

Spatial modeling improves understanding patterns of invasive species defoliation by a biocontrol herbivore

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Abstract Spatial modeling has proven to be useful in understanding the drivers of plant populations in the field of ecology, but has yet to be applied to understanding variation in biocontrol impact. In this study, we employ multi-scale analysis (Moran's Eigenvector Maps) to better understand the variation in tree canopy exposed to defoliation by a biocontrol beetle (*Diorhabda* spp.). The control of the exotic tree *Tamarix* in riparian areas has long been a priority for land managers and ecologists in the American southwest. *Diorhabda* spp. was introduced as a bio-control agent beginning in 2001 and has since become an inseparable part of *Tamarix*-dominated river systems in the southwest. Between 2013 and 2016 tamarisk dieback was assessed at 79 sites across Grand County,

Utah, arguably the epicenter of *Diorhabda* impact in the U.S. Canopy cover of *Tamarix* was between 73 and 81% at these sites, with the percent that was live cover fluctuating by year with a minimum of 42%. Using a traditional general linear model, we found that readily and commonly measured environmental factors could explain only up to 26% of the variation in *Tamarix* live canopy each year. The number of defoliations was correlated with an increase rather than a decrease in percent live canopy, suggesting compensatory growth. Spatial structure alone explained 22–40% of variation. We found fine scale spatial structure at less than 10 km and broad scale spatial structure from 10 to 30 km. Combining both traditional and novel spatial statistical methods we increased that percentage to 43–63%, depending on year. These results suggest that scientists and land managers must look beyond commonly measured environmental variables to explain non-random biocontrol impact in this system. In particular,

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this study points to the potential for biotic interactions and variation in flood cycles for further exploration of the identified spatial structure.

Keywords Biological control · *Diorhabda* spp. · Moran's Eigenvector Maps · Spatial modeling · *Tamarix* spp.

Introduction

Ecological phenomena display geographical patterns as a result of the underlying abiotic conditions being spatially structured (spatial dependence) or through contagious biotic processes in the community (true spatial autocorrelation, SAC) (Legendre 1993; Fortin et al. 2002; Borcard et al. 2004; Legendre and Legendre 2012). This spatial structure was, until recently, largely ignored in ecological studies. However, a new analytical framework has been developed to incorporate spatial structure into the analysis of ecological systems (Moran's Eigenvector Maps, Legendre and Legendre 2012). Recent studies have demonstrated the value of identifying spatial patterns of ecological communities to increase understanding of community drivers (Andersen et al. 2011; Sharma et al. 2011). An understanding of spatial structure may be particularly valuable in the context of restoration outcomes and invasive species community dynamics (Muster et al. 2014; Bourgeois et al. 2016; Venugopal et al. 2016). Early in the study of biological control (biocontrol), spatial patterns were also recognized as an important element to understanding this management tool (Levins 1969). The impact of invasive species removal through biocontrol presents a particularly difficult scenario to predict, given that biocontrol effects are both spatially and temporally variable. However, to our knowledge, no published study has incorporated spatial modeling to better understand patterns of biocontrol impact. Here we combine traditional approaches with a new modeling tool to explore patterns of defoliation by a biocontrol herbivore.

Determining the drivers of the response by invasive plant species to biological control based solely on environmental conditions without regard for spatial patterns may be insufficient due to the complexity of interactions between small- and large-scale processes.

Biocontrol has a myriad of potential drivers, from top-down factors such as predation to bottom-up factors such as soil nutrients and competition among target plant species (Seastedt 2015). While environmental conditions can influence the effects of a biocontrol herbivore on its target plant, other factors such as population genetics and dispersal, which may be heavily spatially structured, also play a role. For example, gene flow among species of both the biocontrol agent and target species before and after the introduction of the biocontrol agent can make biocontrol impact more difficult to predict (Seastedt 2015). Additionally, it is difficult to predict how far and in what manner an agent will disperse in a new environment (Nagler et al. 2014).

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

In this study, we apply MEM analysis to examine the defoliation of an invasive tree, *Tamarix* spp. (tamarisk, saltcedar), by a biocontrol beetle in riparian corridors and intermittent watercourses of the Southwestern United States. *Tamarix* was introduced in the early 19th century as a bank stabilizer, windbreak and ornamental. Although naturalized prior to the widespread practice of hydrological engineering (Birken and Cooper 2006), river regulations and thus changing flood regimes partially facilitated the dominance of *Tamarix* (Stromberg et al. 2007; Sher 2013). In the Southwestern U.S., it is now the third most common

woody species and second highest tree cover in the (Friedman et al. 2005). Given the difficulty of distinguishing species in terms of biology and ecology, *Tamarix* refers to the two most common species in the U.S. and their hybrids—*T. ramosissima* and *T. chinensis* (DiTomaso 1998; Gaskin 2013). *Tamarix* reproduces throughout the growing season, with wind and water dispersed seeds that are sensitive to desiccation, and thus no seed bank is maintained (DiTomaso 1998; Hultine and Dudley 2013). *Tamarix* has been called a “paradox plant” as it has seemingly contradictory life history traits (reviewed in Sher 2013): It is both long-lived and produces large amounts of small seeds, is both drought and flood tolerant, and is an excellent competitor as a mature tree while easily overtopped as a seedling. *Tamarix* is a passenger of degraded ecosystems (sensu MacDougall and Turkington 2005), but once established it drives tenacious changes in the ecosystem including higher soil salinity, increased fire frequency, and altered river geomorphology (reviewed in Johnson 2013). As a costly invasive species (Zavaleta 2000), its control has been a high priority in the American Southwest.

