fig. 2** Map showing the site locations along a 140 km reach in the Virgin River Watershed from St George, UT to Lake Mead in Nevada. Site coordinates are listed in Table 1

density. A defoliation event was defined as  $>50\%$  of the *Tamarix* canopy being desiccated (i.e. defoliated) by the beetle, although in most cases plants were 95–100% defoliated (Dudley, unpublished data). Trees at the original release site experienced a total of seven defoliation events since the release of the beetles in 2006 (Table 1). The furthest downstream sites near Lake Mead experienced the fewest defoliation events (2), while trees at all of the other sites were defoliated four and six times (Dudley, unpublished data) (Table 1). Sites 1–9 were located in riparian areas along the Virgin River between St George (Site 1) and its delta entering Lake Mead (Site 9). Site 10 was located on the Muddy River near Overton Nevada approximately 10 km upstream from its confluence with the Virgin River (Fig. 2). All of the sites were located within the active floodplain with approximate heights above the active channel (determined from satellite imagery) ranging from 0 to 0.9 m at Site 8 to 1.5–3.7 m at Site 3 (Table 1). The Virgin and Muddy River's both have limited flow controls upstream from the field sites and therefore

experience regular episodic flooding. Two recent floods, one in 2005 and the other in 2010 were characterized as having return intervals of 52 and 39 years, respectively, resulting in significant changes in the channel morphology of both of the river's floodplains. Mean annual maximum and minimum temperatures at the upper end of the reach (Site 1) are 25.4 °C and 6.9 °C, respectively with on average 210 mm of precipitation falling annually (Western Region Climate Center). Mean annual maximum and minimum temperatures at the upper end of the reach (Site 10) are 29.2 and 9.9 °C, respectively with on average 210 mm of precipitation falling annually (Western Region Climate Center).

At each site, 100 live, healthy trees were selected for monitoring. Although tree selection was haphazard, minimum tree height, canopy vigor and canopy dieback were roughly equal for each site and only mature trees that had evidence of prior or current reproduction were used. With the exception of Site 1, all of the trees were confined to an area of ca. 100 m radius. Site 1 included two locations approximately

**Table 1** Coordinates, elevation, distance in river kilometers from the original release site, approximate height (min and max) of site above the active river channel, mean tree height of analyzed *Tamarix* trees and number of defoliation events by a specialist herbivore, *Diorhabda carinulata* in the lower Virgin River Watershed

Site #	Coordinates	Elev (m)	Distance: release point (km)	Height above channel (m)	Mean tree height (m)	# of Def. events
1	37°05'12.52"N 113°33'20.49"W	781	1	0.3–0.9	4.5 (0.1)	7
2	36°54'38.38"N 113°53'41.89"W	565	55	0.9–1.5	3.9 (0.1)	6
3	36°50'33.07"N 113°58'47.23"W	514	68	1.5–3.7	3.5 (0.1)	6
4	36°48'30.06"N 114°00'24.97"W	496	73	1.5–3.0	3.5 (0.1)	5
5	36°47'33.33"N 114°04'38.04"W	477	80	1.5–2.4	3.4 (0.1)	5
6	36°47'35.05"N 114°05'03.05"W	473	81	2.4–3.4	3.4 (0.1)	5
7	36°40'54.40"N 114°17'08.33"W	410	104	0.6–1.8	4.0 (0.1)	4
8	36°35'03.41"N 114°20'13.70"W	379	117	0.0–0.9	3.4 (0.1)	2
9	36°28'04.49"N 114°21'56.65"W	353	135	0.9–1.2	2.7 (0.1)	2
10	36°29'53.26"N 114°24'27.10"W	367	140	0.9–1.2	2.9 (0.1)	2

one km from each other, with 50 trees selected at each location. A numbered aluminum tag was placed on each tree and a GPS unit was used to identify the tree's coordinates to within approximately 1 m. The trees were categorized by percent canopy dieback (of total canopy volume) and approximate tree height. Tree height was estimated for each tree and mean tree height ranged from 4.5 m at Site 1 to 2.7 m at Site 9 (Table 1). Canopy dieback ( $C_d$ ) was estimated in increments of 0, 25, 50 and 75 %, or 100 % if there was no evidence of live canopy in which case the tree was categorized as dead. Where no live canopy was visible, but live re-sprouts were present at the base, the tree was estimated to have 90 % dieback.

In May of 2013 and May of 2014, the trees were monitored for canopy condition and mortality. Because some trees were either cleared during management activities or were unidentifiable because the tags were removed, our final census count was 866 trees in 2013 and 892 trees in 2014.

