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# DO BEAVERS PROMOTE THE INVASION OF NON-NATIVE *TAMARIX* IN THE GRAND CANYON RIPARIAN ZONE?

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*Abstract:* Beavers (*Castor canadensis* Kuhl) can influence the competitive dynamics of plant species through selective foraging, collection of materials for dam creation, and alteration of hydrologic conditions. In the Grand Canyon National Park, the native *Salix gooddingii* C.R.Ball (Goodding's willow) and *Salix exigua* Nutt. (coyote willow) are a staple food of beavers. Because *Salix* competes with the invasive *Tamarix ramosissima* Ledeb., land mangers are concerned that beavers may cause an increase in *Tamarix* through selective foraging of *Salix*. A spatial analysis was conducted to assess whether the presence of beavers correlates with the relative abundance of *Salix* and *Tamarix*. These methods were designed to detect a system-wide effect of selective beaver foraging in this large study area (367 linear km of riparian habitat). Beavers, *Salix*, and *Tamarix* co-occurred at the broadest scales because they occupied similar riparian habitat, particularly geomorphic reaches of low and moderate resistivity. Once the affinity of *Salix* for particular reach types was accounted for, the presence of *Salix* was independent of beaver distribution. However, there was a weak positive association between beaver presence and *Salix* cover. *Salix* was limited to geomorphic settings with greater sinuosity and distinct terraces, while *Tamarix* occurred in sinuous and straighter sections of river channel (cliffs, channel margins) where it dominated the woody species composition. After accounting for covariates representing river geomorphology, the proportion of riparian surfaces covered by *Tamarix* was significantly greater for sites where beavers were present. This indicates that either *Tamarix* and beavers co-occur in similar habitats, beavers prefer habitats that have high *Tamarix* cover, or beavers contribute to *Tamarix* dominance through selective use of its native woody competitors. The hypothesis that beaver herbivory contributes to *Tamarix* dominance should be considered further through more mechanistic studies of beaver foraging processes and long-term plant community response.

*Key Words:* *Castor canadensis*, Colorado River, herbivory, plant-animal interactions, riparian vegetation, *Salix*, tamarisk

## INTRODUCTION

Selective foraging and utilization of woody materials by North American beavers (*Castor canadensis*) can exert profound effects on the species composition and structure of plant communities (Rosell et al. 2005) and may shift community structure toward non-preferred species (Johnston and Naiman 1990). For instance, selective felling of *Populus deltoides* Bartram ex. Marsh (cottonwood) by beavers has facilitated the growth of *Tamarix* (tamarisk) and *Elaeagnus angustifolia* L. (Russian olive), two non-native invasive shrubs, along several rivers in eastern Montana (Lesica and Miles 2004). Along the Marias River in north-central Montana, beaver browsing was three times more likely on *P. deltoides* than on *E. angustifolia*, and the damage to *Populus* trees was more severe, with beaver damage to the main stem on *Populus* as opposed to the basal branches on *E. angustifolia* (Lesica and Miles 1999). Pearce and Smith (2001) also found that *Populus* was more susceptible to beaver harvesting than *E. angustifolia*, which led them to predict that *E. angustifolia* will become more abundant at the expense of *Populus* along the Milk River, Montana. Beavers have also greatly reduced the abundance of *Populus* along the Green and Yampa rivers of the upper Colorado River Basin, and sapling predation by beavers threatens continued recruitment of *Populus* (Breck et al. 2003a). Beavers are capable of altering the competitive relationships between preferred and non-preferred forage species.

Bank-dwelling beavers colonize dens on the banks of large-order rivers and influence vegetation by forage selection for preferred species. *Salix* (*S. exigua* and *Salix gooddingii*) is a staple food for beavers (Johnson 1991, Baker and Hill 2003), leading to the concern that abundant beaver populations in the Grand Canyon National Park (GCNP) may lead to an increase in invasive *Tamarix* over native riparian plant species. Beaver utilization is apparent in the majority of *Salix* stands and threatens the persistence of *Salix gooddingii* (Goodding's willow) stands. The potential effect of beavers on the native *S. gooddingii* is of more imminent concern because few stands of *S. gooddingii* remain. Beaver foraging contributes to the decline of *S. gooddingii* populations along the main channel of the Colorado River in the Grand Canyon (Johnson 1991).

Plants respond differently to herbivory depending on a variety of factors including timing, nutrient availability, and intensity of grazing (Maschinski and Whitham 1989). Plant competition can cause a more negative reaction (i.e., lower fitness) to biomass removal (Harper 1977). Foraging of *Salix* by beavers may yield areas for future establishment of *Tamarix*, particularly when foraging occurs in late summer when annual growth has subsided and compensatory growth is not possible (Kindschy 1989). Alternatively, when foraging occurs in early spring, beaver damage may increase the cover of *Salix*, as has been observed for *Populus fremontii* S. Wats. (McGinley and Whitham 1985). In Utah, *P. fremontii* changes growth forms from a tree to a shrub due to beaver herbivory; repeated branch removal by beavers causes production of many branches below the original *Populus* branch (McGinley and Whitham 1985). Similar to *Populus*, this type of growth pattern could increase canopy cover and, possibly, increase the competitive ability of *Salix* if browsing occurs early in the growing season.