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

Diorhabda adults and larvae feed exclusively from *Tamarix* foliage, resulting in leaf desiccation and defoliation (DeLoach et al. 2003; Lewis et al. 2003). They are gregarious, and swarms are known to intensively defoliate entire stands of trees at a time (Bean et al. 2013a). Following such an event, *Diorhabda* tend to abandon the stand, resulting in areas that were heavily defoliated in 1 year having small or absent populations of larvae in the following year (Jamison et al. 2015). Conversely, areas that are only partially defoliated tend to retain an

overwintering population, affecting the spatial distribution of beetle populations in future years (Jamison et al. 2015). Adult beetles are attracted to new food sources by sensing chemical compounds in tree foliage that are released through feeding activity as well as aggregation pheromones produced by mature males (Cossé et al. 2005, 2006). They have been measured to travel up to 65 km in one dispersal event (Jamison et al. 2015; Nagler et al. 2014).

One defoliation event does not usually kill a stand or even a tree; leaves will often regrow on some or all of the defoliated branches depending on degree of carbon starvation (Bean et al. 2013a). Multiple defoliation events are generally required to cause branch or whole-tree mortality, however the number of defoliation events that is required for this to occur varies greatly (Bean et al. 2013a). Some studies suggest that the variation in number of defoliation events required to kill a tree is related to resource allocation governed by tree genetics or response to water availability (Hultine et al. 2013; Williams et al. 2014). Specifically, trees that allocate more resources to root growth and nutrient storage may be more resilient to herbivory than trees that invest more in above ground growth and leaf production (Williams et al. 2014). Recent studies show that beetle defoliation may affect ecosystem processes such as evapotranspiration, although at lower rates than were anticipated prior to release (Nagler et al. 2017).

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

In general, studies examining the response of *Tamarix* to biocontrol are highly variable (Hultine et al. 2015; Kennard et al. 2016; Nagler et al. 2017). Despite 15 years of biocontrol, the impact of *Diorhabda* on *Tamarix* remains inconclusive and nearly impossible to predict (Hultine et al. 2015; Kennard et al. 2016; González et al. 2017; Sher et al. 2018). To date, variation in defoliation and mortality has been primarily studied in terms of environmental factors influencing tree response (but see Jamison et al. 2015), but no consensus has been reached about what

environmental conditions mediate tree mortality in *Tamarix* stands. For example, Hultine et al. (2015) found a positive relationship between soil salinity and canopy dieback, but no correlation with the number of defoliation events or drought stress. In contrast, Kennard et al. (2016) found that defoliation was positively correlated with soil percent sand and negatively correlated with drought stress.

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

Methods

Site description and data collection

A total of 79 defoliation monitoring sites were established throughout the landscape of Grand County, Utah (Fig. 1), arguably the epicenter of *Diorhabda* spp. beetle impact in the Southwestern U.S. (Tamarisk Coalition 2016). The Northern tamarisk beetle (*Diorhabda carinulata*) was released at 12 locations (Fig. 1) between 2004 and 2006 throughout the study area and has since expanded across the western United States. This region has an average high temperature of 22.1 °C and low temperature of 5.6 °C with average annual precipitation in rainfall of 241 mm and snowfall of

152 mm (US Climate Data 2016). Sites were established at every known *Tamarix* population within Grand County that was (1) accessible and (2) large enough to accommodate the sampling design (described below). Distances between adjacent sites ranged from 30 m to 15.1 km, with a mean of 8.8 km ($s = 4.3$ km). All sites were individual stands, with the exception of two sites that were each a combination of two, smaller, adjacent stands in order to meet the size requirement while maintaining good geographic coverage across the study area. The resulting study area reached from the Book Cliffs (mountain range running East to West along the northern edge of study area) to the Colorado River or Green River, representing a wide variety of ecosystem types, including ephemeral washes, cattle stock ponds and two rivers with permanent flow. As such, this location provided the diversity in environmental variables that exist where *Tamarix* occurs without confounding other spatial variables such as climate.