#### Leaf $\delta^{13}\text{C}$ , and leaf nitrogen content and Leaf C:N

Leaf carbon isotope ratios of bulk leaf tissue ( $\delta^{13}\text{C}$ , ‰), leaf nitrogen content per unit leaf mass ( $N_{\text{mass}}$  mg g<sup>-1</sup>) and leaf carbon to nitrogen (C:N) ratios were measured in foliage collected from *Tamarix* trees at each site. Approximately 30–40 sun leaflets were collected from each tree at each site. The leaves were collected at approximately mid-canopy, immediately placed into labeled ziplock bags and stored on ice until they were transferred to a freezer in the lab. Although leaves were

collected from every tagged tree, we randomly selected 12 trees to analyze per site. The most recent fully expanded sun leaves were collected from the south side of the canopy from mid-canopy above the ground surface. Foliage was oven-dried for 72 h at 70 °C, ground to a fine powder and analyzed for nitrogen and carbon content, and carbon isotope ratios using a DELTA Advantage ratioing mass spectrometer (ThermoFisher Scientific, Waltham, MA), configured with a CONFLO III interface to a Carlo Erba NC2100 Elemental Analyzer (Milano, Italy) at the Colorado Plateau Stable Isotopes Laboratory at Northern Arizona University. Carbon isotope ratios were calculated using  $\delta$  notation:

$$\delta = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \quad (1)$$

where  $R$  is the ratio of the heavy isotope (<sup>13</sup>C) to the lighter isotope (<sup>12</sup>C), and the standard was V-PDB. The instrument error (twice the standard deviation) associated with each observation was  $\pm 0.1$  ‰.

#### Soil characterization

Bulk soil samples were collected during the dry season in 2013 near the center of each monitoring site, from a depth of approx. 20–30 cm to represent soil status in the rooting zone while avoiding anomalies associated with the soil surface as well as from recent precipitation events. Samples were collected using a hand-auger, first removing the upper 20 cm and retaining the sub-surface material in a paper bag to initiate drying before

processing for soil texture, salinity and pH. In the lab samples were dried at 60° C for 48 h, then passed through a soil sieve to remove particles greater than 2 mm. Texture was determined by the hydrometer method of measuring particle size fractionation based on differential sedimentation rates (Gee and Bauder 1979) in which 100 gr of soil were suspended in 1,000 ml of water, with hydrometer readings taken at 40 s and 2 h. To determine salinity, 60 ml of 0.1 M calcium chloride was added to 20 g of soil (3:1 mixture) and mixed on an orbit shaker for 30 min. Electrical conductivity was measured at  $21.0 \pm 0.5$  °C using an EC Testr 11+ m (Eutech Instruments Pte LTD).

### Remote sensing of canopy dieback

To assess whether our estimates of canopy dieback from our tree surveys reflect site-scale changes in canopy cover, we measured the Normalized Difference Vegetation Index (NDVI; Rouse et al. 1973), calculated as:

$$NDVI = \frac{NIR - Rd}{NIR + Rd} \quad (2)$$

where *NIR* is the reflectance of the near infrared bands and *Rd* is the reflectance of the red band. As canopy dieback occurs and photosynthetic area decreases, the NDVI value also decreases. NDVI was measured using remote sensing imagery acquired from the Moderate Resolution Imaging Spectroradiometer (MODIS), an approach previously used to measure patterns of *Tamarix* defoliation by *D. carinulata* (Dennison et al. 2009; Nagler et al. 2012, 2014). Unfortunately, MODIS has a relatively low spatial resolution (250–500 m) that cannot fully resolve many *Tamarix* stands in our study. Therefore, for each site we calculated the ratio of NDVI measured in 2013 ( $NDVI_{13}$ ) with the maximum NDVI ( $NDVI_{max}$ ) between 2006 (the year *D. carinulata* was first released into the watershed) and 2012. For each year, NDVI was calculated from MODIS scenes acquired on day 145 (May 25) because previous surveys have shown that no significant herbivory by *D. carinulata* had occurred in the watershed prior to this date (T. Dudley, unpublished). NDVI was not evaluated for 2014 because we did not have data on whether canopy defoliation was already present by May 25, which would result in over estimates of canopy dieback.