We investigated the potential for selective foraging by bank-dwelling beavers to correlate with coarse-scale spatial patterns of riparian vegetation along the Colorado River in the Grand Canyon National Park. Our analyses were designed to assess: 1) correlations in the distribution of beavers, *Salix*, and *Tamarix*, 2) the spatial association of species occurrence after accounting for the distribution in the form of large-scale geomorphic variables, and 3) the relatedness of beaver presence to canopy cover of *Tamarix* and *Salix*. Because beavers and *Salix* co-occur in similar habitats in GCNP (Ruffner 1983), a negative association between beavers and *Salix* after accounting for habitat variability may suggest that beavers have had a significant effect on riparian plant community composition. A positive association may not necessarily indicate a causal relationship, but only that beavers and *Salix* exist in similar habitats. In contrast, because beavers rarely feed on *Tamarix* (Lesica and Miles 2004, unpublished data), a positive association would imply that beavers prefer habitats high in *Tamarix* or suggest a potential effect of beavers for facilitating *Tamarix* at the expense of native plant species.

It is unknown whether beaver herbivory along the lower Colorado River has contributed to the invasion of the non-native *Tamarix*. This question is important for managers, as evidenced by a recent proposal by the Hualapai Tribe to conserve native riparian vegetation through a 50% reduction of the beaver population in the Lower Grand Canyon (E. Leslie, National Park Service, pers. comm., 2005). There are also important ecological implications of a system-wide effect of beaver foraging on shrub species composition. If beavers strongly influence the species diversity of riparian ecosystems, the current bottom-up view of riparian systems with hydrology and geomorphology as the key structuring processes (Tickner et al. 2001) should be reconfigured to better incorporate biotic interactions as recommended by Naiman and Rogers (1997).

## STUDY AREA

The study area encompasses the riparian habitat along the Colorado River in the Grand Canyon National Park from Lees Ferry to 383.8 km downriver (Figure 1). From Lees Ferry to Diamond Creek (river km 387) the Colorado River drops 542 meters, and the majority of elevation loss occurs in short rapids created by debris flows at tributary mouths (Schmidt and Graf 1990). Eleven geomorphic reaches from Lees Ferry to Diamond Creek have been proposed by Schmidt and Graf (1990). These reaches differ fundamentally in their bedrock composition which causes variation in channel width, slope, and other landform characteristics. In 1963 the Glen Canyon Dam was completed and, thereafter, has drastically reduced the annual streamflow discharge, increased daily water-level fluctuations, and altered the season of high flows of the Colorado River. Flow stabilization has created more riparian habitat, and many shrub species have colonized this newly-available habitat including *Salix exigua* (coyote willow), *Pluchea sericea* Nutt., *Tamarix ramosissima*, and *Baccharis* spp. Beavers are also thought to have become more common

