

TAMARISK, WILLOW AND BEAVER IN GRAND CANYON
NATIONAL PARK:
A PRELIMINARY LANDSCAPE-SCALE ANALYSIS

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SUMMARY

Beaver have been increasing in Grand Canyon National Park since construction of the Glen Canyon Dam in 1963 resulted in flow stabilization and enhanced development of riparian vegetation. The native coyote willow is a staple food species of beaver, leading to the concern that overabundant beaver populations may lead to an increase in exotic tamarisk (*Tamarix ramosissima*) over native riparian plant species. A preliminary spatial analysis, using existing data sources, was conducted to assess whether beaver have influenced the relative distributions of willow and tamarisk. The investigation was considered preliminary because the data utilized were either still at a preliminary stage (vegetation database) or were spatially imprecise (beaver database).

Beaver, willow and tamarisk co-occur at the broadest spatial scales because they prefer similar riparian habitat, particularly geomorphic reaches of low and moderate resistivity. However, the occurrence and relative cover of willow were independent of beaver distribution, once the preferences of the two species for particular reaches were accounted for. Willow is limited to geomorphic settings with greater sinuosity and greater availability of vegetated terraces, while tamarisk also occurs on straighter sections of river channel (cliffs, channel margins) where it dominates the woody species composition. The relative cover of tamarisk was greatest for sites where beaver were present, after accounting for covariates representing river geomorphology. This indicates either that tamarisk and beaver prefer similar habitats even at fine spatial scales, or that beaver contribute to tamarisk dominance through selective use of its native woody competitors.

Given these preliminary results, the hypothesis that beaver herbivory contributes to tamarisk dominance should be considered further, through more mechanistic studies of beaver foraging processes and long-term plant community response. The Park should act promptly to establish a network of monitoring plots for beaver effects, including exclosure studies and appropriate controls, and to actively protect the few remaining groves of large native trees along the river corridor.

INTRODUCTION

Selective foraging and utilization of woody materials by the North American beaver (*Castor canadensis*) can exert profound effects on the species composition and structure of plant communities (Rosell et al. 2005), in many cases shifting community structure toward non-preferred species (Johnston and Naiman 1990). Beaver have increased in Grand Canyon National Park (GCNP) since construction of the Glen Canyon Dam in 1963. With enhanced development of riparian vegetation following flow stabilization, beaver have become well established (Breck and Kellett 2000). Coyote willow is a staple food species, leading to the concern that overabundant beaver populations in GCNP may lead to an increase in exotic tamarisk (*Tamarix ramosissima*) over native riparian plant species. Beaver facilitation of tamarisk and Russian olive, due to selective felling of cottonwood, has been observed along several rivers in eastern Montana (Lesica and Miles 2004). Beaver have greatly reduced the abundance of cottonwood along the Green and Yampa Rivers of the upper Colorado River Basin (Breck et al. 2003a). However, it is unknown whether beaver herbivory along the lower Colorado River has contributed to tamarisk invasion. This question is an important one, as evidenced by a recent proposal by the Hualapai Tribe to conserve native riparian vegetation by trapping 50% of the beaver population in the Lower Grand Canyon (E. Leslie, National Park Service, personal communication, 2005).

The purpose of this study was to use spatial pattern analysis to assess whether beaver have influenced the relative distributions and abundances of willow and tamarisk in GCNP. Existing data sources were used to conduct a preliminary analysis of spatial correlations among beaver occurrence and riparian vegetation. Specifically, beaver occurrence data at the spatial resolution of 0.1 river mile units were compared with tamarisk and willow occurrence data, derived from a remote sensing classification and aggregated to the same spatial resolution. Since beaver and willow are expected to occur in similar habitats in GCNP (Ruffner 1983), a negative association between beaver and willow over fine spatial scales would suggest that beaver have had a significant effect on riparian plant community composition. A positive association would not necessarily indicate a causal relationship, but only that beaver and willow select similar habitats.

METHODS

GIS Data Layers

There were two primary spatial data layers used in this study, a point coverage of beaver distribution¹ and a vegetation map² developed by the Grand Canyon Monitoring and Research Center (GCMRC) from 2002 digital infrared aerial photography. 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 (Stevens RM) units. The 2274, 0.1 RM units between Lees Ferry (RM 0) and RM 238.5, but 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 both beaver and vegetation data sets.

¹ The beaver database was obtained from the Science Center at Grand Canyon National Park.

² The vegetation classification was obtained from B. Ralston of the Grand Canyon Monitoring and Research Center. At the date provided (1/15/06), this map was considered to be preliminary.