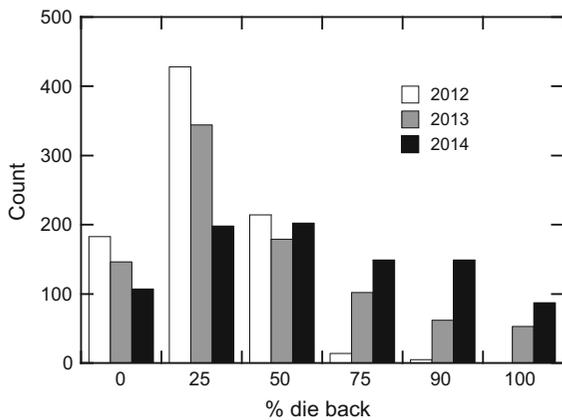
### Statistical analysis

Statistical modeling was performed using mean site variables as replicates and individual trees as pseudo replicates within each site. We used a stepwise autoregression model to determine whether canopy dieback in 2013 was correlated with environmental factors, soil electrical conductivity, percent silt and clay, number of defoliation events and tree height after testing for linearity. A similar model was used to analyze canopy dieback in 2014, but this model did not include the number of defoliation events since we did not have an accurate account through the 2013 growing season. Leaf  $\delta^{13}C$ , leaf N content and leaf C:N were evaluated against environmental factors, soil electrical conductivity, percent fine sediments (silt and clay), number of defoliation events and tree height using a stepwise autoregression model with backstepping to evaluate autocorrelation among the independent variables after testing for linearity. Relationships between canopy dieback in 2013 and  $\delta^{13}C$  and  $NDVI/NDVI_{max}$  were tested using analysis of variance (ANOVA). JMP 8.0 (SAS Institute, Cary, NC) was used for all statistical analyses with a significance level of  $P \leq 0.05$ .

### Results

Across all sites,  $C_d$  shifted from 27 % in the spring of 2012 to 41 % in the spring of 2013, to 54 % in the spring of 2014. Site 8 displayed the largest shift in dieback in 2013 from 17 % in 2012 to 84 % despite experiencing only two defoliation events (one in 2011 and one in 2012). Conversely, Site 1 that had experienced seven defoliation events but displayed less than 2 % dieback in all 3 years it was measured.

Overall only 19 trees surveyed in 2012 had greater than 50 % dieback, and of these only five were classified as having 90 % dieback (i.e. only had live sprouts at the base of the trunks). A year later in 2013, 62 trees (7 %) showed 90 % dieback and 53 trees (6 %) were dead (Fig. 3). Site 8 yielded the most dieback (84 %) with 64 % of the trees exhibiting 90–100 % dieback, while Site 3 had the highest percentage of dead trees at 38 %. Conversely, three sites (Sites 1, 5, and 10) had no trees with either 90 or 100 % dieback in 2013. Percent dieback increased between 2013 and 2014 at eight of the 10 sites from a



**Fig. 3** The comparison of percent canopy dieback of *Tamarix* trees between surveys conducted in the spring of 2012 and surveys conducted in the spring of 2013 and 2014 in the Virgin River Watershed

1.5 % increase at Site 5 to a 31 % increase at Site 9. Dieback recorded at Sites 1 and 4 were virtually unchanged between years. Site 8 continued to yield the greatest dieback in 2014 at over 90 %, although Site 9 also had 85 % dieback. Overall, nearly 17 % of the surveyed trees had 90 % dieback and 10 % of the total population was classified as dead in 2014 (Fig. 3).

Patterns of  $C_d$  were tested against key biotic (number of defoliation events, tree height) and abiotic (soil salinity, soil texture) parameters to evaluate potential drivers that underscore *D. carinulata*'s impact on *Tamarix*. Canopy dieback in 2013 was not correlated with either the number of defoliation events or tree height (Fig. 4a, b; Table 2). Likewise, there was no relationship between canopy dieback and soil texture (Table 2), although a simple regression model yielded a relationship when Site 8 (obvious outlier in Fig. 4c) was removed ( $C_d = 0.33 + 1.04 \cdot \text{Clay:Silt}$ ,  $R^2 = 0.61$ ,  $F = 11.07$ ,  $P = 0.0126$ ). Alternatively, there was a weak relationship between soil electrical conductivity and canopy dieback ( $C_d = 8.91 + 0.03 \cdot \text{EC}$ ,  $R^2 = 0.39$ ,  $F = 5.02$ ,  $P = 0.055$ , Fig. 4d; Table 2).

Unlike in 2013, percent canopy dieback was correlated with mean tree height in 2014 ( $C_d = 171 - 33.8 \cdot \text{height}$ ,  $R^2 = 0.50$ ,  $F = 10.26$ ,  $P = 0.015$ , Fig. 5a; Table 2). Again there was no relationship between  $C_d$  and soil texture (Fig. 5b; Table 2), but  $C_d$  in 2014 was moderately correlated soil electrical conductivity, explaining 56 % of the variation ( $C_d = 9.20 + 0.04 \cdot \text{EC}$ ,  $F = 10.26$ ,  $P = 0.015$ , Fig. 5c; Table 2).

