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RESEARCH ARTICLE

Northern tamarisk beetle (*Diorhabda carinulata*) and tamarisk (*Tamarix* spp.) interactions in the Colorado River basin

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Northern tamarisk beetles (*Diorhabda carinulata*) were released in the Upper Colorado River Basin in the United States in 2004–2007 to defoliate introduced tamarisk shrubs (*Tamarix* spp.) in the region's riparian zones. The primary purpose was to control the invasive shrub and reduce evapotranspiration (ET) by tamarisk in an attempt to increase stream flows. We evaluated beetle–tamarisk interactions with MODIS and Landsat imagery on 13 river systems, with vegetation indices used as indicators of the extent of defoliation and ET. Beetles are widespread and exhibit a pattern of colonize–defoliate–emigrate, so that riparian zones contain a mosaic of completely defoliated, partially defoliated, and refoliated tamarisk stands. Based on satellite data and ET algorithms, mean ET before beetle release (2000–2006) was 416 mm/year compared to postrelease (2007–2015) ET of 355 mm/year ($p < 0.05$) for a net reduction of 61 mm/year. This is lower than initial literature projections that ET would be reduced by 300–460 mm/year. Reasons for the lower-than-expected ET reductions are because baseline ET rates are lower than initially projected, and percentage ET reduction is low because tamarisk stands tend to regrow new leaves after defoliation and other plants help maintain canopy cover. Overall reductions in tamarisk green foliage during the study are 21%. However, ET in the Upper Basin has shown a steady decline since 2007 and equilibrium has not yet been reached. Defoliation is now proceeding from the Upper Basin into the Lower Basin at a rate of 40 km/year, much faster than initially projected.

Key words: biological control, Colorado Plateau, *Diorhabda*, endangered species, remote sensing, riparian evapotranspiration, saltcedar

Implications for Practice

- Tamarisk biocontrol programs will not necessarily result in large-scale water savings as previously assumed.
- Episodic defoliation events do not necessarily result in replacement of tamarisk by more desirable native plants and defoliated areas have negative effects on fauna.
- Restoration projects would be needed to provide alternative habitat for riparian birds such as the Southwestern Willow Flycatcher that use tamarisk for nesting.
- Evapotranspiration has been decreasing after beetle arrival, so an equilibrium condition has not yet occurred; further reductions in evapotranspiration can be expected.
- Although based on the best science available at the time, several key assumptions in the original biological assessment have not been met; therefore, predator–prey biocontrol programs (e.g. tamarisk beetles) must be viewed as having potentially unpredictable results.

Introduction

Tamarisk (*Tamarix ramosissima* and related species and hybrids; Gaskin & Schaal 2002) is an introduced shrub or small tree that has spread widely in riparian zones in the western United States. Tamarisk is salt tolerant and can also extract groundwater from greater depths than native phreatophytes such as cottonwoods (*Populus* spp.) and willow (*Salix* spp.) (reviewed in Busch & Smith 1995; Glenn & Nagler 2005). These two traits have allowed it to replace native trees on floodplains that have become saltier and have deeper water tables due to human alterations of river systems (Busch & Smith

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1995). Tamarisk is now the second most dominant western North American riparian tree after cottonwood (Friedman et al. 2005).

Starting in the 1950s, projects have been undertaken to remove tamarisk from western U.S. floodplains (Chew 2009). The primary motivation has been to salvage water for human use. Early lysimeter studies suggested that tamarisk had higher transpiration rates than native trees and other riparian vegetation, and that removal of tamarisk and replacement with native vegetation could result in augmented river flows (Johns 1987). Zavaleta (2000), relying on evapotranspiration (ET) estimates in Johns (1987), estimated that tamarisk used on average 300–460 mm/year more water than native riparian vegetation. More recently, a case has been made that removal of tamarisk, combined with active restoration projects, will allow native trees to return to the floodplains, improving their ecological value for wildlife (Shafroth et al. 2008; Dudley & Bean 2012).

In 1999, populations of tamarisk beetles (*Diorhabda* spp.) were imported into the United States from their native range in Asia for testing as biocontrol agents for tamarisk (DeLoach et al. 2004). The experiments successfully demonstrated that tamarisk beetles were host-specific and readily defoliated tamarisk shrubs in the United States (Richard 2003; DeLoach et al. 2004). The final Environmental Assessment (USDA 2005) recommended release of *Diorhabda carinulata* (northern tamarisk beetles, then classified as *Diorhabda elongata deserticola*, see Tracy & Robbins 2009) in 13 states. Beneficial effects expected from biocontrol included reduction of water consumption (citing Johns 1987 and Zavaleta 2000), as well as reduction in soil salinity, increase in floral and faunal biodiversity, reduction in fires, and other benefits (USDA 2005).

Initial predictions were that northern tamarisk beetles (originally from northwest China and Kazakhstan) would spread slowly (DeLoach et al. 2004; USDA 2005), allowing time for native trees and other vegetation to replace tamarisk (USDA 2005). However, the spread of the beetles has been much faster than predicted, resulting in many thousands of hectares of completely or partially defoliated tamarisk on riparian floodplains without replacement vegetation in the early stages of infestation (Dudley & Bean 2012; Nagler et al. 2010; Nagler et al. 2014).

The original Environmental Assessment (USDA 2005) recognized that tamarisk provides nesting habitat for the endangered Southwestern Willow Flycatcher (*Empidonax traillii extimus*) when its preferred willow habitat is not available (Sogge et al. 2008). However, the Environmental Assessment (USDA 2005) cited literature showing that *D. carinulata* would only slowly penetrate into Southwestern Willow Flycatcher territory. Originally introduced populations of *D. carinulata* had a photoperiod requirement for entering diapause (dormancy), which would confine it to the Upper Colorado River Basin above about 38°N (Lewis et al. 2003) while Southwestern Willow Flycatchers nest in riparian areas below 35°N (Sogge et al. 2008).