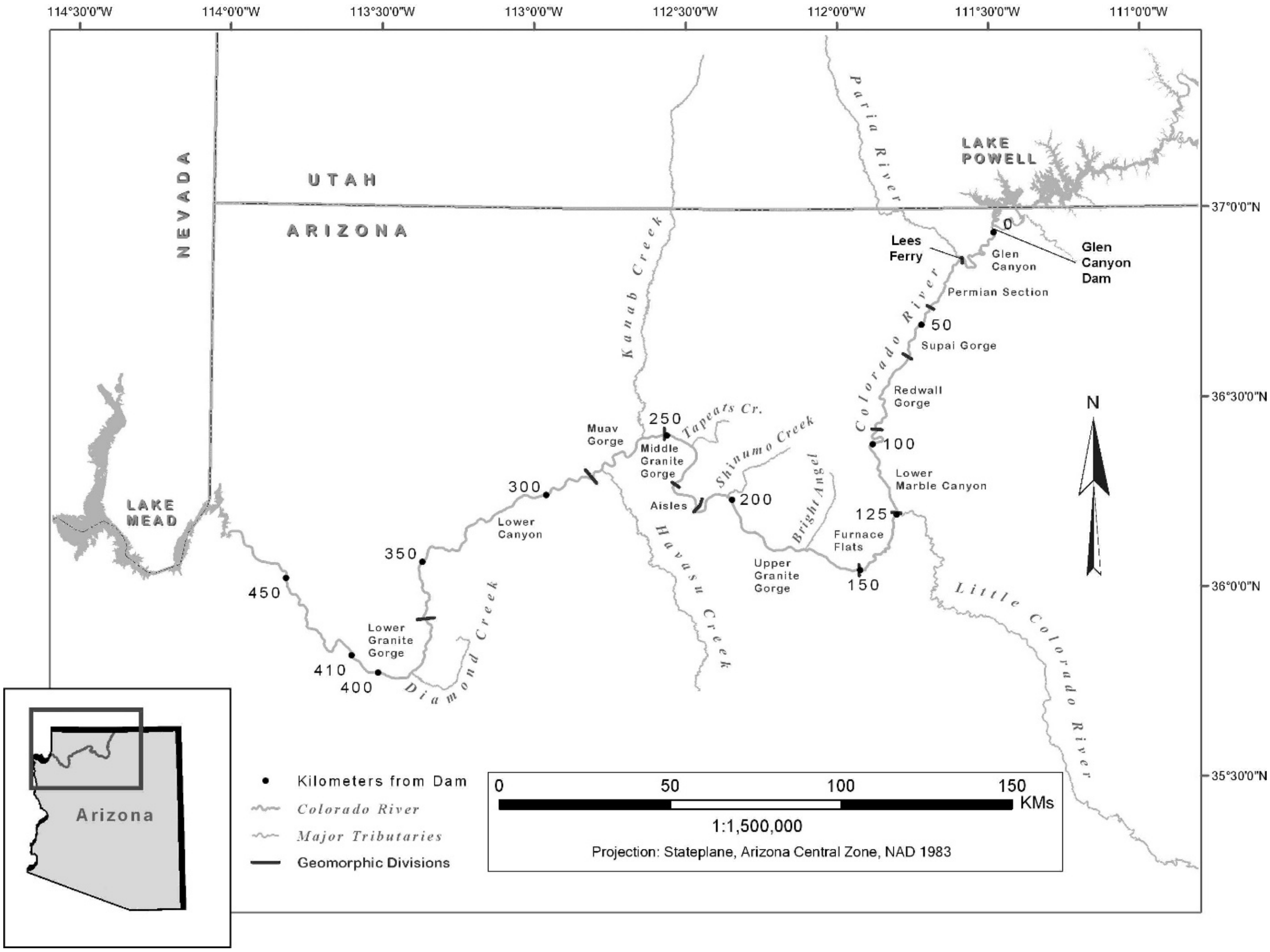


Figure 1. The Colorado River through the Grand Canyon. The twelve geomorphic reaches identified by Schmidt and Graf (1990) are shown. The study area encompasses Lees Ferry to river km 408 but excludes the section from 162 km to 178 km.

because of this increase in available habitat (Turner and Karpiscak 1980). *Tamarix*, an Eurasian native, was distributed as isolated individuals prior to the Glen Canyon Dam, but spread prolifically with native riparian vegetation after 1963. No major flood has occurred in Grand Canyon since 1983. Currently, *Salix exigua* and *Tamarix* are the two of the most dominant riparian shrubs in the Grand Canyon (Turner and Karpiscak 1980).

## METHODS

### GIS Data Layers

Beaver occurrence data at the spatial resolution of 0.1 river mile units along the longitudinal axis of the river were compared with *Tamarix* and *Salix* occurrence data, derived from a remote sensing classification and aggregated to the same spatial resolution. There were two primary spatial data layers used in this study, a point coverage of beaver observations obtained from the Science Center at Grand Canyon National Park and a vegetation map developed by the Grand Canyon Monitoring and Research Center (GCMRC). From these layers and others, several GIS variables were derived and used for analysis (Table 1). All variables were sampled at the level of 0.1 Stevens river mile (RM) units, the common distance system used in GCNP (Stevens 1990). This measurement system refers to Lees Ferry as RM 0, and downstream locations are referred to by their distance downstream from RM 0 along the river centerline. The 2274, 0.1 RM units between Lees Ferry (RM 0) and RM 238.5, excluding the section from 85.8 RM to 96.0 RM, formed the set of observations used in this analysis; these comprised the extent of river length common to beavers and the vegetation data sets.

Table 1. Spatial variables used in the nested multiple linear regression models. All vegetation variables are derived from 2002 aerial photography according to the Grand Canyon Monitoring and Research Center vegetation classification. "RM" = Stevens river mile.

| Ecological Variable | Abbreviation | Description |
|---|---|---|
| Beaver Occurrence | BEAV | Presence/Absence at each 0.1 RM, pooled for 1999–2003 |
| *Salix* Occurrence | paSALIX | Presence/Absence of *Salix* spp. in a 120-m radius circle centered on each 0.1 RM point, as classified from 2002 aerial photography. |
| *Tamarix* Occurrence | paTARA | Presence/Absence of *Tamarix* spp. in a 120-m radius circle centered on each 0.1 RM point, as classified from 2002 aerial photography. |
| *Salix* Cover | cvSALIX | Proportion of riparian surfaces in 2002 covered by *Salix* |
| *Tamarix* Cover | cvTARA | Proportion of riparian surfaces in 2002 covered by *Tamarix* |
| Riparian Surface Area | VegArea | Area within the 4.52 ha plot with riparian surfaces where vegetation is or could be established ($m^2$) |
| **Geomorphic Variable** | **Abbreviation** | **Description** |
| Geomorphic Reach | GeoReach | The 11 bedrock- and landform-defined geomorphic reaches of the Grand Canyon derived from Schmidt and Graf (1990) |
| Rock Resistivity | Resistivity | Classifications of rock resistivity at river level, interpreted from major geologic formations between Lees Ferry and Phantom Ranch. Three levels: Low, Moderate, High. |
| Sinuosity | Sinuosity | River sinuosity index, calculated as the quotient of channel length and straight-line distance, for 1.0 RM channel lengths centered on each 0.1 RM point. |