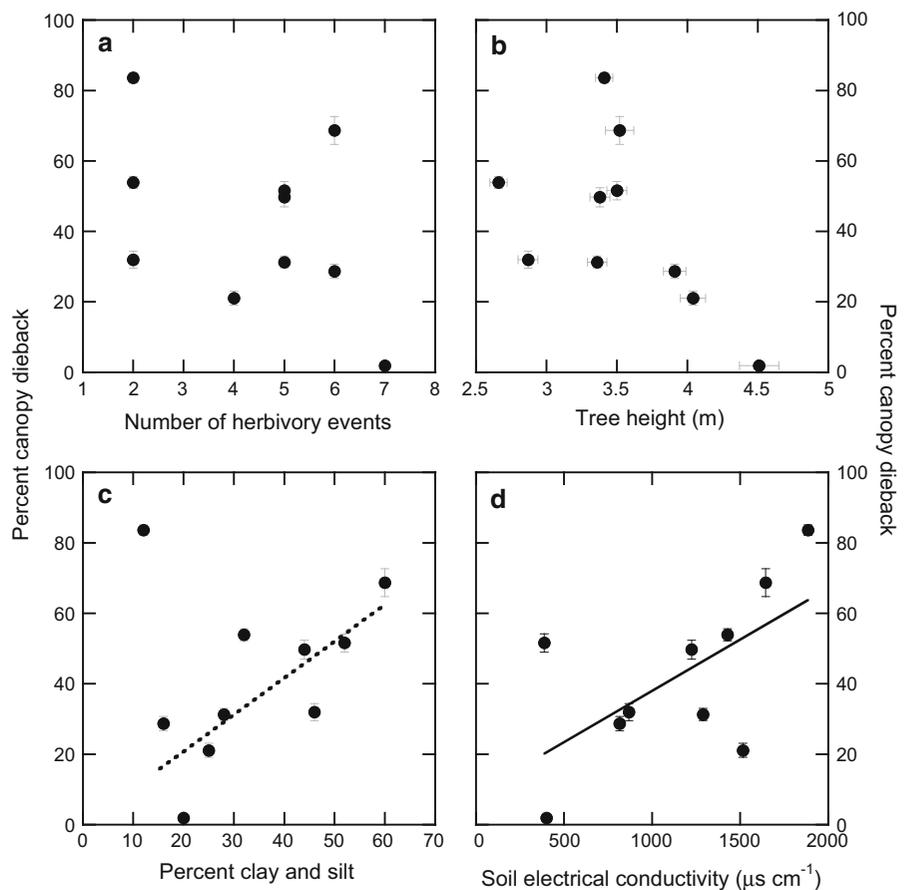
Percent canopy dieback in 2013 was weakly correlated with bulk leaf  $\delta^{13}\text{C}$ , a proxy for plant photosynthetic activity and drought stress ( $C_d = 448 + 15.71 \cdot \delta^{13}\text{C}$ ,  $R^2 = 0.38$ ,  $F = 4.08$ ,  $P = 0.078$ , solid line in Fig. 6a). Again when the obvious outlier was removed from the analysis (Site 3), the relationship between canopy dieback and  $\delta^{13}\text{C}$  improved dramatically ( $C_d = 710 + 26.11 \cdot \delta^{13}\text{C}$ ,  $R^2 = 0.86$ ,  $F = 44.53$ ,  $P = 0.0003$ , dashed line in Fig. 6). However, a stepwise regression model placing  $\delta^{13}\text{C}$  against the other explanatory variables revealed significant co-linearity with the number of defoliation events ( $\delta^{13}\text{C} = -24.11 - 0.39 \cdot \text{Def}$ ,  $R^2 = 0.64$ ,  $F = 14.17$ ,  $P = 0.0055$ , Fig. 6b), suggesting that repeated herbivory may have impacts on the physiological function of regrowth foliage.

Mean leaf N content ( $N_{\text{mass}}$ ) and mean leaf C:N were not correlated with any of the explanatory variables (data not shown), except when data from Site 8 was removed from the analysis. For the remaining sites,  $N_{\text{mass}}$  increased significantly with the number of defoliation events ( $N_{\text{mass}} = 1.31 + 0.28 \cdot \text{Def}$ ,  $R^2 = 0.54$ ,  $F = 8.31$ ,  $P = 0.0236$ , data not shown) and C:N decreased with the number of defoliation events ( $\text{C:N} = 26.86 - 2.18 \cdot \text{Def}$ ,  $R^2 = 0.67$ ,  $F = 11.12$ ,  $P = 0.0125$ , data not shown).

We used remote sensing from MODIS imagery to assess whether our plant surveys represented quantitative changes in canopy cover at each site. On day 145, when *Tamarix* is typically fully leafed out throughout the watershed but before *D. carinulata* becomes active, mean NDVI of all 10 sites between 2006 and 2011 was 0.381, ranging from 0.365 (SE  $\pm 0.028$  in 2006 to 0.402 (SE  $\pm 0.033$ ) in 2010. In 2012, NDVI dropped to 0.306 (SE  $\pm 0.026$ ) and declined further to 0.300 (SE  $\pm 0.021$ ) in 2013, its lowest level since the 2006 introduction of *D. carinulata* into the watershed (Fig. 6a) (MODIS imagery was not analyzed for 2014 due to potential confounding effects of present defoliation by *D. carinulata*). The reductions of NDVI in 2012 and 2013 were largely a function of a dramatic decrease in NDVI at site 8 (i.e. the site with the highest soil salinity and largest canopy dieback), declining from a high of 0.654 in 2008 to values of 0.509 and 0.276 in 2012 and 2013, respectively (Fig. 7a).