Initial successful releases surrounding the Upper Colorado River Basin were made in 2001 on the Arkansas River at Pueblo, Colorado, on the Sevier River near Delta, Utah, and in the Humboldt Basin near Lovelock, Nevada (DeLoach et al. 2004). Later, releases of the northern tamarisk beetle inside the Upper Basin were made on the Dolores, Colorado, and San Juan Rivers from 2004–2007 (Hultine et al. 2010*b*; Jamison et al. 2015). A separate release on the Virgin River in Saint George, Utah, occurred in 2006 (Bateman et al. 2010). By 2014 tamarisk beetles were present on virtually all river systems and their tributaries in the Upper Basin but had not yet widely colonized rivers and streams in the Lower Basin (Bloodworth et al. 2016). The rapid spread of the tamarisk beetle has been attributed to its ability to establish satellite populations through long-range dispersal flights of the winged adults (so-called Levy flights, Nagler et al. 2014) and aggregation of adults at new sites via release of a pheromone by males (Coss et al. 2005).

In this study we used ground-validated remote sensing methods to estimate the extent of defoliation and rates of ET by tamarisk growing on the Dolores, San Juan, Upper Colorado, and Virgin Rivers and their tributaries. Our objectives were, first, to estimate the reduction in ET and therefore potential water savings that has been achieved in the Upper Colorado River Basin and, second, to track the movement of the beetles from the Upper Basin into the Lower Basin. This study covered a wider area and longer time span than previous remote sensing studies of tamarisk and beetle interactions (e.g. Dennison et al. 2009, 2010; Meng et al. 2012; Nagler et al. 2012; Nagler et al. 2014). It provides an overview of these interactions over the whole Colorado River Basin since introduction of the beetles in the Upper Basin.

Methods

Study Sites

We collected remote sensing data for determination of ET from 13 sites on the Colorado, Dolores, and San Juan Rivers and their tributaries (Fig. 1, Table 1, and Appendix S1, Supporting Information). At each site, we selected four to seven individual sampling points, and, where possible, two or more sample sites located on each river system. Sampling points were 0.5–2.0 km apart. The satellite imagery we used did not allow us to distinguish tamarisk from other plants; hence, we relied on ground surveys to determine the vegetation composition of our sites. Sites on the Lower, Middle, and Upper Dolores River, the Colorado River near Moab, the San Juan River, and tributary streams have been monitored through annual summer field surveys since 2008 (van Riper unpublished data; Jamison et al. 2015; Nagler et al. 2012). Sites on the Virgin River have been monitored since 2009 (Bateman et al. 2010; Bateman & Ostoja 2012; Nagler et al. 2014; Mosher & Bateman 2016). Other sites have been surveyed from 2007–2015 by the Tamarisk Coalition and reported in presence-absence maps (Tamarisk Coalition 2015). In addition to the sites for which ET was determined, the progress of defoliation down the Virgin River and into the Lower Colorado River was followed through remote sensing images at five additional sites where tamarisk beetles and defoliation of tamarisk were reported from ground surveys (Table S1).

Figure 1. Major sampling sites for defoliation trends and evapotranspiration. 1 = Colorado River near Grand Junction; 2, 6 = Colorado River at Moab; 3–5 = Dolores River; 7, 8 = Dove Creek, Kane Creek; 9, 10 = San Juan River at Mexican Hat and Shiprock; 11 = Navajo Springs; 12 = Moenkopi Wash at Tuba City; 13 = Upper Virgin River; 14 = Lower Virgin River; 15 = Las Vegas Wash, 16 = Lake Mohave; 17 = Big Bend State Park; 18 = Bill Williams River delta at the Colorado River.

Satellite Imagery

This study used images from the Moderate Resolution Imaging Spectrometer (MODIS) on the Terra satellite and Landsat images. For rivers that were wide enough, MODIS Enhanced Vegetation Index (EVI) data (250 m resolution) were obtained as single pixels from the Oak Ridge National Laboratory website (http://daacmodis.ornl.gov). The website displays the approximate pixel footprint on a high-resolution digital image. Pixels that fit wholly within the riparian zone of a river were selected to avoid sampling nonriparian areas (Nagler et al. 2012, 2014). We used the MOD13Q1 EVI product, which consists of 23 images per year representing composites over each 16-day period. Images are supplied to end users as georectified and atmospherically corrected products. Landsat images (30 m resolution) were used to estimate ET along streams that were too narrow to sample with MODIS imagery. Whereas MODIS is obtained at near daily return times, Landsat images are obtained every 16 days. Twenty-nine Landsat 5 (2000–2011) or Landsat 8 (2013–2015) images were obtained from the USGS LSDS Science Research and Development website (http://espa.cr.usgs

Table 1. Comparison of EVI and NDVI values before and after beetle arrival by paired *t* tests across site and years. MODIS EVI values are for eight river reaches wide enough to support MODIS pixels; Landsat NDVI values are for five rivers too narrow for MODIS pixels. Numbers following means are SE.

	MODIS EVI	*Landsat NDVI*
Mean before	0.177 (0.001)	0.379 (0.010)
Mean after	0.158 (0.001)	0.371 (0.010)
N	5,005	160
p	0.001***	0.302

.gov/). One cloud-free image per year was obtained between May and July, with some years missing due to lack of adequate imagery (Appendix S1). As with MODIS, band values are converted to at-surface reflectance by USGS and further band processing by end users is not required. Images were converted to Normalized Difference Vegetation Index (NDVI) images from the red and near infrared bands using ArcGIS software. Shapefiles were prepared representing approximately 250 m stretches of rivers, with four to seven shapefiles prepared per sample site. For five of the sites, both MODIS and Landsat images were sampled to compare ET estimates, since different algorithms were used for each type of imagery. For these sites, Landsat shapefiles overlapped areas covered by MODIS pixel footprints.