Continuous sampling for beaver activity was conducted by National Park Service employees from rafts. Indications of beaver presence and location (i.e., RM) were noted. The beaver database included 929 beaver observations from 1999–2003, distributed among years as follows: 2 in 1999, 494 in 2000, 123 in 2001, 142 in 2002, and 168 in 2003. The vast majority (97%) of these observations was taken from April–June. This data set encompassed the river corridor from Lees Ferry to Lake Mead, and included the following variables: observer, date, river mile (to the nearest one-tenth), bank (left or right), whether the observation was active or inactive, density, and comments which sometimes indicated the type of observation (i.e., slide, burrow, lodge, den, tracks, holes, cuttings, animals). In order to achieve consistency in the analysis, we simplified the beaver data set by considering only signs of beaver presence or absence at each 0.1 river mile (Table 1; Figure 2a). Because beaver sampling was *ad hoc* and inconsistent between sample periods, levels of sampling effort differed among years. Therefore, this data set cannot be used to assess patch occupancy dynamics of beaver populations.

The vegetation classification was derived from airborne digital imagery collected between May 25 and June 3, 2002, when dam release was approximately 8,000 cfs. The resulting four-band image mosaics (blue, green, red, and near-infrared) were aggregated to a resolution of 44 cm. The vegetation base map was constructed through a combination of ground surveys, image processing, and automated supervised classification procedures to identify vegetation classes (Ralston et al. 2008). The accuracy of the classified database was estimated by sampling approximately 10% of the river corridor and comparing areas at least 100 $m^2$ in size. The overall accuracy of the vegetation map was 80%. We used the single-species level vegetation classification, which differentiated *Salix* and *Tamarix* from other species. *Salix exigua* and *Salix gooddingii* were combined into a common class for *Salix* spp. following a river reconnaissance trip which suggested that the classification did not accurately distinguish the two species. The fuzzy accuracy assessment (Gopal and Woodcock 1994) revealed 92% accuracy in omission and 50% accuracy in commission for the *Salix* class values, while *Tamarix* had values of 80% accuracy in omission and 78% accuracy in commission.

The vegetation classification was used to determine the aerial cover of each species, and each observation describes the vegetation of a circular plot of 120-m radius, comprising 4.52 ha, centered on each 0.1-RM point. Circles of different radii were compared, and the 120-m distance was chosen because it minimized overlap with neighboring circular buffers, while capturing all vegetation within 60-m from water, the maximum foraging distance reported for beavers (Rosell et al. 2005). The proportion of riparian surfaces covered by *Tamarix* and *Salix* were used as response variables. Therefore, the area covered by water at a flow of 8,000 cfs and the area covered by desert vegetation