Relationships between NDVI and percent canopy dieback were further established by comparing percent dieback with the ratio of  $\text{NDVI}_{13}$  and  $\text{NDVI}_{\text{max}}$ . Across all of the sites, percent canopy dieback in 2013

**Fig. 4** Patterns of *Tamarix* canopy dieback along the Virgin River in 2013 in relation to: **a** The number of defoliation events by *Diorhabda carinulata* swarms, **b** Mean tree height, **c** percent silt and clay at a 20 cm soil depth, and **d** soil electrical conductivity at a 20–30 cm soil depth. The dashed line in Fig. 4c represents the regression line when the outlier site (Site 8) was removed from the analysis. Error bars represent  $\pm$  the standard error of the mean



**Table 2** F ratio and probability values from a stepwise regression model of percent canopy dieback in mature *Tamarix* stands against the number of defoliation events by *Diorhabda carinulata*, soil electrical conductivity, percent silt and clay and mean tree height in the Virgin River watershed in the southwestern US. Bold text represents model results that are statistically significant

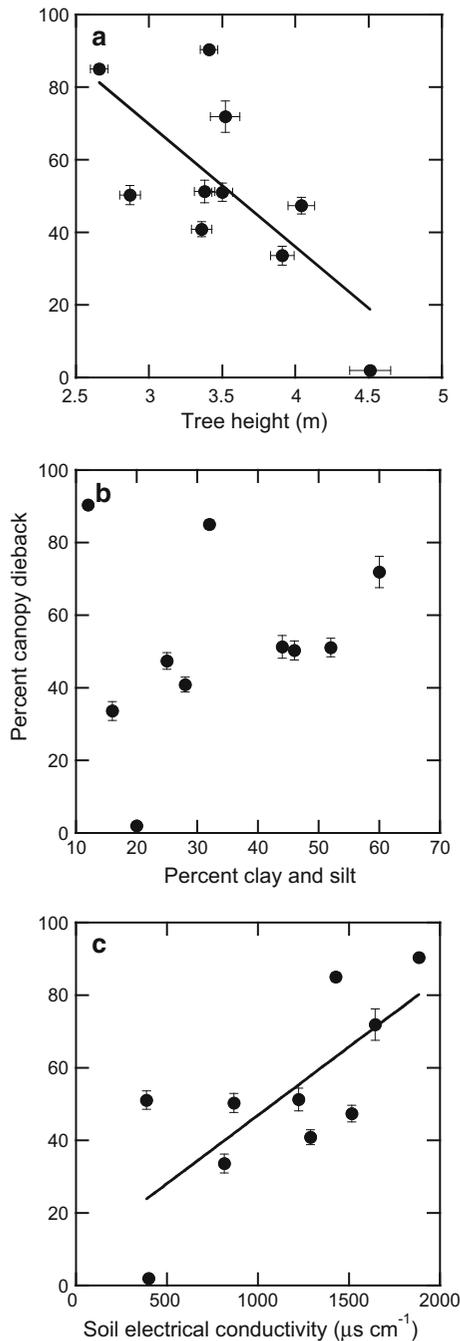
Parameter	F ratio	Probability >F
<i>2013</i>		
Defoliation events	0.36	0.57
Mean tree height	1.85	0.21
Percent silt and clay	1.58	0.25
Soil electrical conductivity	5.02	<b>0.055</b>
<i>2014</i>		
Mean tree height	8.22	<b>0.025</b>
Percent silt and clay	0.10	0.76
Soil electrical conductivity	10.26	<b>0.015</b>

explained 61 % of the variation in  $NDVI_{13}:NDVI_{max}$  ( $NDVI_{13}:NDVI_{max} = 1.0002 - 0.0065 * C_d$ ,  $F = 12.32$ ,  $P = 0.008$ , Fig. 6b). Again Site 8 had the

lowest  $NDVI_{13}:NDVI_{max}$  at 0.42, while Site 1 (i.e. site with the most defoliation events, but lowest canopy dieback) had a  $NDVI_{13}:NDVI_{max}$  of 1.00 (Fig. 7b), suggesting that herbivory by *D. carinulata* had no measurable impact on *Tamarix* at this site.