To compare reductions in EVI or NDVI caused by defoliation, the bare-soil value of the vegetation index was first subtracted from pre- and postbeetle values (bare soil = 0.092 for EVI and 0.094 for NDVI, determined by sampling bare soil sites in images). This allowed a comparison of the reduction in green foliage density above the soil baseline values.

ET Algorithms

The MODIS algorithm for ET took the form used by Nagler et al. (2005, 2013) and Guerschman et al. (2009):

$$ET = ET_o \left[1.65 \left(1\text{-}e^{(-2.25EVI)}\right) \text{-}0.169\right] \quad (1)$$

where ET_o is reference ET calculated for a hypothetical freely transpiring grass crop from meteorological data (Allen et al. 1998; Brouwer & Heibloem 1986) and a, b, and c are fitting coefficients. The term $(1 - e^{(-bEVI)})$ is derived from the Beer–Lambert Law modified to predict the fraction of incident radiation absorbed by a canopy (Nagler et al. 2004). As formulated for plant canopies, LAI normally replaces N in the Beer–Lambert equation for light absorption by a solution, $(1 - e^{(-N)})$, where N is the density of light absorbing particles. In our application EVI replaces LAI, assuming a linear relationship between EVI and LAI over LAI values from 0 to approximately 4 (Potithep et al. 2013).

To determine the coefficients a, b, and c, multi-year monthly ground data from eddy covariance moisture flux towers and basin water balance analyses from 17 riparian and agricultural sites were regressed against EVI using Equation (1) as the model algorithm (Nagler et al. 2013). The final equation of best fit was:

$$ET = ET_o \left[1.65 \left(1\text{-}e^{(-2.25EVI)}\right) \text{-}0.169\right] \quad (2)$$

The equation had $r^2 = 0.78$ ($p < 0.001$). The standard error of the mean (SE) across sites was 21% for monthly values and 5.4% for annual values of ET (Nagler et al. 2013).

For Landsat data, we calculated ET from ET_o and NDVI by an algorithm developed by Groeneveld et al. (2007) for phreatophyte communities in the western U.S. NDVI is first scaled ($NDVI_{sc}$) between bare soil and full vegetation cover using values for $NDVI_{min}$ and $NDVI_{max}$ of 0.094 and 0.790, respectively, derived from a sampling of bare soil and dense vegetation areas across images:

$$NDVI_{sc} = 1 - \left(NDVI_{max} \text{-} NDVI\right) / \left(NDVI_{max} - NDVI_{min}\right) \quad (3)$$

ET was calculated as:

$$ET = NDVI_{sc} * ET_o \quad (4)$$

This method assumes that the ratio of ET/ET_o is constant over the growing season. The method had SE = 5% for western phreatophyte communities compared to eddy covariance flux tower results (Groeneveld et al. 2007).

ET_o was determined from monthly temperature data and latitude by the Blaney-Criddle equation (Brouwer & Heibloem 1986). Temperature data were obtained from NOAA Cooperative Reporting Stations nearest in location and elevation to the sample sites (Table S1). Tamarisk is deciduous in the Upper Basin. For the sites surveyed by Landsat imagery, ET_o during the May to October growing season was used to estimate ET. For MODIS sites, monthly ET_o values over the whole year were used because the dormant period is captured by low EVI values during dormancy.

Tamarisk Beetle Abundance

Tamarisk beetle abundance on the Virgin River was measured from Littlefield, Arizona, to Gold Butte, Nevada, approximately 22 km from near the terminus of the river at Lake Mead from 2009 to 2014 (Bateman & Ostoja 2012; Bateman et al. 2013). The study area stretched for about 50 km. Beetles were monitored in pitfall traps associated with a large research effort to monitor herpetofauna, habitat, and ground arthropods (Bateman et al. 2013; Mosher & Bateman 2016). Pitfall traps were 19-L buckets installed at ground level. The sampling array consisted of four traps set at the ends of three 6 m drift fences and one in the center designed to capture herpetofauna. Fences were set under and adjacent to riparian trees including tamarisk. These were live traps. Beetles were counted in one trap per array and we removed all animals. Although animals could interact in the live traps, we compared arthropod counts with and without predators (lizards, mice) and found no statically significant difference in arthropod abundance (data not shown). When beetle larvae were present, they swamped the predators in abundance

Table 2. Comparison of annual ET rates (mm/year) for beetle-infested tamarisk sites in the Upper Colorado River Basin, 2000–2015. The Virgin River site was considered to be infested first in 2009; all other sites were considered infested first in 2007. Asterisks denote significant levels at 0.05 (*), 0.01 (**), or 0.001 (***). [a]Sites surveyed by van Riper since 2008. [b]Sites surveyed by Bateman 2010–2014. [c]Sites mapped by Tamarisk Coalition since 2008 (Tamarisk Coalition 2015). T, tamarisk; W, willow; CW, cottonwood; RO, Russian olive.

Site-Type	*Tree Species*	*ET Before, mm/year*	*ET After, mm/year*	*Difference, mm/year*	*% Reduction*	*p Values*
Colorado River near Moab[a]	50% W, 50% T	511 (25)	284 (29)	227	44.4	< 0.001***
Dove Creek	90% T, 10% RO	403 (43)	380 (23)	23	5.17	0.007**
Mathieson Wetland Preserve, Moab[a]	60% T, 40% W, CW	807 (24)	710 (32)	97	12.0	0.029*
Lower Dolores[a]	90% T, 10% W, CW	270 (16)	295 (13)	−25	−9.3	0.071
Middle Dolores[a]	70% T, 30% W	289 (11)	322 (12)	−33	−11.4	0.001***
Upper Dolores[a]	90% CW, 10% W, No T	537 (7)	514 (11)	23	4.3	0.108
Navajo Springs[a]	100% T	163 (10)	146 (10)	17	10.4	0.274
Kane Springs Creek[a]	80% T, 20% W, CW	497 (14)	479 (20)	0	0	0.090
San Juan at Shiprock[a]	60% T, 40% RO	343 (19)	272 (17)	71	20.7	0.006**
San Juan at Mexican Hat[a]	60% T, 40% RO	350 (22)	319 (19)	31	8.9	0.042*
Moenkopi Wash[a]	100% T	251 (11)	178 (16)	73	29.1	< 0.001***
Lower Virgin[b]	100% T	651 (19)	376 (79)	275	42.2	< 0.001***
Colorado R. at Grand Junction[c]	70% T, 30% CW, W	332 (11)	334 (14)	−2	−0.6	0.889
Mean all		416 (50)	355 (41)	61(26)	14.7	0.035*

and we counted hundreds to thousands of beetle larvae daily during these periods. Traps were monitored daily in June and July of each year, encompassing the period of beetle activity. We recorded tamarisk beetles per site at 14–21 sites each year. Results were expressed as beetles captured per trap per day, averaged across all sites (Bateman et al. 2013).