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

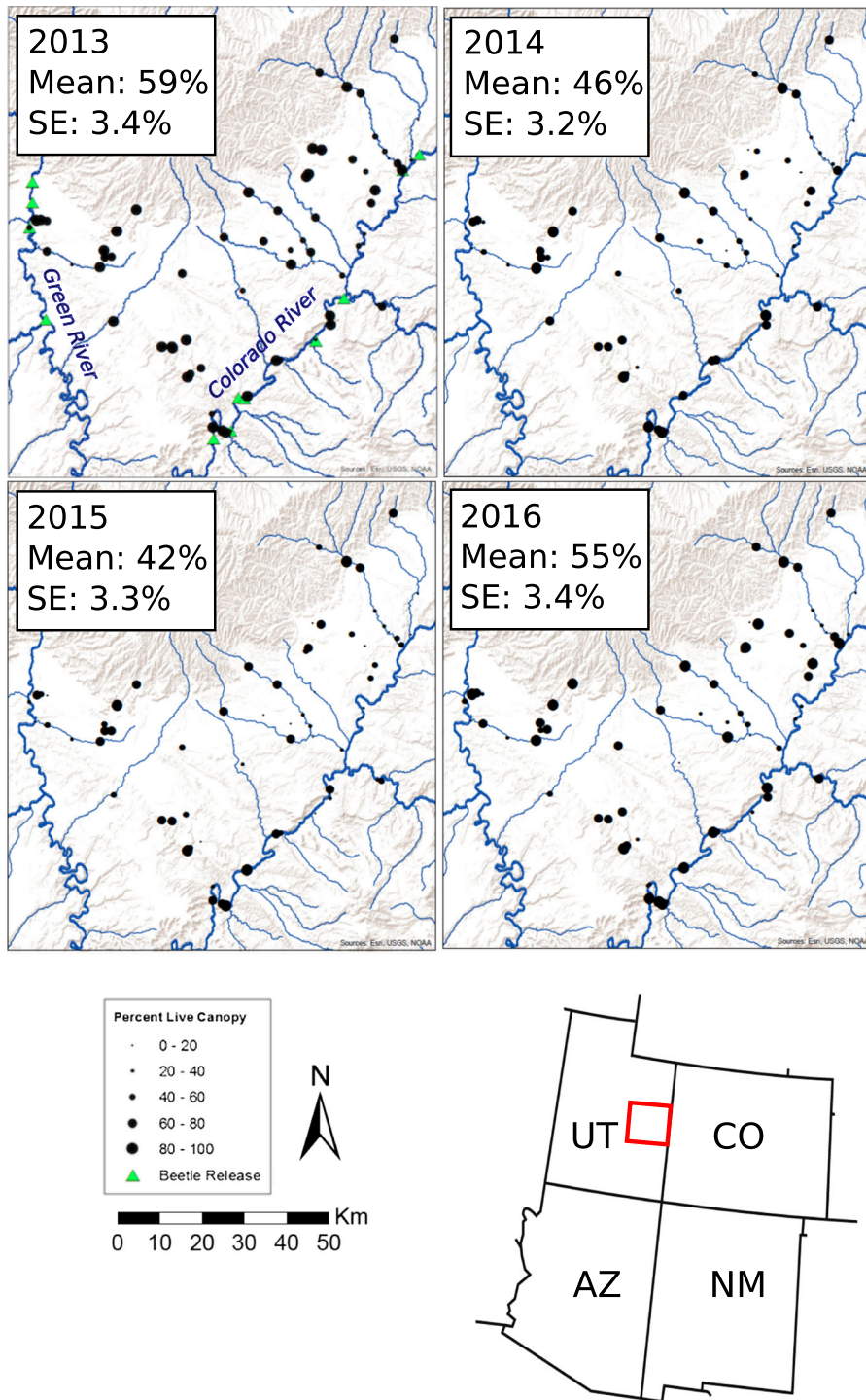


Fig. 1 Percent live canopy. Percent live canopy (as indicated by size of circle) of *Tamarix* in southeastern Utah for each of the 79 sites recorded annually between 2013 and 2016. The red box

in the overview represents the study area. UT-Utah, CO-Colorado, AZ-Arizona, NM-New Mexico

total points sampled that intersected *Tamarix* (“live” or “dead”). Canopy cover was calculated as the number of points that intersected *Tamarix* divided by the total number of points sampled. All 79 sites were sampled for *Tamarix* canopy from 2013 to 2016 for a total of 4 years of data (Fig. 1). Given the number of sites, sampling began in late spring once *Tamarix* had greened up and was finished by late summer before autumn browning began.

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

Stand characteristics

The circumference of the largest tree per transect was measured and averaged for each site. This variable represents a proxy for stand age, with larger trees representing older stands (Brotherson et al. 1984; Ohrtman et al. 2012). Hultine et al. (2010a) have shown that older trees have reduced vigor and fewer leaves and so fewer resources to recover from defoliation, thus we expect to see lower percent live canopy in stands with larger (and thus older) trees. The number of years since the first defoliation was assessed from data collected by the continuous monitoring of the sites since beetle release in 2006. We predicted that more years since first defoliation would be associated with lower live canopy, given that Hudgeons et al. (2007) have shown that multiple defoliation events are required to cause tree mortality. If beetles are returning to stands that have re-greened, then stands that were defoliated in earlier years are expected to have higher mortality over time. Using Google Earth, we measured the as-the-crow-flies distance from each site to the nearest release site. We predicted that stands farther from release sites would have lower live canopy based on Jamison et al.’s (2015) finding that average defoliation was a function of distance from release site. Beetles were seen at all sites at least once, indicating that all stands represent a potential food source for the beetles. Cattle impact was assessed on a scale of zero to three, with three being highest impact based on a visual inspection of cattle damage on adjacent plants and presence of excrements in the area. Cattle may graze *Tamarix* seedlings if desirable vegetation is lacking, despite

having no nutritional benefit (DiTomaso et al. 2013). Additionally, cattle can cause physical damage to *Tamarix* stands through trampling and branch breakage (personal observation). We therefore predicted that higher cattle presence in a site would be correlated with lower percent live canopy.

