RIPARIAN VEGETATION AND FOREST STRUCTURE OF TWO UNREGULATED TRIBUTARIES, COMPARED TO THE REGULATED SNAKE RIVER, GRAND TETON NP, WY

by

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ABSTRACT

The dynamic nature of rivers shapes riparian plant communities, and changes to the flow regime can have profound effects on these diverse ecosystems. To examine how riparian plant communities of the dam-regulated Snake River in Grand Teton National Park, WY respond to hydro-geomorphological factors, I studied the vegetation of two unregulated tributaries, Pacific Creek and Buffalo Fork, in relation to the main river. I considered three perspectives in this analysis. In chapter 2, I examined hydro-geomorphological processes shaping riparian vegetation in naturally flowing systems, by evaluating 15 environmental variables, and determining which were most related to vegetation. Using cluster analysis, I identified six distinct communities. I described environmental conditions associated with each community, using the unconstrained ordination technique NMDS, coupled with generalized additive models (GAMs). Community types occur on characteristic geomorphologic landforms. Depth to gravel, soil texture, pH, distance to bankfull channel, and elevation above water are all related to vegetation, and interact to determine where community types occur. In my third chapter, I compared the vegetation of the unregulated tributaries to the Snake River, as a means of assessing dam effects. Species richness per plot is higher on the tributaries, despite higher overall richness on the Snake River. Through the use of NMDS ordination and clustering techniques, I found the composition of the upper section of the Snake River, immediately below the dam, to be distinct. However, this section is naturally more incised, and the lower sections of the river do not seem to be influenced, suggesting dam impacts on vegetation are minimal. Environmental variables related to vegetation composition include elevation above water, depth to gravel, and geomorphological landform. In chapter 4, I compared age class distributions of spruce and cottonwoods across river sections, and found no evidence for a late-successional trend on the regulated river, versus unregulated tributaries. Age distribution is related to geomorphological landform, and browing also influences forest structure through root coppicing. Forest understory communities are structured by cottonwood age.

CHAPTER 1

INTRODUCTION

The unique, complex, and diverse nature of riparian ecosystems is largely a result of flow regime, and the dynamic nature of rivers (Nilsson and Svedmark, 2002). Riparian zones are considered to be the most diverse terrestrial ecosystems in the world (Naiman *et al.*, 1993), and, as ecotones, they contain habitat crucial for both terrestrial and aquatic organisms (Naiman and Decamps, 1997). On dam-regulated rivers, biodiversity can decline as cottonwood-dominated forests senesce (Marston *et al.*, 2005, Uowolo *et al.*, 2005). Cottonwood regeneration typically occurs on recently deposited, damp alluvial surfaces, created by large flood events in early spring (Naiman *et al.*, 2005, Mahoney and Rood, 1998). To examine how riparian plant communities of the dam-regulated Snake River in Grand Teton National Park, WY respond to hydro-geomorphological factors, I studied the vegetation of two unregulated tributaries, Pacific Creek and Buffalo Fork, in relation to the main river. I considered three perspectives in this analysis.

In chapter 2, the primary objective was to identify plant communities in this area, and describe the variables associated with these communities. I used ordination techniques to explore vegetation patterns, and identify environmental variables underlying community structure. I evaluated a wide range of environmental variables, either directly or indirectly related to hydro-geomorphological processes, to determine which are most influential in structuring the vegetation ordination. I also identified community types and described the associated environmental conditions, via Cluster Analysis.

The primary objective of the third chapter was to determine whether riparian community structure along the Snake River and tributaries is related to river regulation, and to examine relevant hydro-geomorphological factors in these systems. I hypothesized that unregulated river sections would consist of early successional, disturbance-associated communities compared to regulated sections, and that differences would be most pronounced immediately below the dam. I compared species richness and community composition across these sections. Similarly to Chapter 2, I used ordination and clustering techniques to model composition, and determined the role of river section, and of various hydro-geomorphological factors in structuring vegetation.