Statistical Tests

The data were analyzed as a repeated measures experiment (Paine et al. 2014) with results before and after beetle arrival analyzed by paired *t* tests. MODIS imagery resamples the same pixel location with each satellite pass with a registration error of no greater than 50 m per 250 m pixel hence these were regarded as paired samples within a site. MODIS has a near-daily return time and the data were binned by the NASA data source into 16-day intervals (23 dates per year). The same sample intervals were repeated each year. The sample dates were also treated as paired samples that accounted for seasonal differences in EVI within each year. We divided the EVI data into two treatments representing years before beetle arrival (7 years) and after beetle arrival (7 years). Eight sites were analyzed by MODIS imagery. Landsat NDVI data were also divided into years before and after beetle arrival and the four to seven sample locations per site were subjected to paired *t* tests to compare NDVI before and after beetle arrival. Five sites were analyzed by Landsat imagery.

Annual estimates of ET were calculated for each site from MODIS EVI or Landsat NDVI values. The first year of beetle infestation was considered to be 2007 for all sites except the Lower Virgin River, for which the first year of infestation was considered to be 2009. The overall comparison of ET estimates before and after beetle arrival was analyzed by paired *t* test. We also plotted changes in annual ET over all sites from 2000 through 2015 and conducted a linear regression analysis to test if there was an overall trend in ET by year after release of beetles.

Results

Impacts of Beetles on EVI, NDVI, and ET

For the eight sites surveyed by MODIS imagery, EVI was reduced by 11% in years after beetle introduction ($p < 0.001$, Table 1). For the five sites survey by Landsat, NDVI was not significantly reduced ($p = 0.302$) (Table 1). ET was significantly reduced at eight of the sites for an overall reduction of 14.7% across sites ($p = 0.035$, Table 2),

Patterns of Defoliation at Individual Sites in the Upper Basin

Basic patterns of defoliation determined by changes in EVI are illustrated for three rivers within the original Upper Basin release areas in Figure 2, with MODIS EVI as a surrogate for defoliation. Results for the Colorado River at Moab are in Figure 2A (data were from sites in the Scott M. Matheson Wetlands Preserve, see Table S1). Beetles were first released in 2004 and defoliation was first noted in 2006 in ground surveys (Dennison et al. 2009). EVI decreased by about 30% relative to the bare soil value from 2005 to 2008, but showed recovery in 2010–2011, then a second cycle of apparent defoliation followed by recovery to about 90% of prebeetle levels in 2014 and 2015. ET was reduced by 44% in postbeetle years ($p < 0.001$, Table 2).

Prebeetle and postbeetle EVI values on the Lower Dolores River (Fig. 2B) were not significantly different ($p > 0.05$) although beetles were present from 2007 on; the period of defoliation was brief and plants produced new leaves after defoliation (Hultine et al. 2010*a*, 2010*b*).

Beetles were first released on the San Juan River near Bluff, Utah, in 2007 (Jamison et al. 2015). Prebeetle EVI was higher than postbeetle values at the Shiprock, New Mexico site. After a two-year lag, EVI values started to decrease and by 2011–2014 peak summer values above the soil baseline value were only 50% of prerelease values (Fig. 2C). However, by 2015 EVI