Stands with less access to ground water may have a lower capacity to recover from herbivory based on the relationship between tree mortality, resource availability and disturbance studied in other plant species (Bean et al. 2013a). Thus, we measured water availability with several indirect measures, including by surveying understory plants for each transect. Species identification in the field was verified later in an herbarium. Using the PLANTS Database of the U.S. Department of Agriculture we determined the Wetland Indicator Status of each plant species found for the “Arid West” Ecoregion (USDA-NRCS 2016). We assigned a wetland status to each site based on the most wetland-dependent plant present at the site (Table 1). These categories were used as proxies to indicate low lying areas of floodplains that are more connected to the river than higher and therefore drier areas (Corenblit et al. 2009; Merritt 2013; González et al. 2017).

Geographic features

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

Table 1 Summary statistics for all environmental variables sampled

	Mean	SE			
Geographic					
Absolute elevation (m)	1349.06	12.35			
River width (m)	35.89	7.09			
Longitudinal site slope (m)	5.47	0.89			
River category (permanent or intermittent)	Intermittent (1) = 59	Permanent (2) = 20			
Soil					
Ec ($\mu\text{S}/\text{cm}$)	1937.04	164.23			
% Sand	45.85	2.54			
pH	8.08	0.02			
Wetland status	UNK(1) = 8	FACU(2) = 12	FAC(3) = 40	FACW(4) = 13	OBL(5) = 6
Stand characteristics					
Tree circumference (cm)	41.50	2.41			
Distance from release site (km)	12.95	0.97			
Years since first defoliated	9.34	0.08			
Cattle impact (0–3)	0 = 19	1 = 10	2 = 20	3 = 30	

Mean \pm 1 SE are presented for all continuous variables. Counts are presented for categorical and ordinal variables. See “Methods” section for explanation of variables

Soil characteristics

A soil sample was collected from one randomly selected location along each transect. Transect samples were mixed to create a composite site-level soil sample. Soil samples were collected using a soil corer to a depth of 10 cm. Samples were placed in a paper bag to air dry until returning to the lab where they were dried in an oven at 60 °C and processed to measure soil texture, salinity and pH. Soil texture was measured as the percentage of sand ($> 63 \mu\text{m}$) present, pH was determined using a 1:1 water solution and soil salinity was measured as the electrical conductivity of the soil (González et al. 2014, 2017). We predicted that sites with higher soil salinity would have lower live canopy, given that a previous work on *Tamarix* response to *Diorhabda* beetles found dieback positively correlated with salinity in two of the 3 years surveyed (Hultine et al. 2015).

Statistical methods

To address our first question of whether environmental factors explain variability in live canopy we used a general linear model with stepwise selection, variables selected based on Akaike information criterion (AIC),

maximum likelihood fit and normal distribution to test the relationship between percent live canopy in each year and environmental conditions. Sites were at least 30 meters from the nearest neighboring site (an exception), while most were separated by several kilometers or more (see above under “Site Description”). Nevertheless, this type of analysis may lead to type I error due to pseudo-replication related to the spatial dependency of environmental variables. To account for and incorporate this spatial dependency into our analysis, the results of the linear model were then considered in the context of the following spatial analyses.

To determine spatial patterns in present live canopy we used MEM (Borcard and Legendre 2002; Dray et al. 2006). In preliminary analyses we incorporated down-river directionality in the modeling of spatial processes using Asymmetric Eigenvector Matrices (AEM, Blanchet et al. 2008). However, the AEM increased the complexity of the model but did not improve our ability to explain patterns of *Tamarix* live canopy (results not shown), therefore we proceeded with MEMs that do not use directionality. We used two defined relationships—overland proximity (using Euclidean distance, henceforth referred to as MEM overland) and proximity along waterways

(MEM waterway). Using overland distances for the MEM overland model and distance along waterways for the MEM waterway model, we generated sets of spatial variables for each model called spatial eigenfunctions (Borcard et al. 2004; Dray et al. 2006; Legendre and Legendre 2012). For this, a site-by-distance matrix based on either raw overland distances or raw distances along waterways was submitted to a principal component analysis. The resulting eigenvectors corresponded to the spatial eigenfunctions representing independent (i.e., orthogonal) spatial structure acting at decreasing scales. For both models, raw distances as well as two geographic weighting functions were tested representing linear and concave-down spatial relationships (Dray et al. 2006). The weighting function with the highest adjusted R^2 was used (raw distances for the overland model and concave down for the waterway model).

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

To explore the shape and scale of significant spatial patterns, we plotted the significant eigenfunctions on a map of the study sites. For the MEM overland model, the significant spatial variables were plotted and then visually inspected to identify broad and fine relative spatial scales. Scales were identified simply by visually exploring the size of clusters in the plot and assigning the spatial variables as broad or fine relative to each other (Borcard and Legendre 2002; Borcard et al. 2004). These two sub-sets of spatial variables made up a large-scale spatial structure and a fine-scale spatial structure to be used in variation partitioning (see below). For the MEM waterway model, the significant spatial variables were plotted and visually

inspected, however, no visual discernment could be made for the scales of these variables.