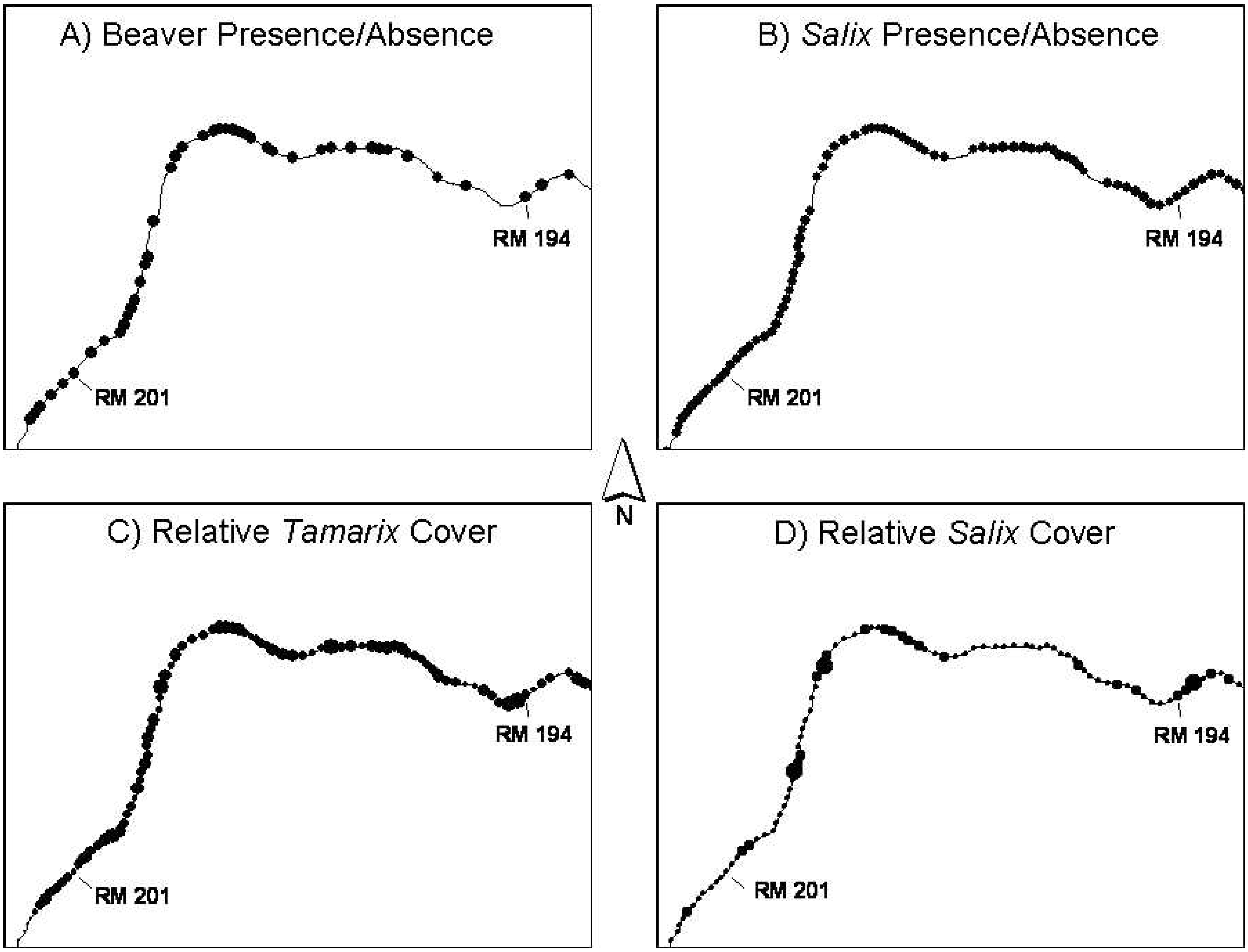


Figure 2. Occurrence of A) beaver and B) *Salix* and relative cover of C) *Tamarix* and D) *Salix* for a representative section of the Colorado River from Stevens River Mile 194–201. For (a) and (b) a circle indicates presence of beaver or *Salix*, respectively, in the 120-m radius plots centered on each 0.1 River Mile. For C) and D) larger sizes reflect greater values for the proportion of riparian surfaces covered by *Tamarix* and *Salix*.

were not considered in the analysis. The variables derived from the vegetation classification and used in this analysis are described in Table 1.

Three geomorphic variables were developed for use as covariates in the statistical analyses: geomorphic reach, rock resistivity, and sinuosity index (Table 1). Eleven geomorphic reaches were adopted from Schmidt and Graf (1990) and include the Permian Gorge, the Supai Gorge, the Redwall Gorge, the Marble Canyon, Furnace Flats, Upper Granite Gorge, The Aisles, Middle Granite Gorge, Muav Gorge, Lower Canyon Reach, and Lower Granite Gorge (Figure 1). In addition, we considered three levels of rock resistivity (low, moderate, high) as interpreted from major geologic formations at river level between Lees Ferry and Phantom Ranch (Ruffner 1983). High resistivity reaches tend to have more constrained river channels, less riparian vegetation, and rocky banks because the bedrock is not easily eroded. A river sinuosity index was calculated as the ratio of channel length to Euclidean distance for each circular plot, where distances were calculated from 0.5 RM above to 0.5 RM below each focal 0.1 RM point. All spatial variables were extracted from the 120-m buffer polygons in ArcGIS and exported to S-Plus software for statistical analysis.

### Statistical Analysis

The standard chi-square test, ANOVA analysis, and Bonferroni multiple comparisons tests were used to test whether occurrence or mean cover of the three taxa varied according to geomorphic river reach or rock resistivity class. Contingency table analyses were used to test for association among beaver occurrence, *Salix* occurrence (Figure 2b), and the two reach type variables (geomorphic reach and rock resistivity). *Tamarix* occurrence (presence-absence) was not analyzed further because *Tamarix* was nearly ubiquitous along the river corridor. The spatial association between beavers and *Salix* was assessed using contingency table analysis, for the entire river corridor as well as individually within rock resistivity classes. A chi-square test was used for bivariate contingency tables, and the Mantel-Haenszel chi-square test (Legendre and Legendre 1998) was used to test for bivariate associations (e.g., *Salix* and beaver occurrence) after accounting for a third categorical covariate (e.g., rock resistivity class).

Nested multiple linear regression models were used to test whether beaver occurrence significantly predicted the proportion of riparian surface area covered by *Salix* and *Tamarix* (Figures 2c, d), after accounting for the environmental covariates of geomorphic reach, river sinuosity, riparian surface area, and proportion of riparian shrub cover (Table 1). This analysis allowed us to determine the relative importance of beaver presence to *Salix* and *Tamarix* distribution and abundance after removing the correlation attributed to their shared environments. *Salix* and *Tamarix* cover values were first transformed using the natural logarithm to achieve more normal distributions. Multicollinearity among predictor variables was low. Rock resistivity was not included in regression models because this variable was not available for the entire river corridor. Akaike's Information Criterion (AIC) was used to rank the effectiveness of alternative covariate models for fitting the data, given the number of parameters included. Models were compared on the basis of the ΔAIC, or the difference in AIC between the model with smallest AIC value and the current model, and Akaike weights ($w_i$), where the weights of all models considered are constrained to sum to unity. Thus, for AIC differing by at least 2, the most parsimonious model was that with the lower AIC value (Burnham and Anderson 1998). A drop-in-deviance test (Ramsey and Schafer 2002) was then used to test whether addition of the "beaver" variable to the more parsimonious covariate model significantly improved model fit.