In chapter 4, I compared age class distributions of spruce and cottonwoods across river sections, and geomorphological landforms. I had two hypotheses regarding cottonwood regeneration on the Snake River. First, I expected that cottonwood regeneration was historically impacted by the dam, with recruitment inhibited between the years of 1916 and 1957 when peak flows occurred late in the spring. During these years, floods did not correspond with the release of cottonwood seeds, and new seedlings would have been scoured. As a result, trees between the ages of 50 and 90 should be sparse. My second hypothesis was that age gaps and possible trends towards late succession should be most prevalent in the sections of the Snake River immediately below the dam, where the tributaries have not had a mitigating effect on the magnitude of peak flows. In this chapter I also examined the effects of beaver and ungulate browsing, as well as how forest understory communities are structured by cottonwood age.

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CHAPTER 2

RIPARIAN PLANT COMMUNITIES OF PACIFIC CREEK AND BUFFALO FORK

Abstract

Riparian plant communities are largely structured by fluvial processes such as flood regime and geomorphology. On two naturally flowing tributaries to the dam-regulated Snake River, in Grand Teton National Park, WY, I evaluated 15 environmental variables, either directly or indirectly related to hydro-geomorphological processes, to determine which variables are most related to the vegetation of this area. Using clustering techniques, I identified six distinct communities. To describe the environmental conditions associated with each community, I used the unconstrained ordination technique NMDS, coupled with generalized additive models (GAMs). Community types occur on characteristic geomorphologic landforms. Depth to gravel, soil texture, pH, distance to bankfull channel, and elevation above water are related to vegetation composition, and interact to determine where community types occur.

Introduction

The unique, complex, and diverse nature of riparian ecosystems is largely a result of flow regime, and the dynamic nature of rivers (Nilsson and Svedmark, 2002). Riparian zones are considered to be the most diverse terrestrial ecosystems in the world (Naiman *et al.*, 1993), and, as ecotones, they contain habitat crucial for both terrestrial and aquatic organisms (Naiman and Decamps, 1997). Riparian plant communities are structured by hydrology, and by the resulting geomorphology (Bendix and Hupp, 2000).

The factors promoting species richness in riparian systems are complex, and include high spatial heterogeneity (Naiman *et al.*, 1993, Nilsson and Svedmark, 2002), reduced competitive exclusion due to flooding disturbance (Pollock *et al.*, 1998), and high dispersal through hydrochory (Jansson *et al.*, 2005, Nilsson *et al.*, 1994). On dam-regulated rivers, biodiversity can decline as cottonwood-dominated forests senesce (Marston *et al.*, 2005, Uowolo *et al.*, 2005). Cottonwood regeneration typically occurs on recently deposited, damp alluvial surfaces, created by large flood events in early spring (Naiman *et al.*, 2005, Mahoney and Rood, 1998). The dynamic nature of flow regimes is integral to the biodiversity of these areas, and any modifications to the magnitude, frequency, timing, duration, or rate of change of floods can have impacts on riparian vegetation (Nilsson and Svedmark, 2002).

Hydro-geomorphological processes, including erosion and deposition, structure riparian plant communities as they create and destroy landforms (Bendix and Hupp 2000, Ward, 1998). Geomorphological landforms, such as floodplains, terraces, and gravelbars, have characteristic flooding regimes, substrates, and elevations above water, and are associated with distinct plant communities (Hupp and Osterkamp, 1985, Bendix and Hupp, 2000).

In addition to geomorphological landform, many other important environmental variables have been identified as influencing riparian vegetation. Inundation duration, (Greulich *et al.*, 2007, Gregor *et al.*, 1994), depth to water, salinity, soil organic content, (Busch and Smith, 1995), elevation above water, pH, (Sagers and Lyon, 1997), soil moisture (Merigliano, 2005), geomorphologic valley type (Harris, 1988), sediment size (Hupp and Osterkamp, 1985) and stream power (Bendix, 1994) all play a role. In general, these variables are either directly or indirectly related to hydro-geomorphological processes. Individual river systems can respond differently to these gradients, making local factors an important consideration (Tabacchi *et al.*, 1996).