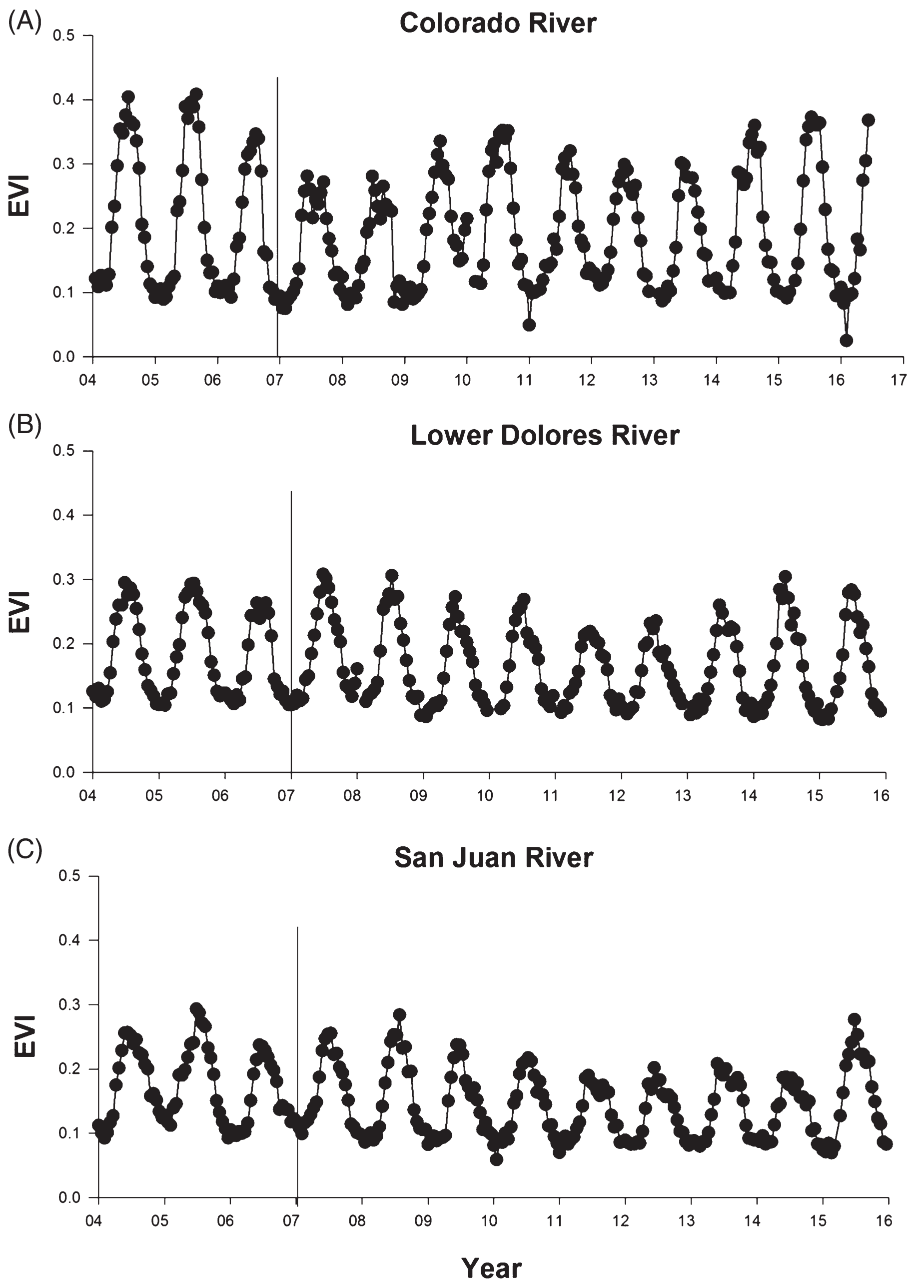

Figure 2. Patterns of EVI at riparian sites in the Upper Colorado River Basin, 2000–2015. Data for the Colorado River are from sites in the Scott M. Matheson Wetland Preserve (A); the Lower Dolores data are from sites near the junction with the Colorado River (B); and the San Juan River is from sites near Shiprock, New Mexico (C). The dividing line shows when beetle damage first became apparent at the site based on ground surveys.

had returned to prerelease values. ET was reduced by 20.7% in postbeetle years ($p = 0.006$, Table 2).

Defoliation Patterns on the Virgin River and Lower Colorado River

Beetles were first released in 2006 at St George, Utah, the dividing line between the Upper Colorado River Basin and the Lower Basin (Bateman et al. 2010). EVI values at sites near St. George were low to start with and did not show an overall decline from 2006–2015 (Fig. 3A). However, ground surveys showed the beetles moved downstream, reaching Littlefield, Arizona, by 2009 and near the terminus of the river at Lake Mead by 2011 (Bateman et al. 2013; Nagler et al. 2014). Prebeetle values were higher than postbeetle values for this river reach ($p < 0.001$). By 2011, EVI values from Littlefield to Lake Mead began to decrease and showed a marked dip then recovery in mid-summer of 2011. EVI was lower in 2012, and by 2015, EVI was only 25% of prebeetle values. Beetles were quantified in pitfall traps over the same river reach from 2009 to 2014 (Fig. 3B). Beetle