A second-order spatial point pattern analysis technique (Ripley's K) was applied to the distributions of *Salix* and beaver observations (Getis and Boots 1978). Each presence of either species at a 0.1 RM plot (with the 120-m radius applied for *Salix*) was extracted as a point observation, and then analyzed by plotting Ripley's K functions with a 95% confidence envelope indicating the k-function

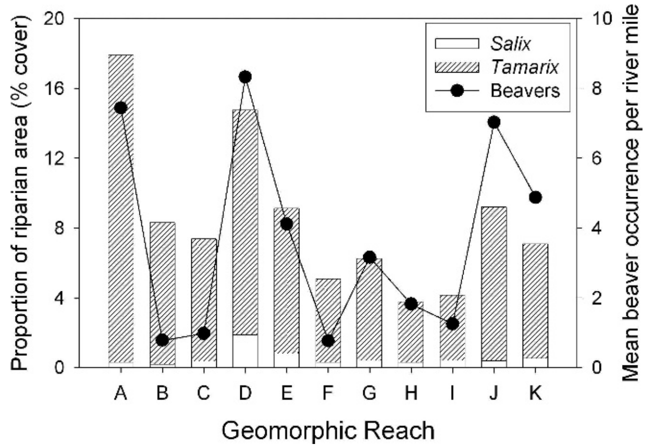


Figure 3. The proportion of riparian surfaces covered by *Tamarix* and *Salix* and the number of beaver occurrences divided by the length of each geomorphic reach in river miles. One occurrence indicates that there was some sign of beaver activity during one of the years (1999–2003) of beaver surveys. The reach abbreviations are: (A) Permian Gorge, (B) Supai Gorge, (C) Redwall Gorge, (D) Marble Canyon, (E) Furnace Flats, (F) Upper Granite Gorge, (G) The Aisles, (H) Middle Granite Gorge, (I) Muav Gorge, (J) Lower Canyon, and (K) Lower Granite Gorge.

for completely spatially random (CSR) data. In this manner, distributions can be described as clustered, random, or uniform over a range of spatial scales. The Ripley's K analysis allowed us to further investigate the spatial patterns of beaver and willow occurrence.

## RESULTS

### Abundance and Distribution of *Tamarix* and *Salix* on the Colorado River

*Tamarix* occurred at 2,265 of 2,274 (99.6%) plots, and *Salix* occupied 1,796 of 2,274 (79%) plots. These frequency rates were high because occupancy was assessed at a coarse spatial scale. Greater differences between the two species were apparent for the proportion of riparian surface area covered (Figure 3). *Tamarix* dominated an average of 7.8% (95% CI: 7.4–8.1%) of riparian area (including rock and unvegetated surfaces) across all plots, while the cover of *Salix* was an order of magnitude lower, with a mean of only 0.52% (95% CI: 0.44%–0.60%).

*Salix* occurrence was not independent of geomorphic river reach ($\chi^2 = 183.16$, df = 11, $p < 0.001$), with *Salix* species occurring more commonly in some reaches than in others. *Salix* presence/absence varied according to resistivity of the rock formation at river level ($\chi^2 = 71.90$, df = 2, $p < 0.001$), with a higher proportion of *Salix* occurrences than expected in reaches of low and moderate resistivity.

Table 2. *A priori* candidate models explaining variation in *Salix* cover according to various combinations of geomorphic and vegetation variables (abbreviations defined in Table 1). K indicates the number of parameters plus one. Only candidate models with ΔAIC ≤ 10 are shown.

| VARIABLES | K | AIC | ΔAIC | AIC WEIGHT |
|---|---|---|---|---|
| GeoReach VegArea Sinuosity | 15 | 1908.4 | 0.0 | 0.86 |
| GeoReach VegArea | 14 | 1912.2 | 3.8 | 0.14 |

Similarly, mean *Salix* cover differed across geomorphic river reach types ($F_{11,\ 2262} = 54.16$, $p < 0.001$) and rock resistivity classes ($F_{2,\ 855} = 97.50$, $p < 0.001$). *Salix* cover was greatest in reaches of moderate resistivity (mean = 1.42%), intermediate in reaches of low resistivity (mean = 1.07%), and lowest in reaches of high resistivity (mean = 0.29%). *Tamarix* cover also varied according to the eleven geomorphic reaches considered ($F_{11,\ 2262} = 49.70$, $p < 0.001$) (Figure 3), as well as by rock resistivity class ($F_{2,\ 855} = 9.02$, $p < 0.001$). *Tamarix* cover was greatest in reaches of moderate resistivity (mean = 12.84%), but did not differ significantly between reaches of low and high resistivity (mean = 9.84% and 8.98%, respectively).