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, Stevens 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). However, many of these variables were recorded inconsistently. The bank of the river was not recorded for 113 (12%) of observations. Whether the beaver observation was active or inactive was not recorded for 366 (39%) of observations. The density of beaver observations was not recorded for 183 (20%) of observations, and has an inconsistent interpretation in that sometimes it refers to the number of animals, and at other times to the number of signs (tracks, cuttings, etc.). In order to achieve consistency in the analysis, we therefore simplified the beaver data set by considering only the presence or absence of beaver sign at each Stevens 0.1 river mile (Table 1; Fig. 1a).³

The vegetation classification was provided by GCMRC in a preliminary stage, not having been fully ground-truthed. Therefore, results from this study need also to be considered preliminary. The classification was derived from airborne digital imagery acquired between May 25 and June 3, 2002, when dam release was approximately 8,000 cfs. Spatial resolution was 22 cm, and subsequently aggregated to 44 cm for the four color bands, including a near-infrared band. The vegetation data layer classified vegetation at both an aggregated (alliance) level and a single-species level, the latter of which was deemed to be least accurate. However, this analysis depended upon separating willow and tamarisk from other species, so we utilized the single-species level only. *Salix exigua* and *Salix gooddingii* (Gooding's willow) were combined into a common class for *Salix* spp., following a river reconnaissance trip which suggested that the classification may not accurately distinguish the two species. Variables derived from the vegetation classification and used in this analysis are described in Table 1. Each observation describes the vegetation condition for a circular area of 120-m (394-ft) radius, comprising 4.52 ha, centered on each 0.1 RM site. Circles of different radii were compared, and the 120-m distance was chosen since it minimized overlap with neighboring circular buffers, while capturing all vegetation within 60-m from water, the maximum foraging distance reported for beaver (Rosell et al. 2005).

Three geomorphic variables were developed for use as covariates in the statistical analyses: geomorphic reach, rock resistivity, and sinuosity index (Table 1). Twelve geomorphic reaches were adopted from Schmidt and Graf (1990) and include the Glen Canyon Reach, 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. These reaches differ fundamentally in their bedrock and landform characteristics. 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). The

³ See Discussion section for suggestions regarding development of a more effective database for future monitoring and research of beaver distribution and effects in the Grand Canyon.

Shinarump, Kaibab, Toroweap, Coconino, Supai, Redwall, and Granite/Schist formations were classified as having high resistivity. The Hermit, Bright Angel, and Grand Canyon Series formations were classified as having low resistivity. The Muav and Tapeats formations were classified as having moderate resistivity. Finally, a river sinuosity index was calculated as a continuous variable for each 0.1 RM site, as ratio of channel length to Euclidean distance, where distances are calculated from 0.5 RM above, to 0.5 RM below, each focal 0.1 RM site. All spatial variables were intersected with the 120-m buffer polygons in the ArcGIS environment, and exported as a single table into S-Plus software for statistical analysis.

Statistical Analysis

The proportion of 120-m radius sites occupied by beaver, willow and tamarisk was reported for discrete geomorphic and geological reach units. 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, willow occurrence (Fig. 1b), and each of the two reach type variables. Tamarisk occurrence (presence/absence) was not analyzed further because tamarisk was nearly ubiquitous along the river corridor (present at over 99% of sites). The spatial association between beaver and willow was assessed using contingency table analysis, for the entire river corridor as well as individually for rock resistivity classes. The standard chi-square test was used for bivariate contingency tables, and the Mantel-Haenszel chi-square test was used to test for bivariate associations (e.g. willow 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 willow and tamarisk relative areal cover (Figs. 1c, d), after accounting for the environmental covariates of geomorphic reach, river sinuosity, riparian surface area, and proportion of riparian shrub cover (Table 1). Proportion of riparian shrub cover was used to predict willow cover only, since the high correlation of this variable with tamarisk cover was not considered meaningful for predicting tamarisk, due to the dominance of this species. Rock resistivity was not included in regression models because this variable was not available for the entire river corridor. Willow and tamarisk cover values were first transformed using the natural logarithm to achieve more Gaussian distributions. Cover values indicate “relative cover” or the proportion of area classified as this species, and indicate level of dominance rather than absolute cover. The 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 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 willow and beaver observations. Each presence of either species at a 0.1

RM site (with the 120-m radius applied for willow) was extracted as a point observation, and then analyzed by plotting Ripley's K functions along with a 95% confidence envelope indicating the k-function for completely spatially random (CSR) data. In this manner, distributions can be described as clustered, random, or uniform over a range of spatial scales.

RESULTS

Abundance and Distribution of Tamarisk and Willow Species on the Colorado River

Tamarisk was the dominant woody species along the Grand Canyon section of the River, according to the GCMRC preliminary vegetation classification. Tamarisk occurred at 2265 of 2274 (99.6%) sites. One reason this percentage was so great is that presence/absence was calculated for extensive areas (4.52 ha), increasing the probability that any given species will occur. Willow occurred at 1791 of 2274 sites, or 79%. Greater differences between the two species were apparent for areal relative cover. Tamarisk 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 relative cover of willow was an order of magnitude lower, with a mean of only 0.52% (95% CI: 0.44% - 0.60%).