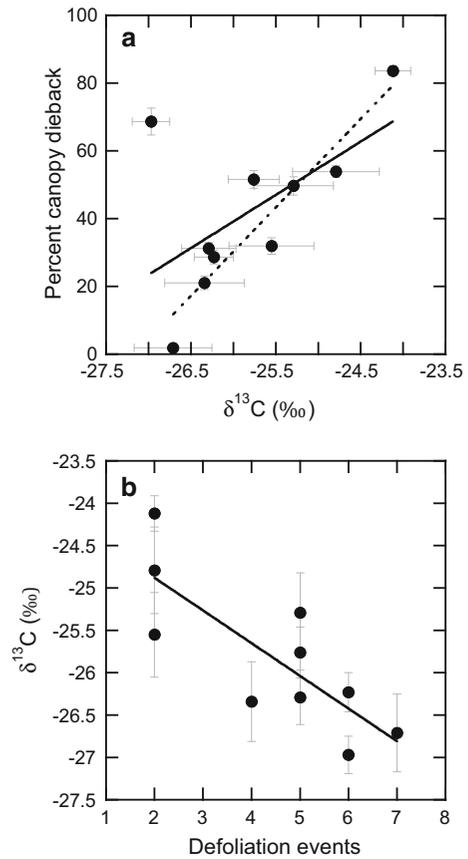
## Discussion

Most plant species have evolved to tolerate consumers, and have accordingly developed a wide range of strategies to reduce and survive herbivory (Ayres 1993). Unfortunately for plants, most of these strategies require allocation of limited resources and therefore increase the minimum resource requirement for survival or requires tradeoffs with other important functions such as growth and reproduction (Bloom et al. 1985; Chapin et al. 1990). Since the availability of resources such as water, nutrients and sunlight can



**Fig. 5** Patterns of *Tamarix* canopy dieback along the Virgin River in 2014 in relation to: **a** Mean tree height, **b** percent silt and clay at a 20–30 cm soil depth, and **c** soil electrical conductivity at a 20 cm soil depth. Error bars represent  $\pm$  the standard error of the mean

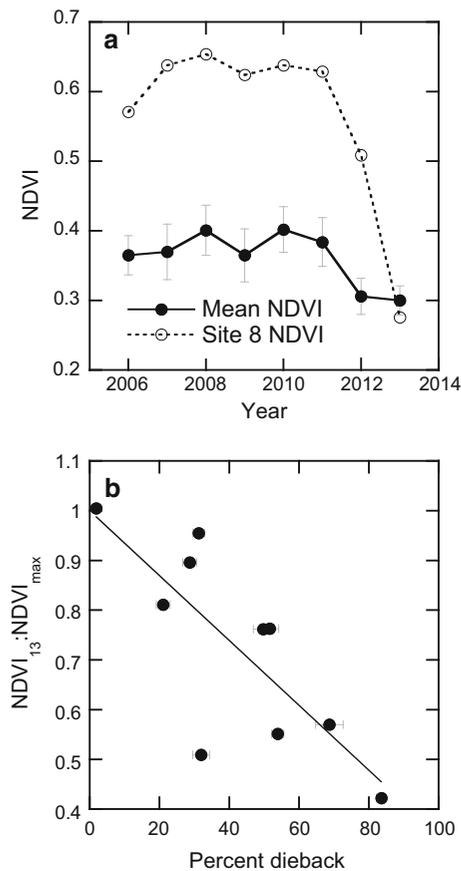
vary from one location to the next, and since resource allocation strategies can shift dramatically within and among species, predicting the impacts of herbivory on



**Fig. 6** Patterns of bulk tissue carbon isotope ( $\delta^{13}\text{C}$ ) ratios in *Tamarix* leaves collected in the Virgin River watershed. **a** Percent canopy dieback in relation to Bulk leaf  $\delta^{13}\text{C}$ . The dashed line represents the regression line when the outlier site (Site 3) is removed from the analysis. **b** Bulk leaf  $\delta^{13}\text{C}$  in relation to the number of defoliation events by *Diorhabda carinulata* swarms in the Virgin River Watershed. Error bars represent  $\pm$  the standard error of the mean

plant fitness and survival at large scales is challenging. Thus, teasing apart the primary factors that underpin plant responses to herbivory will improve our capacity to better understand how herbivory, coupled with global change forces will impact ecosystem structure and function.

In the present study, patterns of canopy dieback and subsequent mortality were unrelated to the number of episodic foliage herbivory events. One potential explanation is that herbivory intensity was not uniform and episodic events resulted in varying levels of canopy defoliation and stress. However, a characteristic feature of this plant/herbivore interaction is that *D. carinulata* larvae and adult beetle swarms generally



**Fig. 7** Patterns of site NDVI measured from MODIS satellite imagery and canopy dieback of *Tamarix* trees measured in May of 2013 in the Virgin River Watershed. **a** Patterns of mean NDVI of all of the sites surveyed for percent canopy dieback and NDVI of Site 8: the site that displayed the highest amount of canopy dieback. **b**  $NDVI_{13}:NDVI_{max}$  in relation to percent dieback. Error bars represent  $\pm$  the standard error of the mean

result in complete defoliation of *Tamarix* stands (Hultine et al. 2010; Pattison et al. 2011; Hultine and Dudley 2013). Plant surveys conducted between 2006 and 2012 at all of our monitoring sites in the Virgin River watershed confirm not only the number of episodic events, but also the intensity of events resulting in complete, or near complete defoliation of the *Tamarix* stands (Fig. 1). In other words, there is no evidence that these plants have been successful at deploying defense mechanisms against intense herbivory by *D. carinulata* and instead rely on tolerance to withstand repeated defoliation events (Hultine et al. 2013).