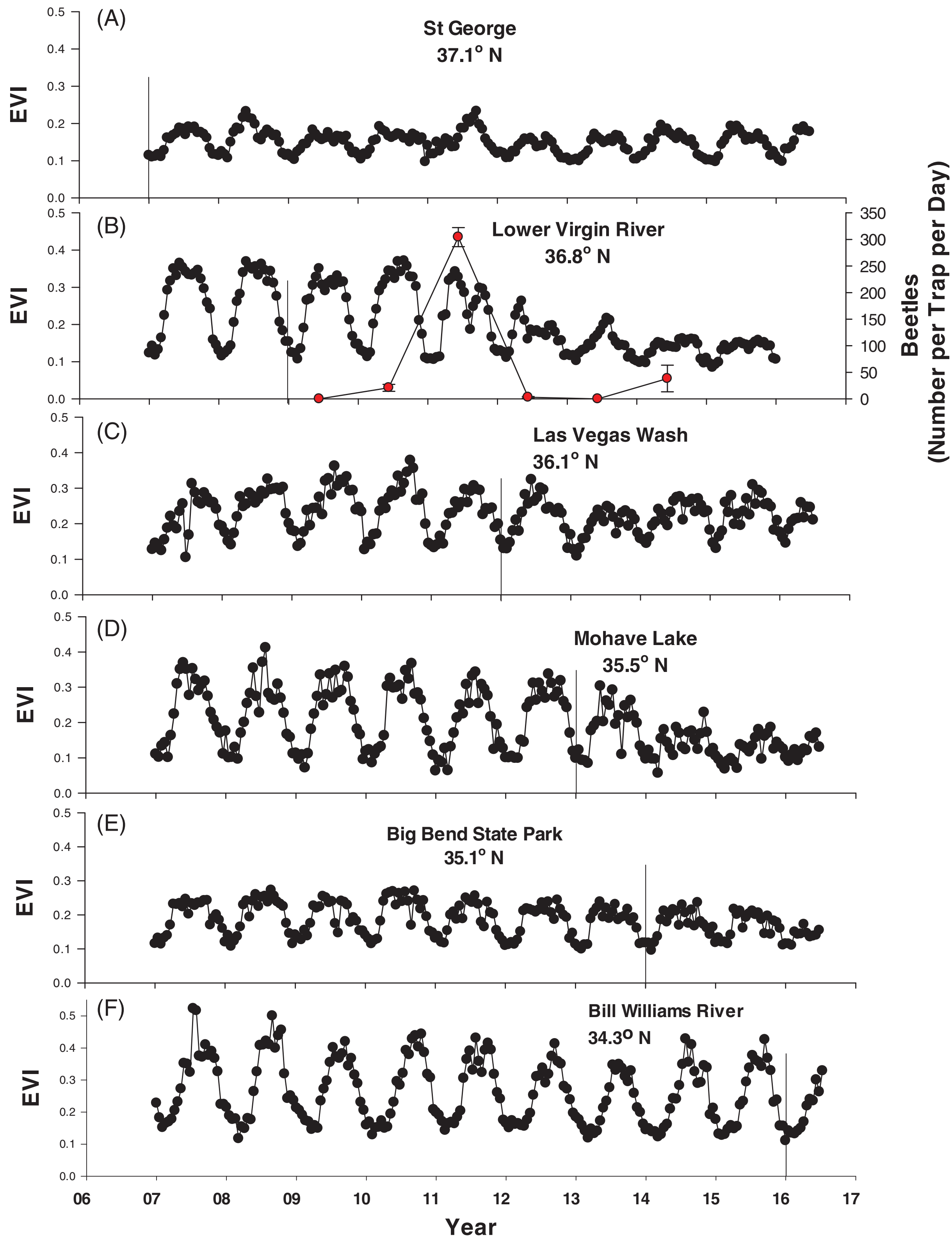

Figure 3. Progression of defoliation activity down the Virgin River and into the Lower Colorado River, with EVI as a surrogate for defoliation. The dividing line shows when beetle damage was first noted at each site, labeled A–F going south from St. George to the Bill Williams River. The red symbols in (B) refer to tamarisk beetle counts; error bars are ±SE.

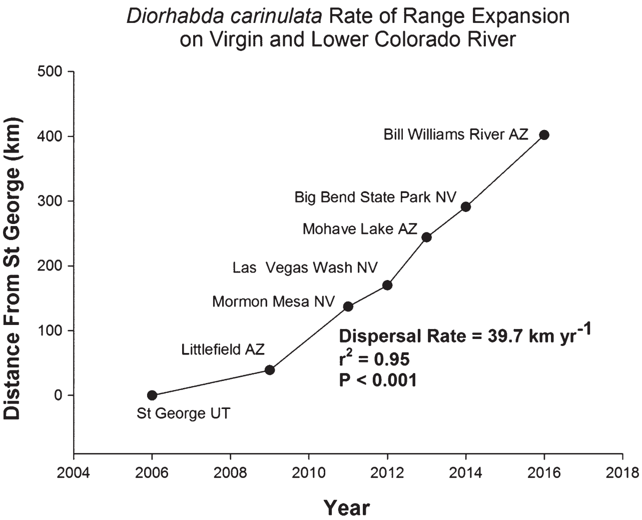

Figure 4. Dispersal of beetles from the Upper to Lower Colorado River Basin via the Virgin River and Lower Colorado River. The timeline is based on the appearance of beetle damage but beetles might have arrived at Mohave Lake and Big Bend State Park a year earlier than shown based on beetle trap data (B. Bloodworth, Tamarisk Coalition, personal communication).

abundance was highest in 2011 but fell to near zero by 2013 with a slight recovery in numbers in 2014 (Fig. 3B).

Figure 3C–E show the progression of defoliation south into the Lower Colorado River Basin. Beetles, as well as defoliation, were documented at Las Vegas Wash at its entry point into Lake Mead in 2012 (Eckerg & Rice 2016) (Fig. 3C). Relative to bare soil values, EVI was reduced by 17% in postbeetle years compared to prebeetle years ($p < 0.001$). Beetles reached Mohave Lake in 2012 (Tamarisk Coalition 2015) and resulted in a 75% reduction in peak EVI ($p < 0.001$, Fig. 3D) in the patch surveyed. Beetle occurrence below Mohave Lake is so far discontinuous. No beetles have been reported for Havasu National Wildlife Refuge, which has large areas of tamarisk monocultures (L. Miller 2016, Manager, Havasu National Wildlife Refuge, U.S. Fish and Wildlife Service, personal communication). Downriver, beetles were noted in Big Bend State Park, Nevada, in 2013 (Dr D. Bean 2016, personal communication) and in the delta of the Bill Williams River in 2016 (Dr K. Blair 2016, Ecologist, Bill Williams National Wildlife Refuge, U.S. Fish and Wildlife Service, personal communication). EVI above the soil baseline decreased by 36% following arrival of beetles at Big Bend State Park ($p < 0.001$; Fig. 3E) while not enough time has elapsed to assess beetle impacts at the Bill Williams River (Fig 3F). The rate of dispersal from St. George, Utah, to the delta of the Bill Williams River was 39.7 km/year, some of which could be due to human-assisted movement of beetles (B. Bloodworth 2016, Tamarisk Coalition, personal communication) (Fig. 4).

Annual ET Estimates

It was necessary to use two types of imagery with different algorithms to estimate ET. MODIS imagery had near-daily temporal

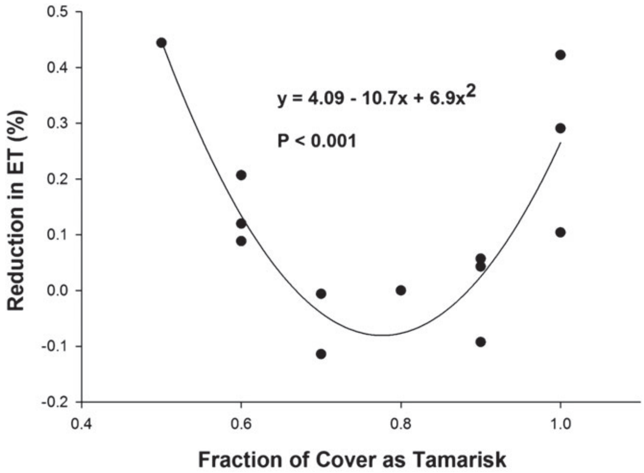

Figure 5. Relationship between reduction in ET after beetle infestation and the fraction of plant cover that was tamarisk.

cover but the spatial resolution was too low for estimating ET in the narrower riparian zones. In those riparian areas, annual ET was estimated with Landsat imagery. The two methods were compared at five sites and gave equivalent results, with mean values of 278 mm/year (SE = 21) for the Landsat method compared to 280 mm/year (SE = 20) for the MODIS method ($p = 0.75$ by paired t test) (see Fig. S1).