Willow presence/absence was not independent of geomorphic river reach ($\chi^2 = 183.16$, d.f. = 11, $p < 0.001$), with willow species occurring more commonly in some reaches than in others (Table 2). Willow presence/absence also varied according to resistivity of the rock formation at river level ($\chi^2 = 71.90$, d.f. = 2, $p < 0.001$), with a higher proportion of willow occurrences than expected in reaches of low and moderate resistivity (Table 3). Similarly, mean willow cover differed across geomorphic river reach types ($F_{11, 2262} = 54.16$, $p < 0.001$) and rock resistivity classes ($F_{2, 855} = 97.50$, $p < 0.001$). Willow 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%; Table 4).

Tamarisk cover also varied according to the 12 geomorphic reaches considered ($F_{11, 2262} = 49.70$, $p < 0.001$), as well as by rock resistivity class ($F_{2, 855} = 9.02$, $p < 0.001$). Tamarisk 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 Beaver along the Colorado River

Between 1999 and 2003, observations of beaver or their sign were reported for 444 of 2274 (19.4%) 0.1-RM sites. Of the 444 observations, 278 sites (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 2 (0.5%) for all five years. It should be kept in mind that beaver sampling was *ad hoc* and inconsistent between sample periods, and that different years had different levels of sampling effort. Unfortunately, this data set cannot therefore be used to assess patch occupancy dynamics of beaver populations. Beaver presence/absence was not independent of geomorphic river reach ($\chi^2 = 228.38$, d.f. = 11, $p < 0.001$). Beaver were more likely to be present in Permian Gorge, Marble Canyon, and Lower Canyon Reach. Beaver were scarce in Supai Gorge, Redwall Gorge, Upper Granite Gorge, Middle Granite Gorge, and Muav Gorge (Table 5).

Beaver occurrence also varied according to rock formation resistivity ($\chi^2 = 61.72$, d.f. = 2, $p < 0.001$), with a higher proportion of beaver occurrences than expected in reaches of low and moderate resistivity (Table 6).

Associations among Beaver, Tamarisk and Willow Occurrence and Abundance

Considering all 2274, 0.1-RM sites in the study, beaver and willow occurrence were not independent ($\chi^2 = 27.18$, d.f. = 1, $p < 0.001$). Willow was present in 88% of sites where beaver occurred, even though beaver occurred only in approximately 20% of river units included in the study. Only 54 of the 2274 sites (2.4%) had beaver but apparently lacked willow. The association between willow and beaver occurrence was significant even when the effect of geomorphic river reach was accounted for (Mantel-Haenszel $\chi^2 = 7.186$, d.f. = 1, $p < 0.001$), suggesting that both taxa selected for similar habitat features at spatial scales finer than the geomorphic reach. However, there was no significant association between willow and beaver occurrence after accounting for the effect of rock resistivity (Mantel-Haenszel $\chi^2 = 0.1244$, d.f. = 1, $p = 0.724$). Individual chi-square analyses conducted for each of the three rock resistivity classes also found that willow and beaver occurrences were independently distributed within each rock resistivity unit.

Multiple linear regression models were used to predict willow and tamarisk relative cover as a function of the environmental variables (“covariate model”), and then to assess whether the presence/absence of beaver improved model fit. The most parsimonious covariate model for willow cover included the following variables: GeoReach (effect varied depending upon reach), pRipShrub (positive effect), and Sinuosity (positive effect) (Table 7). The presence/absence of beaver did not significantly improve this model (drop-in-deviance = 1.56, d.f. = 1, $p = 0.212$). It appears from the model comparisons that, of all the variables, GeoReach has the greatest explanatory power for predicting willow cover (Table 7). The most parsimonious covariate model for tamarisk cover (Table 8) included the following variables: GeoReach (effect varied depending upon reach), VegArea (negative effect), and Sinuosity (negative effect). The presence/absence of beaver significantly improved this model (drop-in-deviance = 12.34, d.f. = 1, $p < 0.001$), and there was a positive effect of beaver on mean tamarisk cover. On sites where beavers were present, after holding all covariates constant, tamarisk cover was on average 1.4 % greater. This represents an increase of approximately 18% of the mean tamarisk cover value (7.8%).

Distribution of both beaver and willow occurrences was aggregated across all spatial scales (Fig. 2). The flat portion of the Ripley’s k function plot indicates only that the closest observations were at approximately 110-m apart. The k-functions then 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. The ecological amplitude for beaver along the river corridor appears to be more limited than that for willow, resulting in a more clustered distribution.