We used variation partitioning in the R package *vegan* (Oksanen et al. 2013) to identify the relative importance of environment and spatial structure in *Tamarix* live canopy for each year. For each variation partition we used the undetrended live-canopy data. Variation partitioning was done to identify the exclusive and shared variation of each of the spatial patterns with the environmental variables (Borcard and Legendre 1994; Borcard et al. 2011; Sharma et al. 2011). For the overland model (MEM overland), variation partitioning was also done with the sub-models of fine and broad scale and environmental variables, making a total of four components for variation partition: linear, MEM overland (broad and fine), and MEM waterway. Additionally, we compared each significant spatial model to the environmental variables to identify the spatial scale at which environmental variables influence live canopy for each year. MEM methods have not yet been applied to address time series analysis. In this study, we visualized spatial structure from 1 year to the next by plotting the significant eigenvectors.

Live canopy and environmental data were checked for normality and log-transformed as needed (see supplemental material Appendix 1). Environmental variables were checked for collinearity using pairwise scatterplots (with a 0.6 cut off for correlation coefficients) before including them in the general linear model (Zuur et al. 2010). Model residuals were also checked for normality. All statistical analyses were performed using R version 3.1.2 (R Core Team 2014).

Results

Mean *Tamarix* live canopy in biocontrol sites varied from 42 to 59% during the 4 years of this study (Fig. 1; significant mixed model with live canopy as the dependent variable, year as the fixed effect and site as the random effect, $df = 3$ F-ratio = 25.01, $p < 0.0001$). Average live canopy decreased from 2013 to 2015 and increased from 2015 to 2016. The average percent live canopy in 2016 was higher than 2014, but still lower than 2013. Average canopy cover ranged from 73 to 81% depending on year. There was a weak negative relationship between live canopy and canopy cover that was statistically significant in all years except 2013 (linear regression adj. 2013

$R^2 = 0.015$, NS; 2014 $R^2 = 0.16$, $p < 0.001$; 2015 $R^2 = 0.1$, $p < 0.01$; 2016 $R^2 = 0.04$, $p < 0.05$). Readily and commonly measured environmental factors explained only 19–26% of the variation in *Tamarix* live canopy each year (traditional general linear model, Table 2). However, by combining both traditional and novel spatial statistical methods we increased the percentage of explained variation to 43–63%, depending on year. The portion of live canopy explained through environmental factors and spatial structure had little overlap (Fig. 2).

Environmental variables

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

Spatial structure

A significant linear trend was found in all years of study, explaining from 3.6 to 11.9% of variation in live canopy depending on year. The structure of this trend remained consistent from year to year. Both the waterway and overland models explained a large

portion of the variation in live canopy in all years (Fig. 2). The spatial structure of the waterway model was highly variable from year to year as shown by different clusters of similarly sized and shaded squares in Fig. 3.

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

Variation partitioning

For each of the spatial relationships examined (linear, MEM overland and MEM waterway), we partitioned the variance with the spatial variables and the environmental variables. That is, the variation was partitioned into the portion of variation explained exclusively by environmental variables, spatial variables as well as the portion of variation explained by both variables. Interestingly, there was very little overlap in the percent of live canopy explained by environmental variables and spatial structure from year to year (Fig. 2). An exception to this is that the overland model consistently overlapped with the stand

Table 2 General linear model with stepwise selection of environmental variables collected in 2014 (independent variables) and live canopy for each year studied (dependent variable)

Live canopy (year)	2013	2014	2015	2016
Geographic				
Absolute elevation (m)	n.s.	n.s.	0.133***	0.113**
River width (m)	n.s.	n.s.	n.s.	n.s.
Longitudinal site slope (m)	0.068*	n.s.	n.s.	n.s.
Stand characteristics				
Tree circumference (cm)	– 0.084**	– 0.101***	– 0.0842**	– 0.101**
Distance from release site (km)	0.103**	0.116***	n.s.	n.s.
Years since first defoliated	0.097**	0.075*	0.0844*	0.0895*
Total adjusted R^2	0.228***	0.2562***	0.1988***	0.190***

n.s. not significant

The value associated with each significant variable is the coefficient showing the direction and strength of the relationship

Significance codes: 0.0001 ‘***’; 0.001 ‘**’; 0.01 ‘*’