Annual ET rates before and after arrival of beetles are shown for wide area sites by MODIS in Figure S2 and for narrower sites by Landsat in Figure S3 Sites below the Virgin River are not included because not enough time had elapsed for stable postbeetle patterns to emerge.

Summary statistics are in Table 2. Over all sites ET was reduced from 416 mm/year to 355 mm/year, for a potential overall savings of 61 mm/year of river water (SE = 26). Results were variable across sites even on the same river system. The correlation between % reduction in ET and initial ET was not significant ($r = 0.34$, $p = 0.26$). Interestingly, the lowest reductions in ET were for mixed stands of tamarisk and other vegetation (70–90% tamarisk), with greater reduction in plots with less than 60% tamarisk or for tamarisk monocultures. A plot of percent saltcedar cover versus ET reduction showed that the greatest reductions occurred at the lowest and highest values of cover and could be described by a quadratic equation with $p < 0.001$ (Fig. 5). A time series plot of annual ET across sites showed a steady reduction in ET of 17.4 mm/year from 2007 to 2015 (Fig. 6).

Discussion

Previous studies have shown that satellite vegetation indices can be used to quantify tamarisk defoliation events due to the loss of green leaf tissue when beetles feed on the shrubs (Dennison et al. 2009; Meng et al. 2012; Nagler et al. 2012, 2014). The EVI trends for the Colorado and Dolores Rivers in this study match ground observations at 10 sites in the same area in Kennard et al. (2016). Ground surveys in 2010 showed very high levels of

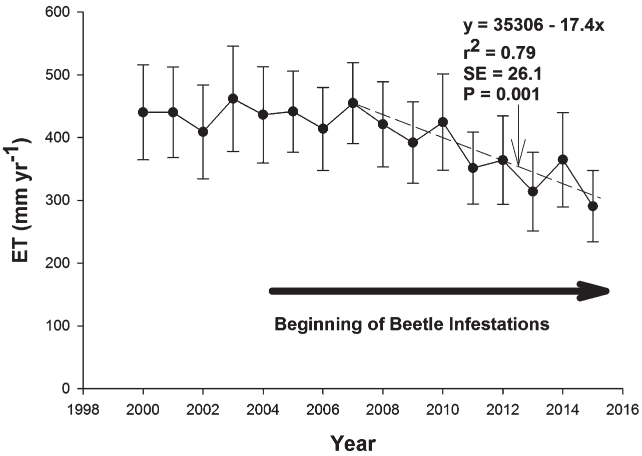

Figure 6. Annual ET across all sites from 2000 to 2015, showing the duration of the impact on ET from the 2004 release of the beetle until present. Error bars are ±SE. The regression analysis is for the years 2007–2015.

defoliation of tamarisk, amounting to 100% at many sites along the river, but beetle abundance was in decline, apparently due to lack of food (Jamison et al. 2015).

The EVI results support the characterization of beetle movements in Jamison et al. (2015) as a series of colonize–defoliate–emigrate events, creating a mosaic of fully defoliated, partially defoliated, and recovering tamarisk stands along rivers. All sites showed at least partial recovery of EVI to pre-release values after 9–10 years. The impact of beetles on riparian ecology and wildlife will be complex depending on the plant successional stages following defoliation of tamarisk, the hydrological conditions, soil nutrient content, and the extent of tamarisk mortality. The beetle data on the Lower Virgin River also support the colonize–defoliate–emigrate model of defoliation seen in the Upper Basin rivers (Jamison et al. 2015) but tamarisk has not yet recovered. The colonize–defoliate–emigrate model is typical of predator–prey interactions, which can be inherently unstable, especially for specialty predators that depend on a single prey species (Ong & Vandermeer 2015). As their food supply runs out, predators either die off or move to other locations, and the prey species can recover. Stability can be introduced into weed biocontrol programs by continually augmenting predator populations with new releases; otherwise, either predators or prey or both can eventually fall to low population levels depending on rates of reproduction (Ong & Vandermeer 2015).

The most striking finding was the variability in beetle/tamarisk interactions among sites. Defoliation impacts ranged from net 0% reduction at sites on the Dolores River, to moderate reductions on the San Juan and Colorado River, and high defoliation rates with little sign of recovery so far on the lower Virgin River. The coefficient of variation for percent defoliation was 147% among sites. Kennard et al. (2016) also noticed high variability among sites but without a correlation with environmental variables measured at the sites. Hultine et al. 2010*a*, Hultine et al. 2010*b*) showed that rapidly growing tamarisks are more susceptible to defoliation damage and mortality than slower growing tamarisks. In this study, however, there was no significant correlation between initial ET values in Table 1 and % defoliation after beetle arrival. In their native range in Asia, tamarisk beetles and tamarisk trees coexist in a state of dynamic equilibrium (Lewis et al. 2003). An estimate can be made of the actual reduction in EVI or NDVI due to beetle activity in the Upper Basin. Assuming that the riparian zones in this study are 70% tamarisk (from Table 1), it can be calculated that beetles have caused a 21% reduction in tamarisk green foliage over an approximately 15 year period, based on the overall reduction in ET in Table 1 (i.e. 14.4% divided by 0.70 = 21% for the tamarisk fraction of cover, assuming beetles do not impact other species). However, the time-course plot of ET versus years after beetle arrival (Fig. 6) shows that ET has shown a steady decline through 2015, indicating that an equilibrium state has not yet been reached.