DISCUSSION

Spatial Relationships Among Beaver, Tamarisk and Willow

This investigation must be considered preliminary because the data utilized are either still at a preliminary stage (vegetation database) or are spatially imprecise (beaver database). It is challenging to infer beaver effects on riparian vegetation purely from spatial patterns of distribution. Such an analysis would require more precise spatial data for beaver, including consistent observations of beaver activity patterns, diet selection, and level of use. Nonetheless, some general conclusions can be made. The three species tend to co-occur because they all prefer similar riparian habitat. As also observed by Ruffner (1983), beaver and willow 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 (Howard and Dolan 1981). Willow occurrence and relative cover were independent of beaver distribution, once the reach-level preference of the two species for low resistivity rock type was accounted for. This neutral association among the two species neither supports nor conflicts with the hypothesis that beaver may be having a negative influence on willow cover along the Grand Canyon river corridor.

Tamarisk currently dominates riparian habitats along the river corridor. Although its presence at coarse spatial scales is nearly ubiquitous, there is considerable variation in relative cover of tamarisk at finer spatial scales. While willow prefers geomorphic settings with greater sinuosity and a greater availability of vegetated terraces, tamarisk relative cover is greatest on straighter sections of river channel where a lower proportion of land is suitable for development of riparian vegetation. Willow and many other important riparian shrub species (*Baccharis*, arrowweed), 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. Tamarisk absolute cover is also high in such settings. However, this species is able to establish and survive even on rocky cliffs in narrow gorges, and so has its highest relative cover on straight channel sections (cliffs and narrow channel margins) where other riparian shrub species cannot establish.

The relative cover of tamarisk was greatest in sites where beaver were present, after accounting for geomorphological covariates. This indicates either that tamarisk and beaver prefer similar habitats even at fine spatial scales, or that beaver contribute to tamarisk dominance through selective herbivory and use of other riparian woody species. Beaver have likely occupied the same sites over the past few decades, since most optimal beaver sites appear to be occupied continuously since approximately 15 years following construction of the Glen Canyon Dam (Ruffner 1983). Prior to dam construction beaver were scarce along the river corridor (Breck and Kellett 2000). 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. Although beaver will use a variety of foods including willow, tamarisk, mesquite, catclaw acacia, cottonwood, and cattail, coyote willow appears to be their primary food source in Grand Canyon (Elaine Leslie, National Park Service, personal communication, 2005). The hypothesis that beaver herbivory

contributes to tamarisk dominance is consistent with our preliminary results and should be considered further, using more mechanistic and detailed studies.

Recommendations for Management, Monitoring and Further Research

Effective science-based management depends upon having accurate information which is updated regularly. Understanding the effects of beaver activities on riparian vegetation composition requires extensive field sampling of vegetation in areas with varying levels of beaver use. It would be advisable to initiate exclosure studies, where beaver-proof fences are constructed around patches of riparian vegetation in areas occupied by beaver. As in Anderson and Cooper (2000), different exclosure types can be used to separate effects of medium-sized mammals (rabbit and beaver) from smaller and larger mammals. For a study on the Green and Yampa rivers, these authors used hardware cloth to exclude small mammals (rodents), hardware cloth or 1.2-m tall ranch wire to exclude medium-sized mammals including beaver, and 2.5-m tall ranch wire fences to exclude large herbivores (ungulates). Ideally, study sites would span different riparian environments and have different initial levels of relative dominance by tamarisk and willow. It is critical that (1) sites be inventoried prior to installation of exclosures (baseline data), and (2) that appropriate control areas without exclosures are also monitored. Monitoring may need to occur on an annual basis for several years before any beaver herbivory effects become apparent. Beaver effects on initial establishment following disturbance may not be evident until a significant flood event has occurred.

In addition to experimental approaches, much could be gained from further descriptive studies, if the quality of spatial databases was improved. More detailed studies of the distribution of riparian woody species are needed, which link field surveys with GIS data layers from remote sensing classifications. More consistent, reliable data describing beaver distribution are also needed. We recommend that the Park develops a single beaver observation protocol that observers on all research river trips can adhere to, so that data will be recorded consistently from trip to trip and year to year. GPS locations should be reported, as opposed to 0.1 river miles, such that observations will be more spatially precise. It is important to specify the nature of the observation; a swimming beaver may merely be dispersing through poor habitat, while an active beaver lodge or trail is more likely to indicate an occupied territory. Beaver observations as such do not provide a reliable indicator of population size, which requires more robust, intrusive methods involving trapping and mark-recapture statistics, or radio telemetry. An accurate population estimate and spatial model of beaver distribution are essential for understanding effects of beaver herbivory.