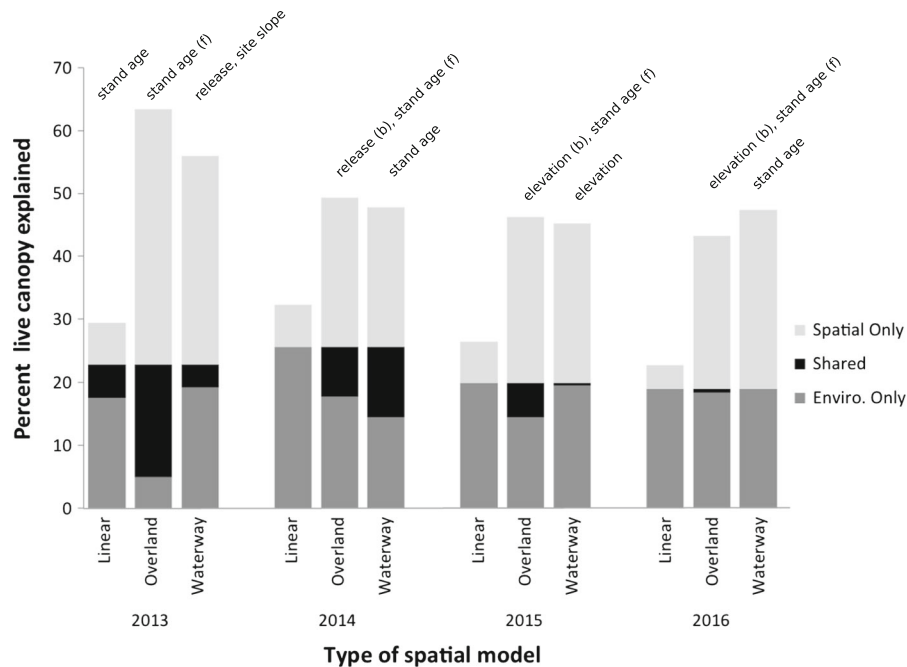


Fig. 2 Percent live canopy explained using variation partitioning with live canopy as the response variable and spatial eigenvectors and environmental variables as explanatory variables. Each bar represents one regression model using variation partitioning. The different shading within each bar shows the percentage of live canopy explained by spatial

variables alone (light grey), environmental variables alone (dark grey), and the shared percent explained by both spatial and environmental variables (black). The text above each bar is the environmental variable that overlaps significantly with the spatial model. For the overland models, the relevant scale was identified for the environmental variable: broad (b) or fine (f)

age at the fine scale. Shared variation with the two other types of spatial models varied from year to year. Particularly, the MEM waterway model showed no consistent trend in overlap from year to year.

Discussion

To the best of our knowledge, this is the first attempt to understand the spatial structure of a plant biocontrol impact using spatial models. By incorporating spatial structure into our analysis of the influence of environmental variables, we were able to describe a much larger portion of the variability in live canopy in biocontrol sites than using environmental variables alone. We were able to show that environmental variables underlie some of the spatial structure (overlapping in the variation partitioning) but that most of the variability in live canopy that is described by spatial structure is not related to the measured environmental variables (non-overlapping), which opens new research pathways to understand the factors governing

biocontrol effects on plants. We will discuss these results in terms of beetle defoliation, as this is the phenomenon of interest, bearing in mind that live canopy is the variable we measured. While it is likely that most dead *Tamarix* branches in the study area are a result of beetle defoliation based on observations over the past decade by the Weed Department of Grand County Utah (W. Robinson, personal observation), we cannot entirely rule out other causes of dead branches, such as drought stress or self-pruning in response to competition.

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

Both of the environmental variables that correlated significantly with live canopy—stand age and time since first defoliation—were under the category of “stand characteristics”, not an underlying property of soil, water, etc. This is not surprising given the lack of consensus on what environmental characteristics are important, despite several studies addressing this