### Distribution of Beavers along the Colorado River

Between 1999 and 2003, observations of beavers or their sign were reported for 444 of 2,274 (19.4%) plots. Of the 444 observations, 278 plots (63%) had recorded beaver observations for only a single year, 117 (26%) had beavers recorded for two years, 36 (8%) for three years, 11 (2.5%) for four years, and only two (0.5%) for all five years. Beaver presence/absence was not independent of geomorphic river reach ($\chi^2 = 228.38$, df = 11, $p < 0.001$) (Figure 3). Beaver occurrence also varied according to rock formation resistivity ($\chi^2 = 61.72$, df = 2, $p < 0.001$), with a higher proportion of beaver occurrences than expected in reaches of low and moderate resistivity.

### Associations among Beaver, *Tamarix*, and *Salix* Occurrence and Abundance

Considering all 2,274 plots in the study, beaver and *Salix* occurrence were not independent ($\chi^2 = 27.18$, df = 1, $p < 0.001$). *Salix* was present in 88% of plots where beavers occurred, even though beavers occurred only in approximately 20% of plots. The association between *Salix* and beaver occurrence was significant even when the effect of geomorphic river reach was accounted for (Mantel-Haenszel $\chi^2 = 7.186$, df = 1, $p < 0.001$). However, there was no significant association between *Salix* and beaver occurrence after accounting for the effect of rock resistivity (Mantel-Haenszel $\chi^2 = 0.1244$, df = 1, $p = 0.724$). Individual chi-square analyses conducted for each of the three rock resistivity classes also found that *Salix* and beaver occurrences were independently distributed within each rock resistivity unit.

The most parsimonious covariate model for *Salix* cover included the following variables: GeoReach (effect varied depending upon reach), VegArea (negative effect), and Sinuosity (positive effect) (Table 2). It appears from the model comparisons that, of all the variables, GeoReach has the greatest explanatory power for predicting *Salix* cover (Table 2). The presence/absence of beavers slightly improved this model (drop-in-deviance = 2.74, df = 1, $p = 0.13$). After holding the three covariates constant, *Salix* cover increased by 1.1% on sites where beavers were present (95% CI = 1.05–1.14). The only parsimonious covariate model for *Tamarix* (ΔAIC ≤ 10) included the following variables: GeoReach (effect varied depending upon reach), VegArea (negative effect), and Sinuosity (negative effect). The presence/absence of beavers significantly improved this model (drop-in-deviance = 12.34, df = 1, $p < 0.001$). On plots where beavers were present, after holding all covariates constant, *Tamarix* cover was on average 1.34% greater (95% CI = 1.24–1.46). This is an increase of 18% of the mean tamarisk cover value (7.8%).

The dispersion pattern of beaver and *Salix* occurrences was aggregated across all spatial scales (Figure 4). The Ripley's k-functions rapidly rise above the confidence envelope for complete spatial randomness, indicating clustered spatial patterns. The beaver k-function shows more intense aggregation over shorter distances, as is expected for the species which is rarer and less diffuse in its distribution.

## DISCUSSION

### Spatial Relationships among Beavers, *Tamarix*, and *Salix*

Beavers, *Salix*, and *Tamarix* tend to co-occur in similar riparian habitat at coarse spatial scales. As also observed by Ruffner (1983), beavers and *Salix*

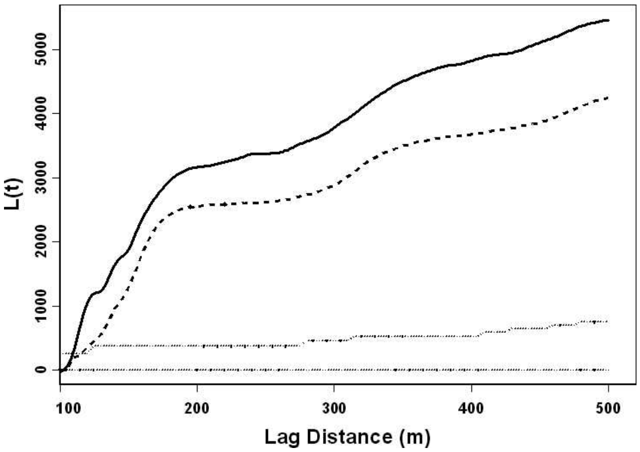


Figure 4. Ripley's K-function for beaver (thick solid line) and *Salix* (thick dashed line) across lag distances from 100–500 meters. The x-axis starts at a lag distance of 100 m because the closest observations are approximately that far apart. The thin dashed lines at the bottom of the graph show the confidence envelope expected for a spatially random distribution. The lines are consistently above the confidence envelope, indicating a clumped distribution.

occur more frequently in reaches of low and moderate resistivity. Such reaches are more likely to have greater channel width, greater sinuosity (more meandering channel), and more extensive terraces for riparian vegetation to establish than high-resistivity reaches (Howard and Dolan 1981). *Tamarix* is the dominant woody species along the Grand Canyon section of the Colorado River. Although its presence at coarse spatial scales is nearly ubiquitous, there is considerable variation in cover of *Tamarix* at finer spatial scales. *Tamarix* cover is greatest on straighter sections of river channel (cliffs and narrow channel margins) where other riparian shrubs cannot establish. *Salix* and many other riparian shrub species (*Baccharis*, *Pluchea*) are more likely to dominate where channels are meandering and geomorphic structures are complex, allowing for formation of marsh habitats and multiple terraces with a mixture of coarse and fine substrates. *Tamarix* absolute cover is also high in such settings. However, this species is dominant on rocky cliffs in narrow gorges likely because of its high drought tolerance relative to native riparian shrubs (Smith et al. 1998).