Surveys of beaver herbivory would also provide essential information. Plots with willow and tamarisk could be randomly selected and monitored over time for number of available live stems and cut stems. Cut stems could be marked to avoid double-counting, such that season or year of cutting could be unambiguously determined, as in Breck et al. (2003b). The proximate effects of beaver herbivory are likely manifested at a spatial grain finer than the 0.1 river mile scale used in this study, and it is imperative that future research quantifies beaver effects at the level of individual plants, for a random sample of field plots from which results can be generalized. This effort would benefit from an initial study of beaver activity patterns (home range size, seasonal and diel activity budgets) to determine the spatial extent of beaver effects at different seasons and times of day. A

study of Great Plains rivers in eastern Montana found signs of beaver foraging at 90% of plots within 50m of the river channel, but at only 21% of plots at greater distances (Lesica and Miles 2004). 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 beaver (Breck et al. 2003b), as well as dramatically alter riparian community composition apart from beaver effects (Stevens et al. 1995).

Even in the absence of scientifically robust information concerning beaver effects, the Park should consider certain management actions which, while of localized scope, would greatly benefit riparian vegetation communities and habitats along the Colorado River corridor. In particular, Park management must act quickly if the last stands of Gooding's willow are to be preserved in the face of intense beaver use. Gooding's willow grows into a large tree that can form solid groves along the riparian corridor, creating a unique and valuable habitat type. Unfortunately, beaver cut the Gooding's willow stands at Buck Farm and Saddle in the mid-1980s, and the sole extant stand at Cardenas Creek is in great jeopardy of also being converted to tamarisk and other shrub species of smaller stature. Wire cages or mesh around tree boles could be used to protect this stand, as is commonly done elsewhere for cottonwoods and other tree species where beaver pressure is intense. The minor aesthetic detriment of the wire mesh would pale in comparison to the ecological, aesthetic, and recreational values gained from preserving the last of the major Gooding's willow stands in the Canyon. More generally, the potential role of beaver in keeping the larger native tree species (cottonwoods, Gooding's willow, box-elder, ash species) from becoming canopy dominants can be quite significant and demands further study. Establishment of larger trees could eventually suppress tamarisk and other exotic species in the understory and subcanopy, as well as provide habitat for songbirds and valuable shade for recreational campsites.

The preliminary analysis described in this report cannot objectively determine the significance of beaver impacts for riparian vegetation community composition, due to data limitations as well as the coarse spatial resolution considered. However, results at least suggest the hypothesis that beaver occurrence may facilitate tamarisk dominance at the scale of 4.5-ha plots. Given the well-documented, dramatic effects of large beaver populations on riparian vegetation elsewhere, it would be prudent for the Park to encourage research on this topic, and to establish a network of monitoring plots with an appropriate scientific design and a mechanism for long-term funding.

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TABLES

Table 1. Spatial variables used in the analysis. All vegetation variables are derived from 2002 aerial photography according to the GCMRC vegetation classification. See text for further explanation. “RM” = Stevens river mile.

<i>Ecological Variable</i>	<i>Abbreviation</i>	<i>Description</i>
Beaver Occurrence	BEAV	Presence/Absence at each 0.1 RM, pooled for 1999 - 2003
Willow Occurrence	paSALIX	Presence/Absence of <i>Salix</i> spp. in a 120-m radius circle centered on each 0.1 RM, as classified from 2002 aerial photography.
Tamarisk Occurrence	paTARA	Presence/Absence of <i>Tamarix</i> spp. in a 120-m radius circle centered on each 0.1 RM, as classified from 2002 aerial photography.
Willow Cover	cvSALIX	Proportion of riparian surfaces in 2002 covered by <i>Salix</i> spp.
Tamarisk Cover	cvTARA	Proportion of riparian surfaces in 2002 covered by <i>Tamarix</i> spp.
Riparian Surface Area	VegArea	Area within the 0.1 RM site (4.52 ha) with riparian surfaces where vegetation is or could be established (m ²)
Proportion of Riparian Shrub Cover	pRipShrub	Proportion of the 0.1 RM site (4.52 ha) dominated by riparian shrub species (i.e. <i>Tamarisk</i> spp., <i>Tessaria</i> spp., <i>Baccharis</i> spp., and <i>Salix</i> spp.)
<i>Geomorphic Variable</i>	<i>Abbreviation</i>	<i>Description</i>
Geomorphic Reach	GeoReach	The 12 bedrock- and landform-defined geomorphic reaches of the Grand Canyon excluding Upper Lake Mead, 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 site.

Table 2. Occurrence of willow across the 12 geomorphic river reaches. Values in the upper row of each cell are actual counts of presence or absence across all 0.1 RM sample units within each reach. Values in parentheses and italics represent the expected value for willow presence or absence, under the assumption of independent distribution with regard to river reach.