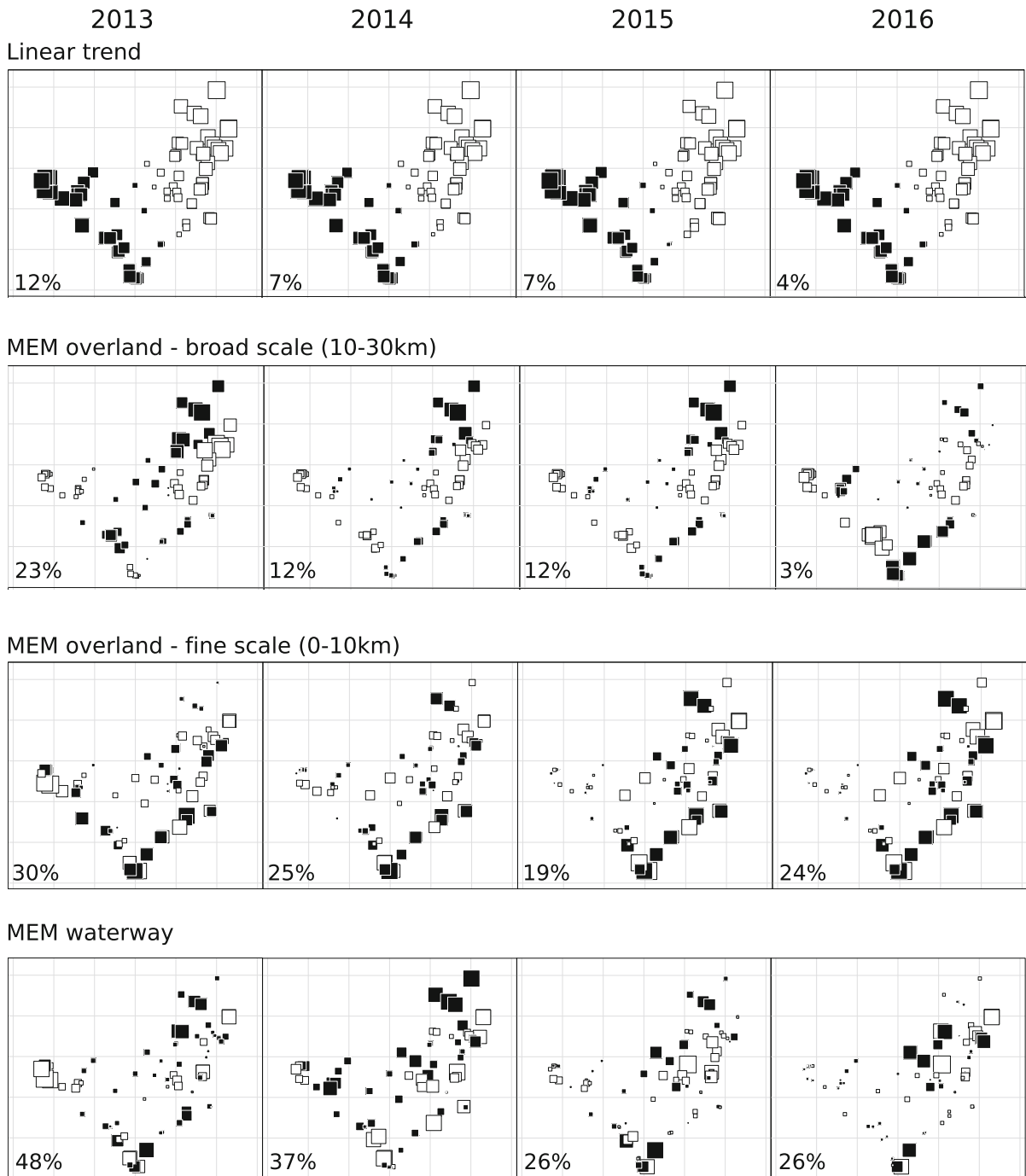


Fig. 3 Plots in geographic space of each spatial model. Each square represents the predicted value of *Tamarix* live canopy for the model. Predicted values are scaled from - 1 to 1 and so should be interpreted in relative terms. Black squares indicate positive values. White squares indicate negative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

lowest predicted live canopy, while large black squares have the highest predicted live canopy. Spatial patterns are interpreted from clusters of similar sized and colored squares. Adjusted R² value is in the bottom left corner of each plot. The predicted values are derived from all spatial variables significant at the 0.05 level

question. Our study supports the hypothesis proposed by Bean et al. (2013a) that older stands would be less able to recover from herbivory and have higher rates of mortality. Older *Tamarix* stands have been shown to have reduced vigor, produce fewer leaves and use fewer resources (Hultine et al. 2010a).

More surprisingly, time since first defoliation was associated with higher live canopy, which is counter to the idea that repeated defoliations eventually lead to the death of the tree (Hudgeons et al. 2007). Given that all of our sites have experienced multiple beetle defoliations, our results suggest that stands not only generally recovered over time but also potentially experienced compensatory growth. *Tamarix* is known to often re-sprout within weeks of beetle defoliation (Hultine et al. 2010a) however these are the first results to show that previously attacked stands were more green. The reason for this may also be that the core of beetle defoliation happens during the first few years following their arrival and tends to level off over time (Hultine et al. 2010b; Kennard et al. 2016; González et al. 2017). As our latest survey year was between 9 and 12 years after the first exposure to beetles (depending on site), we are likely seeing less dramatic beetle impact than would be expected during initial exposure. *Tamarix* persists in this area in high abundance. Given the “boom and bust” cyclical nature of beetle feeding, *Tamarix* decline and recovery to mirror beetle recovery and decline is likely in this area, even after all stands have experienced at least one major defoliation.

Regional scale spatial structure is consistent over time

The temporally-consistent linear trend in live canopy distribution, despite explaining a low percentage of variability, suggests that there is spatial structure on a larger scale than the study area. Previous studies indicate that large scale climatic variation influences *Tamarix* abundance (e.g. geology, soils, valley shape), especially relating to aridity (McShane et al. 2015; González et al. 2017). The present study suggests these types of factors also influence the impact of biocontrol defoliation on canopy status. This linear gradient could at least partly be responsible for regional differences in beetle impact as well as differing outcomes of studies done to predict beetle impact (e.g., Virgin River, Nevada: Hultine et al.

2015; Colorado River and small tributaries, Colorado: Kennard et al. 2016; Dolores River, Colorado and Utah: Sher et al. 2018).

The overland model had a temporally stable spatial structure

Interestingly, the overland proximity-based spatial structure in live canopy remained visually consistent among the 4 years surveyed, while the waterway patterns changed substantially from year to year. This suggests that both processes that are more temporally stable at this time scale (e.g. population genetic structure of *Tamarix*), and less so (e.g., flow regime, beetle dispersal) likely influence defoliation patterns.

Several studies argue that variability in *Tamarix* mortality from beetle defoliation is likely related to variation in plant genotypes among populations (Bean et al. 2013b; Hultine et al. 2013; Williams et al. 2014; Long et al. 2017). Novel hybridization (specifically *T. ramosissima* introgression) in the invaded range has been shown to be variable and associated with higher investment in roots and increased defoliation tolerance (Williams et al. 2014). Conversely, although *Tamarix* is exposed to approximately 320 herbivore species in its native range (Long et al. 2017), the absence of any significant herbivory over the last century in the U.S. may have led to weakening anti-herbivore adaptations (Blossey and Notzold 1995) to varying degrees across the landscape. The mosaic of genotypes created by either of these processes could explain a spatial pattern of beetle defoliation that would remain stable over 4 years.