Among the variables we tested, soil salinity appeared to play the most substantial role in governing *Tamarix* tolerance to defoliation (Fig. 4d). *Tamarix*, like many desert phreatophytic plants, are halophytes that can tolerate high salinity levels (Pataki et al. 2005; Jolly et al. 2008; Armas et al. 2009; Glenn et al. 2012a). Nevertheless, soil and aquifer salinities can exceed the optimum for growth and water uptake even in well-adapted species (Glenn et al. 2012b, 2013). In the present study, soil salinity ranged from 400 to 1,900  $\mu\text{s cm}^{-1}$ , levels that are relatively similar to those reported for another *Tamarix* stand near our Site 7 (Imada et al. 2013) but considerably lower than values reported in other *Tamarix* stands in the lower Colorado River (Merritt and Shafroth 2012; Glenn et al. 2013). One potential explanation for the lower than expected soil salinity values is that episodic overbank flooding that occurred throughout the watershed in December of 2010 flushed a significant proportion of the total dissolved solids from the shallow soils. Thus, the electrical conductivity values recorded in the present study may only serve as a relative indicator of the salinity levels historically experienced by these *Tamarix* stands.

Although *Tamarix* is capable of surviving relatively high salinities, moderate salinity levels have been shown to substantially inhibit water uptake, productivity and presumably carbon assimilation (Glenn et al. 1998, 2013). Inhibition of carbon assimilation would likely reduce the metabolic storage of free sugars and starches (i.e. non structural carbohydrates) that are necessary to construct new foliage following episodic defoliation. Therefore, if chronic resource limitation from high soil salinity was present in some areas such as at Site 8, then episodic defoliation may have triggered a spiraling set of resource deficiencies resulting in significant canopy dieback and a high probability of widespread mortality in the foreseeable future.

Canopy dieback was not related to tree size as indicated by height in 2013, but was moderately well correlated with tree height in 2014, in that taller trees experienced less canopy dieback than smaller trees. In general the pool of total non-structural carbohydrates per unit live biomass increases with total biomass in woody plants (Sala et al. 2012). Thus, it seems plausible that larger trees retained a larger pool of stored carbohydrates to draw upon following episodic defoliation. If so, we might expect recently established

stands, and thus smaller trees, to express a greater sensitivity to defoliation than mature stands if all other factors are equal.

Other environmental factors beyond those we measured could influence resource availability, including depth to groundwater. Reliable estimates of groundwater depth were not available at all of the sites. However, because woody riparian vegetation would not survive without access to reliable water supplies, and all of the trees in the study were within 3.7 m above a perennially flowing river channel (Table 1) [a depth that is well within the rooting depth reported for *Tamarix* spp. (Stromberg 2013)], we can assume that all of the *Tamarix* trees in the study were perennially coupled to the water table. Moreover, at the one site where we did have continuous groundwater height data (Site 8), the water table never fell below a depth of 1.2 m between June 2010 and May 2013 (data not shown). The shallow water table may be a primary contributor to salinity at Site 8 since salts tend to accumulate in the vadose zone via capillary rise followed by evaporation from near-surface soils (Shah et al. 2011). Given that river flow in the lower Virgin River Valley is comprised in part by return flow from agricultural runoff, it would not be surprising if salts from the shallow aquifer contributed significantly to the salinity of the floodplain along the lower reaches of the valley.

Measurements of leaf  $\delta^{13}\text{C}$  ratios are a convenient approach to evaluate plant stress across spatial and temporal gradients (Ehleringer 1991). In the present study, canopy dieback was correlated with  $\delta^{13}\text{C}$  of newly formed leaves following spring bud break (Fig. 5a). However,  $\delta^{13}\text{C}$  was not correlated with either soil salinity or soil texture, but instead with the number of defoliation events (Fig. 5b). Whether repeated defoliation had a direct impact on the  $\delta^{13}\text{C}$  in spring-grown foliage (i.e. foliage that is not grown directly after herbivory) is an open question. One potential explanation is that repeated herbivory reduces the amount of leaf area without altering the whole-plant hydraulic conductance. A reduced leaf area would yield a higher leaf specific conductivity and higher subsequent stomatal conductance (Pataki et al. 1998; Oren et al. 1999), resulting in lower  $\delta^{13}\text{C}$  ratios. This explanation does not seem to fit the data since the site that experienced the most defoliation events (Site 1) also displayed the lowest canopy dieback and highest  $\text{NDVI}_{13}:\text{NDVI}_{\text{max}}$ .