REACH¹	1	2	3	4	5	6	7	8	9	10	11	12	Sum
Willow Present	5 (5)	68 (83)	55 (90)	127 (136)	214 (176)	142 (120)	202 (222)	72 (68)	97 (113)	142 (157)	463 (424)	204 (198)	1791
Willow Absent	1 (1)	37 (22)	59 (24)	46 (37)	9 (47)	10 (32)	80 (60)	14 (18)	47 (31)	57 (42)	75 (114)	48 (54)	483
Sum	6	105	114	173	223	152	282	86	144	199	538	252	2274

¹ Geomorphic river reaches are coded as follows: (1) Glen Canyon Reach, (2) Permian Gorge, (3) Supai Gorge, (4) Redwall Gorge, (5) Marble Canyon, (6) Furnace Flats, (7) Upper Granite Gorge, (8) The Aisles, (9) Middle Granite Gorge, (10) Muav Gorge, (11) Lower Canyon Reach, and (12) Lower Granite Gorge.

Table 3. Occurrence of willow across the 3 rock resistivity classes. Values in the upper row of each cell are actual counts of presence or absence across all 0.1 RM sample units within each reach. Values in parentheses and italics represent the expected value for willow presence or absence, under the assumption of independent distribution with regard to river reach.

RESISTIVITY	LOW	MODERATE	HIGH	Sum
Willow Present	233 (213)	190 (160)	252 (301)	675
Willow Absent	38 (58)	14 (44)	131 (82)	183
Sum	271	204	383	858

Table 4. Willow and tamarisk cover by geomorphic river reach and rock resistivity class. Values are in percentage units. The upper number in each cell gives the mean for that species in that reach class, while the lower (italicized) number gives the half-width of the 95% confidence interval. Geomorphic reach numbers (columns 1 – 12) are coded as for Table 2. Rock resistivity classes are coded as “L” = Low Resistivity, “M” = Moderate Resistivity, and “H” = High Resistivity.

Species / Reach	1	2	3	4	5	6	7	8	9	10	11	12	L	M	H	MEAN
Willow	2.00 3.60	0.30 0.09	0.19 0.08	0.38 0.09	1.87 0.26	0.81 0.19	0.30 0.05	0.41 0.10	0.30 0.08	0.41 0.11	0.40 0.05	0.54 0.06	1.07 0.20	1.42 0.22	0.29 0.07	0.52 0.08
Tamarisk	11.41 11.06	17.59 1.96	8.11 1.06	6.98 1.12	12.87 1.17	8.31 1.12	4.77 0.54	5.83 1.15	3.47 0.63	3.73 0.58	8.80 0.68	6.54 0.77	9.84 0.24	12.84 1.41	8.98 0.80	7.82 0.39

Table 5. Occurrence of beaver across the 12 geomorphic river reaches. Values in the upper row of each cell are actual counts of presence or absence across all 0.1 RM sample units within each reach. Values in parentheses and italics represent the expected value for beaver presence or absence, under the assumption of independent distribution with regard to river reach.

REACH¹	1	2	3	4	5	6	7	8	9	10	11	12	Sum
Beaver Present	2 <i>(1)</i>	38 <i>(21)</i>	6 <i>(22)</i>	13 <i>(34)</i>	83 <i>(44)</i>	33 <i>(30)</i>	12 <i>(55)</i>	11 <i>(17)</i>	12 <i>(28)</i>	13 <i>(39)</i>	174 <i>(105)</i>	47 <i>(49)</i>	444
Beaver Absent	4 <i>(5)</i>	67 <i>(84)</i>	108 <i>(92)</i>	160 <i>(139)</i>	140 <i>(179)</i>	119 <i>(122)</i>	270 <i>(227)</i>	75 <i>(69)</i>	132 <i>(116)</i>	186 <i>(160)</i>	364 <i>(433)</i>	205 <i>(203)</i>	1830
Sum	6	105	114	173	223	152	282	86	144	199	538	252	2274

¹ Geomorphic river reaches are coded as follows: (1) Glen Canyon Reach, (2) Permian Gorge, (3) Supai Gorge, (4) Redwall Gorge, (5) Marble Canyon, (6) Furnace Flats, (7) Upper Granite Gorge, (8) The Aisles, (9) Middle Granite Gorge, (10) Muav Gorge, (11) Lower Canyon Reach, and (12) Lower Granite Gorge.

Table 6. Occurrence of beaver across the 3 rock resistivity classes. Values in the upper row of each cell are actual counts of presence or absence across all 0.1 RM sample units within each reach. Values in parentheses and italics represent the expected value for beaver presence or absence, under the assumption of independent distribution with regard to river reach.

RESISTIVITY	LOW	MODERATE	HIGH	Sum
Beaver Present	72 <i>(56)</i>	70 <i>(42)</i>	34 <i>(79)</i>	176
Beaver Absent	199 <i>(215)</i>	134 <i>(162)</i>	349 <i>(304)</i>	682
Sum	271	204	383	858

Table 7. *A priori* candidate models explaining variation in willow cover according to various combinations of geomorphologic and vegetation variables (abbreviations defined in Table 1).