D. carinulata was initially predicted to move very slowly below 38°N due to its photoperiod requirement for diapause (Lewis et al. 2003; USDA 2005; Bean et al. 2007). However, the beetle has evolved with respect to its photoperiod requirement (Bean et al. 2012) and has now entered Southwestern Willow Flycatcher habitat (Bateman et al. 2010). In 2010 the U.S. Department of Agriculture officially ended its release program due to potential impacts on nesting success of the Southwestern Willow Flycatcher (Dowdy 2010). This study shows that beetles have now spread downriver to 34°N at a rate of 40 km/year, confirming results in Bean et al. (2012) showing the beetles have now adapted to the new environmental conditions. Beetles are now well within the range of Southwestern Willow Flycatchers (Sogge et al. 2008).

ET rates estimated by Landsat and MODIS were within the range estimated by ground methods, which generally have produced much lower values than assumed in Zavaleta (2000) and cited in the Environmental Assessment that led to release of beetles (USDA 2005; Owens & Moore 2007). For example, annual ET estimated for the Lower Dolores River projected from sap flux measurements on 10 trees was 224 mm/year in 2008–2009, with beetles reducing ET by 40 mm/year compared to prebeetle values (Hultine et al. 2010*a*; Hultine et al. 2010*b*). Our results covered a longer time span and were 279 mm/year for prebeetle years and no significant reduction ($p = 0.23$) in postbeetle years. Snyder et al. (2012) measured ET and carbon uptake using an eddy covariance moisture flux tower over four years in a beetle-infested tamarisk patch in the Truckee River in the Great Basin region. ET ranged from 400–500 mm/year and was not greatly affected by beetles. While they defoliated the stand each summer, the periods of defoliation were only 2–4 weeks in duration and new leaves quickly regrew after each defoliation event. Pattison et al. (2011) measured ET of tamarisk with sap flow sensors at sites near the original beetle release in Nevada in 2001. At a site on the Humboldt River they reported prebeetle ET of 518 mm/year and 269–296 mm/year in the first two years of defoliation. Using the same MODIS and Landsat methods used here, Nagler et al. (2012) reported rates of 437 mm/year and 234 mm/year at the same site measured by Pattison et al. (2011). Given the differences in methods and sampling strategies, they concluded that satellite and ground methods gave convincingly similar results for the magnitude of ET and the effect of beetles. Sueki et al. (2015) measured ET at a single eddy covariance moisture flux tower in dense stands of tamarisk on the Lower Virgin River and obtained rates of 953 mm/year in 2010 (before beetles arrived) and 795 mm/year in 2011 and 873 mm/year in 2012 after beetles arrived. These are within the range of values we estimated with MODIS imagery; however, our data show that EVI and projected ET continued to decline after 2012, reaching low levels by 2015. Our estimate of potential water savings was only 61 mm/year and mean ET was only 461 mm/year before beetle arrival. This value is consistent with two recent assessments of potential water savings that could be achieved from tamarisk control (Nagler et al. 2009; Tamarisk Coalition 2009; Zavaleta 2013).

Absolute values of potential water savings can be estimated from the acreage of tamarisk habitat within riparian zones and the amount of water saved per ha. The Tamarisk Coalition (2009) estimated that tamarisk habitat covers 104,000 ha in the Colorado River Basin, of which 65% is tamarisk canopy and the rest is other species, bare soil, or water. They further estimated that 46,957 ha was in the upper basin plus the Virgin River while 57,043 ha was in the Lower Colorado, Gila, and Bill Williams Rivers (Table 1 in Tamarisk Coalition 2009). Our ET estimates include both tamarisk ET and ET from other species. Based on our estimates, total ET in the Upper Basin and Virgin River Valley from 2000–2006 was 195.3 million m^3/year and ET postbeetle introduction was 167.2 million m^3/year, for a potential savings of 28.1 million m^3/year. This is a significant amount of water, equal to 10% of Nevada's allotment of Colorado River water. However, it is only 0.23% of the 12,215 million m^3/year of water that flows in the Colorado River from the Upper Basin to the Lower Basin each year. However, ET reductions have continued each year and it is not possible to predict how much water could eventually be saved.

In the short term, beetles can negatively impact tamarisk habitat quality for a number of organisms (Bateman et al. 2014). On the Lower Virgin River habitat structure was altered by defoliation in monotypic tamarisk stands. Amount of bare ground increased from 9–10% during predefoliation (Bateman & Ostoja 2012), to 23% during postdefoliation conditions (Mosher & Bateman 2016). Canopy cover was reduced from 82% predefoliation to 72% postdefoliation. Mortality was only about 6 to 10% for individual shrubs but canopy was reduced (Bateman et al. 2013; Hultine et al. 2015). After biocontrol, defoliation sites became hotter and drier.

The replacement plants for tamarisk are not necessarily desirable species. Kennard et al. (2016) as well as Hultine et al. (2010*a*, *b*) found that noxious weeds were the most common replacement plants for defoliated tamarisk stands at some sites. Clearly, active restoration steps of affected river reaches will be needed in the reaches that support Southwestern Willow Flycatcher nesting grounds. These could include, first, close monitoring of defoliation events through ground and remote sensing methods. Since defoliation events are episodic and difficult to predict in advance, some form of real-time monitoring and rapid responses would be needed in critical habitats, such as Southwestern Willow Flycatcher nesting sites. Replacement habitat could include plantings of willow, cottonwoods, and other native plants on some sites.

On other sites, soil and groundwater conditions are such that mesic vegetation cannot be re-established, so preservation of some tamarisk stands as refugia might be needed. These are only suggestions to focus attention on the need for new management strategies for the new reality on tamarisk-dominated river reaches. The results support other studies showing that it is difficult to precisely predict the impacts of biocontrol organisms on their target organisms and the associated ecosystems (Howarth 1983).

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Comparison of annual ET estimate obtained by MODIS and Landsat methods at selected river sites, 2000–2015.
Figure S2. Annual ET on rivers wide enough to survey by the MODIS method.
Figure S3. Annual ET on rivers surveyed by the Landsat method.
Appendix S1. Locations of sample sites for ET and defoliation tracking.

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