Natural selection by the environment, unrelated to herbivore pressure, may also lead to traits that affect response to herbivory and thus a spatial structure that is unlikely to change markedly year to year. In particular, increased ability to exploit resources could make trees more vulnerable to defoliation because of tradeoffs between growth and metabolite storage, the latter of which playing a significant part in herbivore resistance and recovery. Hultine et al. (2013) showed that radial growth rates of *Tamarix* were positively associated with beetle-related mortality. Additionally, Friedman et al. (2008) showed that cold-adaptation influenced recovery from episodic herbivory in *Tamarix*. Long et al. (2017) argued that despite gene flow (which one would expect to hinder local adaptation), *Tamarix* is remarkably well adapted to local

environmental conditions. Thus, given this dynamic between the genetic basis for herbivory response and local adaptation, the more stable spatial structure we observed could reflect genotype distribution caused by selection by local conditions, unequal loss of herbivory defense, random hybridization patterns, or some combination of these.

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

The waterway model reveals a temporally dynamic spatial structure

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

We suggest that short-term compensation for flood and drought could be partially responsible for this dynamic structure. If high resource years lead to more growth than carbon storage, trees could be less resilient to defoliation during high-flow years (Hultine et al. 2013). *Tamarix* has been shown to compensate for water availability through high leaf-level transpiration when water tables are high and lower transpiration when water levels are low (Smith et al. 1998). Such climate variability is likely to cause greater beetle induced mortality in some years over others.

Beetle dispersal is also expected to vary from year to year and so may in part explain the source of

unstable spatial variation. Several studies have shown the boom and bust cycles of *Diorhabda* (Jamison et al. 2015; Nagler et al. 2017). Jamison et al. (2015) showed that high densities of beetles led to abandonment of heavily defoliated sites. This gives *Tamarix* the opportunity to re-sprout following defoliation. Given that there is no implicit confinement of this dispersal to river corridors, we anticipated finding evidence of beetle dispersal in our overland model. If beetle dispersal was predominantly characterized by an overland movement, we would expect to see an overland model that varied from year to year. This hypothesis was based on the fact that adult beetles are known to fly vertically into the air and drift on wind currents establishing satellite populations via this long range dispersal events known as Levy flights (Bean et al. 2013a; Nagler et al. 2014). Once away from the stand, they use both aggregation pheromones as well as volatile compounds in *Tamarix* to find new *Tamarix* stands (Cossé et al. 2006). Nagler et al. (2014) showed defoliation at sites 22.5 km from their initial site, with no defoliation in between in one season, suggesting long-range dispersal. These dispersal strategies make overland movement possible, and likely.

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

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

While stand age explained a small portion of the fine scale overland spatial structure of *Tamarix* percent live canopy, no other measured environmental variables corresponded to the spatial patterns observed. This non-overlapping portion of spatial structure is of

particular interest because it reinforces the idea that other factors besides environmental condition measured by classic factors (e.g., distance to river, soil salinity, etc.) related to the invasive tree are causing the variation. As discussed above, the temporally stable elements may be explained by other tree-related factors such as genetics, while those that changed year to year are more likely to be due to factors influencing beetle movement or other underlying contagious biotic processes of tree and beetle (true spatial autocorrelation).

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

Limitations and benefits Moran's Eigenvector Maps in ecological studies

Despite the uncertainty of the underlying causes of the spatial patterns, the distinct spatial structure suggests that the patterns of defoliation are not random. The high percent of variability explained only by spatial structure shows that in cases where measured environmental factors are unable to explain ecological patterns, spatial models offer a tool for better

understanding the variability in the system. In particular, MEM appear of great interest for the description of spatial patterns as it is relatively easy to implement and allows for the use of different connectivity matrices, distances and weighting functions between sites. MEM analysis can be used to conduct spatial analyses with binary dependent variables, making it useful for distribution studies. While our point level data was in fact binary, we scaled up to the site level in this analysis because all explanatory variables were at the site level. A binomial analysis could be useful however in a study designed to understand very fine scale spatial structure. Regardless of data type, MEM results often overestimate the variation explained solely by spatial components and should thus be put in perspective qualitatively rather than quantitatively (Tuomisto and Ruokolainen 2006; Gilbert and Bennett 2010; Hawkins 2011; Kühn and Dormann 2012). Therefore, further studies based on different statistical approaches or experimentally testing hypotheses in the field may be required to fully understand the spatial mechanisms at play in *Tamarix* biocontrol. Despite these limitations, the doubling of explained variation when accounting for spatial processes leaves no doubt here about the existence of strong spatial processes structuring *Tamarix* canopy exposed to biocontrol.

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

Comparing ground surveys to remote sensing methods

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

Additionally, using satellite imagery, Hultine et al. (2015) showed that ground surveys at the tree scale could be accurately scaled up to the stand scale. However, we would caution against scaling up too far, given the patchiness shown in the present study at less than 10 km. Further, Nagler et al. (2017) found through satellite imagery confirmed by on the ground surveys, that *Diorhabda*–*Tamarix* interactions were highly variable among sites even in the same river system, making high resolution sampling important for accuracy.

Conclusions

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

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

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

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