VARIABLES	K	AIC	Δ AIC	AIC WEIGHT
GeoReach pRipShrub Sinuosity	15	1842.3	0.0	0.48
GeoReach pRipShrub Sinuosity VegArea	16	1843.1	0.8	0.32
GeoReach pRipShrub	14	1845.0	2.7	0.12
GeoReach VegArea pRipShrub	15	1845.7	3.4	0.08
GeoReach Sinuosity VegArea	15	1925.7	83.4	0.00
GeoReach VegArea	14	1926.1	83.8	0.00
GeoReach Sinuosity	14	1928.8	86.5	0.00
GeoReach	13	1928.8	86.5	0.00
pRipShrub Sinuosity VegArea	5	2277.6	435.3	0.00
pRipShrub Sinuosity	4	2280.5	438.2	0.00
pRipShrub VegArea	4	2293.2	450.9	0.00
pRipShrub	3	2296.6	454.3	0.00
Sinuosity	3	2444.4	602.1	0.00
Sinuosity VegArea	4	2445.7	603.4	0.00
VegArea	3	2456.5	614.2	0.00

Table 8. *A priori* candidate models explaining variation in tamarisk cover according to various combinations of geomorphologic and vegetation variables (abbreviations defined in Table 1).

VARIABLES	K	AIC	ΔAIC	AIC WEIGHT
GeoReach Sinuosity VegArea	15	5117.1	0.0	1.00
GeoReach VegArea	14	5130.1	13.0	0.00
GeoReach Sinuosity	14	5341.8	224.8	0.00
GeoReach	13	5359.3	242.2	0.00
Sinuosity VegArea	4	5755.2	638.1	0.00
VegArea	3	5756.3	639.2	0.00
Sinuosity	3	5827.4	710.3	0.00

FIGURES

Figure 1. Occurrence of (a) beaver and (b) willow, and relative cover of (c) willow and (d) tamarisk, for a representative section of the Colorado River from approximately GCMRC River Mile 194 – 201. The location of Parashant Wash is shown. For (a) and (b) a green circle indicates presence of beaver or willow, respectively, in the 120-m radius circles centered on each 0.1 River Mile. For (c) and (d) relative willow and tamarisk cover, respectively, are scaled with larger sizes and darker hues reflecting greater values.