After the variation associated with geomorphic reach was accounted for, the positive association of beavers and *Salix* was still significant, suggesting that both taxa selected for similar habitat features at spatial scales finer than the geomorphic reach. However, the ecological amplitude for beavers along the river corridor appears to be more limited than that for *Salix*, resulting in a more clustered distribution (Figure 4). Once the occurrence of the two species in low resistivity rock types was accounted for, *Salix* presence was independent of beaver distribution. However, beaver presence was slightly positively associated with *Salix* cover. Beavers and *Salix* may occupy similar habitats at spatial scales finer than 4.52 ha, or beavers may prefer habitats with greater *Salix* cover. These results are consistent with the idea that *Salix* is a staple food for beavers. This association among the two species does not support the hypothesis that beavers negatively influence *Salix* cover along the Grand Canyon river corridor.

The cover of *Tamarix* was also greatest in 4.52-ha plots where beavers were present, after accounting for geomorphic covariates. This effect was highly significant and greater than the effect of beavers on *Salix* cover. This indicates either that *Tamarix* and beavers occupy similar habitats even at spatial scales finer than 4.52 ha, that beavers prefer habitats with high *Tamarix* cover, or that beavers promote *Tamarix* dominance through selective herbivory and use of competing riparian woody species. Beavers have likely occupied the same sites over the past few decades, given that most optimal beaver sites have been occupied continuously since approximately 15 years following construction of the Glen Canyon Dam (Ruffner 1983). Riparian plant communities can shift rapidly under pressure from intense, selective herbivory because plant community composition depends largely upon initial successional response to frequent, episodic disturbance. For instance, cattle grazing of *Populus* and *Salix* in unregulated riparian habitat indirectly increases *Tamarix* abundance (Stromberg et al. 2007). The hypothesis that beaver herbivory contributes to *Tamarix* dominance is consistent with our results. Beaver occurrence may facilitate *Tamarix* dominance at the scale of 4.52-ha plots.

## Recommendations for Further Research and Management

The effects of beaver activities on riparian vegetation composition should be investigated further using more mechanistic and detailed studies. More specifically, we recommend exploration of the relationship between beavers and *Tamarix* at fine scales. It would be advisable to initiate exclosure studies, where beaver-proof fences are constructed around patches of riparian vegetation in areas occupied by beavers as in Andersen and Cooper (2000). Beaver observations from exclosure studies do not provide a reliable indicator of population size, which requires more robust, intrusive methods involving trapping and mark-recapture statistics, or radio telemetry as in Breck et al. (2001). Accurate population estimates and spatial models of beaver distribution are essential for understanding effects of beaver herbivory. Finally, it is critical to consider beaver effects with respect to life history traits of riparian woody species and the interaction of these with managed flow regimes. Flow regulation may increase availability of favored species to beavers (Breck et al. 2003b), as well as dramatically alter riparian community composition apart from beaver effects (Stevens et al. 1995, Stromberg et al. 2007).

It is important to differentiate between bank-dwelling beaver and dam-building beaver strategies when considering the effects that beavers have on wetland communities. Dam-building beavers are considered ecosystem engineers because they increase landscape heterogeneity through creation of impoundments. Beaver ponds increase beta diversity of herbaceous species in the Adirondacks (Wright et al. 2002) and may shift competitive dynamics in favor of native shrubs. Beaver dams may also inhibit *Tamarix* growth due to the relative intolerance of *Tamarix* for inundation when compared with native *Salix* and *Populus* (Albert and Trimble 2000). The use of *Tamarix* for beaver dam construction in northwestern Colorado may have indirectly enhanced *Salix exigua* distribution and abundance (Baker and Hill 2003).

Dam-building beavers are often introduced to benefit native plants and wildlife in ecological restoration projects (Albert and Trimble 2000), but beaver populations are also controlled (e.g. removed to another habitat, fatally trapped) to reduce their negative influence on rare, native shrubs and trees (Longcore et al. 2007). These treatments obviously contradict each other. Perhaps much of the confusion concerning the effects of beavers on wetland health arises due to the different activities of dam-building and bank-dwelling beavers. Beaver dams may benefit restoration projects that aim for greater diversity, while selective foraging of beavers may favor non-native plant species. The potential for divergent ecological effects of beavers that construct ponds and bank-dwelling beavers should be taken into account in planning for wetland management.

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