An alternative explanation is that repeated defoliation alters leaf chemistry and photosynthetic capacity. In the present study, leaf  $\text{N}_{\text{mass}}$  was generally higher at the sites that experienced the most defoliation events: a trend that has been previously reported in other *Tamarix* populations following defoliation by *D. carinulata* (Uselman et al. 2011). A higher leaf N would result in a higher photosynthetic capacity since the majority of leaf N is present in the chloroplasts and photosynthetic enzymes (Evans and Seemann 1989). If all else is equal, a higher photosynthetic capacity would yield higher  $\delta^{13}\text{C}$  ratios in plant tissues due to the higher demand for  $\text{CO}_2$  by photosynthetic enzymes relative to the supply of  $\text{CO}_2$  entering the leaf. However,  $\delta^{13}\text{C}$  was actually lower, not higher in the leaves of *Tamarix* populations that experienced the most defoliation events.

Another possibility is that repeated defoliation altered the structure of new leaves such that internal resistance from the substomatal cavity to the sites of carboxylation decreased, resulting in reduced  $\delta^{13}\text{C}$  ratios in plant tissues. Recent evidence shows that internal resistance can vary substantially even within species, and result up to a 3 per mil difference in  $\delta^{13}\text{C}$  fixed in plant tissues regardless of other factors (Warren and Adams 2006). While there is currently no direct evidence that herbivory and subsequent defoliation by *D. carinulata* reduces the internal resistance of new *Tamarix* leaves, it remains a possibility worth exploring if measurements of  $\delta^{13}\text{C}$  are to be used to predict future impacts of episodic defoliation on *Tamarix*.

Regardless of environmental conditions and resource availability, some *Tamarix* populations and genotypes may be better suited to cope with episodic herbivory than others (Hultine et al. 2013; Williams et al. 2014). Since its introduction, *Tamarix* has undergone rapid hybridization (Gaskin and Schaal 2002; Gaskin et al. 2012), likely resulting in novel genotypes that are better adapted to their environment and/or disturbance than others. For example, genotypes that have relatively slow growth rates tend to have higher survival rates following defoliation, possibly as a consequence of greater carbon allocation to non-structural carbohydrate storage pools than to tissue growth (Hultine et al. 2013). In a common garden study, *Tamarix* genotypes from higher latitudes and colder climates tended to allocate more biomass to roots than genotypes from lower latitudes

(Williams et al. 2014). As a potential consequence of having a higher belowground allocation, and presumably a higher storage of non-structural carbohydrates, genotypes from northern latitudes were more tolerant of herbivory by *D. carinulata* than genotypes from lower latitudes (Williams et al. 2014). In the present study, it is unlikely that the small temperature gradient between Site 1 near St George, UT and Sites 8–10 near Lake Mead facilitated significant selective pressures or measurable gradients in adaptive tradeoffs among sites. Nevertheless, given the high rate of *Tamarix* hybridization since its introduction in North America (Gaskin and Schaal 2002), it is likely that novel genotypes have emerged and spread throughout the Virgin River watershed, resulting in a mosaic of adaptive strategies among populations.

An improved evaluation of the patterns of *Tamarix* canopy dieback and mortality in response to *D. carinulata* herbivory would have several important management implications, both in the Virgin River watershed and across the southwestern United States and northern Mexico. Among the most biologically relevant, and controversial features of *D. carinulata*'s presence in the Virgin River is its potential negative impact on a federally listed passerine bird, the southwestern willow flycatcher (*Empidonax traillii extimus*) that in some locations builds its nest in *Tamarix* stands. The Virgin River represents the first overlap between *D. carinulata* activity and *E. traillii extimus* nesting (Bateman et al. 2010). Rapid canopy dieback and mortality may result in significant habitat loss for *E. traillii extimus*. Thus, documenting relationships between environmental parameters and patterns of canopy dieback and mortality will assist land managers who are tasked with balancing habitat preservation of *E. traillii extimus* with conservation efforts aimed at removing and/or controlling *Tamarix* (Paxton et al. 2011). These efforts may need to be expanded since *D. carinulata* has extended its range south of Lake Mead and into the lower Colorado River (Bean et al. 2012, 2013). The combination of soil surveys (salinity and texture), plant canopy surveys and satellite-based remote sensing techniques used in the present study coupled with advanced molecular tools to study *Tamarix* landscape genetics could improve the capacity to predict future impacts of *D. carinulata* on *Tamarix* in the lower Colorado River basin and southwestern US and northern Mexico.

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