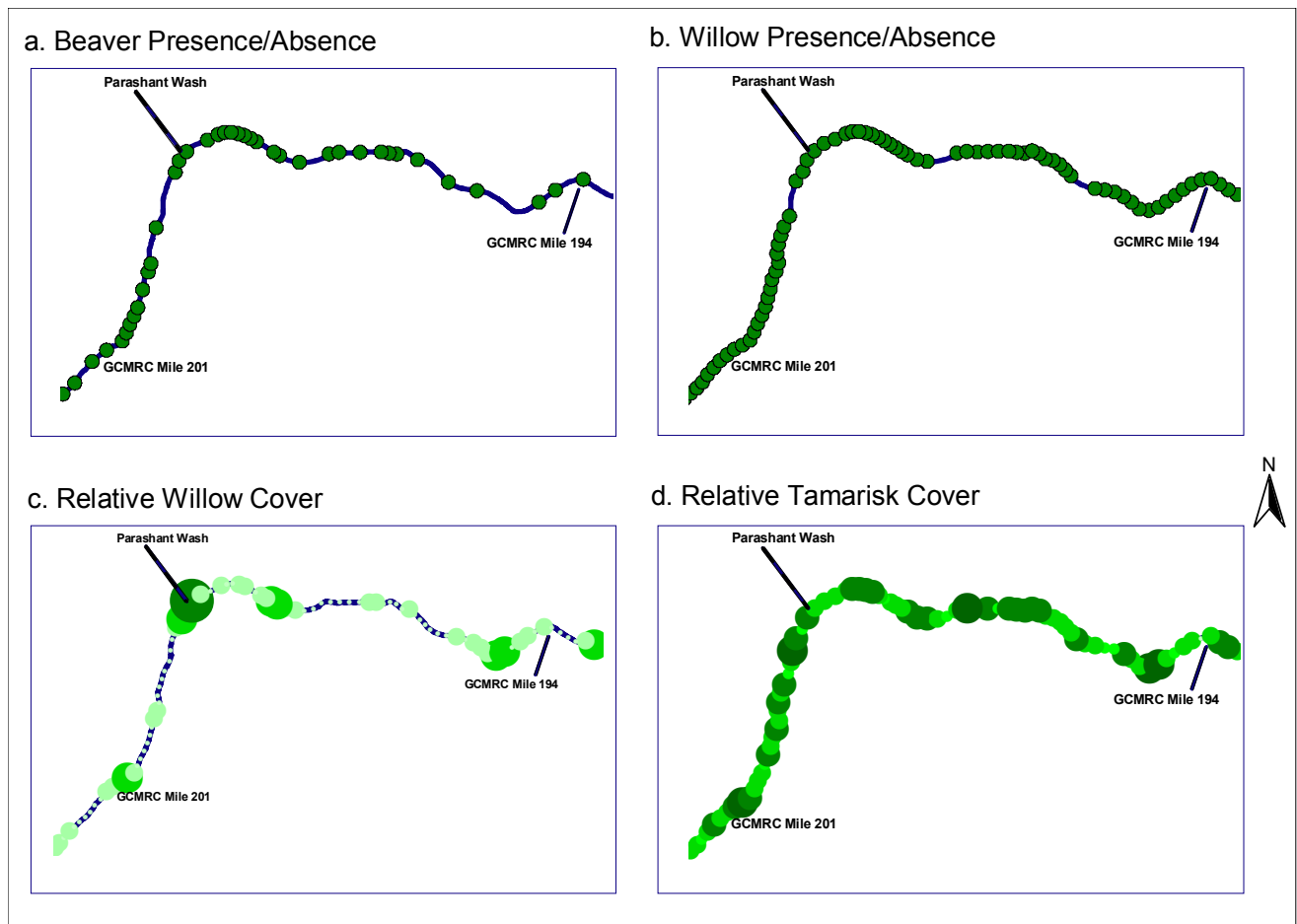
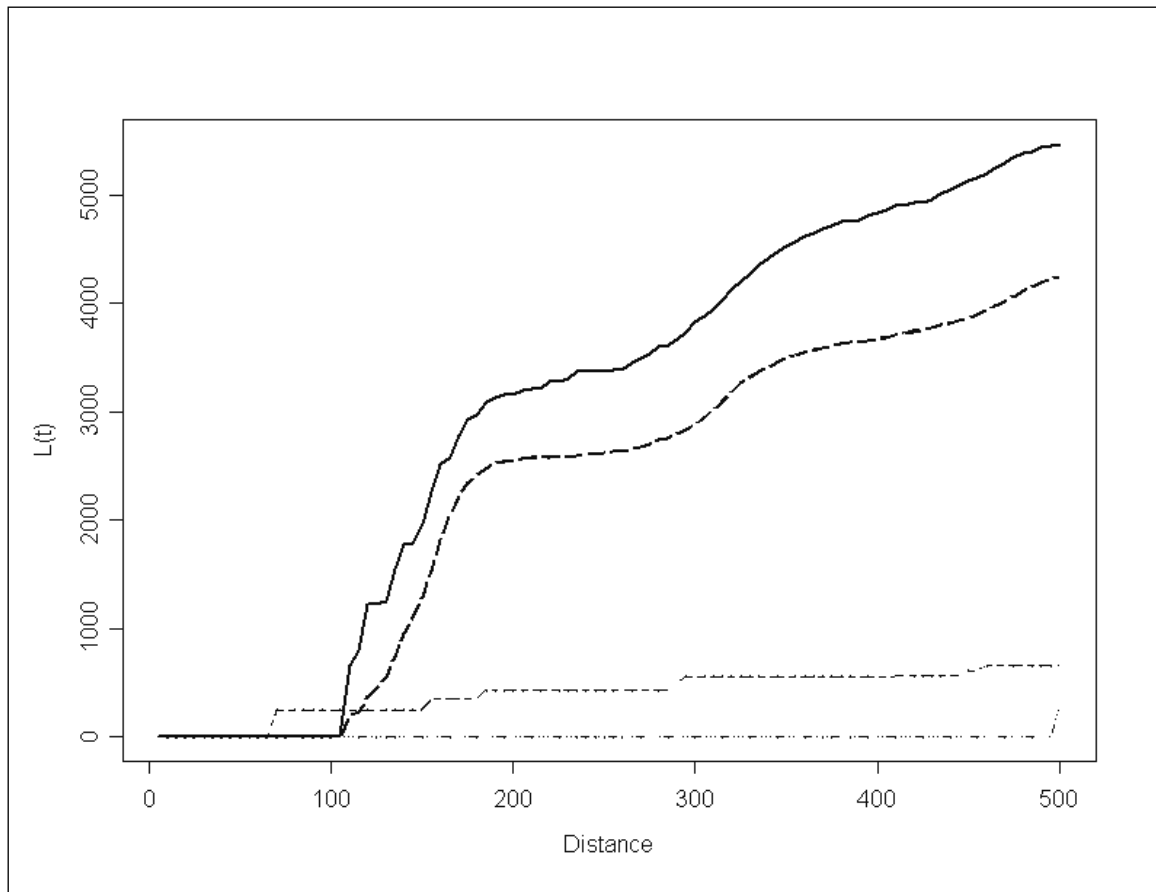


Figure 2. Ripley's K-function for beaver (thick solid line) and willow (thick dashed line), across lag distances from 0 – 500 meters. The thin dashed lines at bottom of the graph show the confidence envelope expected for a spatially random distribution.



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