Despite the vast literature on the subject of riparian vegetation, generalizations are difficult to make. The importance of flow regime and hydro-geomorphological processes has been established (Nilsson and Svedmark, 2002, Naiman *et al.*, 1993), but the manner in which communities respond to these factors can differ across systems (Tabacchi *et al.*, 1996). In the present study, I will describe riparian plant communities on two tributaries to the Snake River, Pacific Creek and Buffalo Fork, in Grand Teton National Park, WY.

Pacific Creek and Buffalo Fork are unregulated, but are otherwise similar to the dam-regulated Snake River. By exploring how hydro-geomorphological processes influence riparian plant communities, I hope to gain a clearer understanding of how these systems function naturally. This knowledge may be directly applicable to management of the Snake River, and will contribute to the growing understanding of riparian ecosystems.

The primary objective was to identify plant communities in this area, and describe the variables associated with these communities. I used ordination techniques to explore vegetation patterns, and identify environmental variables underlying community structure. I evaluated a wide range of environmental variables, either directly or indirectly related to hydro-geomorphological processes, to determine which are most influential in structuring the vegetation ordination. I also identified community types and described the associated environmental conditions, via Cluster Analysis.

Multivariate Techniques

Several multivariate techniques were used in this thesis, including the unconstrained ordination technique NMDS (Non-Metric Multidimensional Scaling), and OPTSIL, a form of Cluster Analysis. Multivariate statistics were performed in R (R Development Core Team, 2007).

NMDS is an ordination algorithm that is “non-metric” in that functions are calculated on rankings, with values simply ranked from minimum to maximum, rather than on a ratio scale (Kruskal and Wish, 1978). The rank distances of samples in the ordination should reflect the rank distances in the dissimilarity or distance matrix, which is often calculated using a Bray-Curtis dissimilarity index (Bray and Curtis, 1957). NMDS, especially based on a Bray-Curtis dissimilarity matrix, is considered to be one of the more robust ordination techniques (Minchin, 1987, Faith *et al.*, 1987). NMDS models involve an algorithm designed to minimize stress, which is calculated as the square root of a normalized “residual sum of squares” (Kruskal and Wish, 1978).

As with many ordination techniques, data from the dissimilarity matrix are condensed into a few dimensions, and 2-dimensional NMDS plots are often very effective. One problem with an NMDS algorithm is selecting a solution with a local minimum of stress, rather than the global minimum (Kruskal and Wish, 1978). To address this problem, multiple iterations can be used, with independent starting configurations, and the model with the lowest stress selected. The correlation between an ordination and the underlying matrix can also be evaluated by a correlation statistic (labdsv package; Roberts, 2007).

Like NMDS, Cluster Analysis is generally based on a similarity, dissimilarity, or distance matrix (Everitt, 1993). The Bray-Curtis dissimilarity index (Bray and Curtis, 1957) is a common index for evaluating the proximity of samples to each other. Clustering techniques are often hierarchical, and can be represented by a dendrogram, showing sample partitioning (Everitt, 1993). Agglomerative methods involve fusing all samples into groups, and divisive methods separate all samples into progressively finer groupings, until only individuals remain (Everitt, 1993). It is also possible to use optimization algorithms to optimize some criterion, typically by reallocating samples to more suitable clusters (Everitt, 1993). One such method is OPTPART (optpart package for R; Roberts, 2008), which is a reallocation algorithm designed to maximize within versus between cluster dissimilarity (Aho *et al.*, 2008). Ideally, samples in the same cluster should have the least dissimilarity to each other. A similar method is OPTSIL (optpart package for R; Roberts, 2008), which optimizes silhouette width. Silhouette width is a measure of cluster suitability, based on the average dissimilarity of samples in a cluster, compared to samples in the nearest neighbor cluster, and is measured as follows (Kaufman and Rousseeuw, 1990):

$$s_i := (b_i - a_i) / max(a_i, b_i)$$

Where a_i is the average dissimilarity between a sample and all other samples in that cluster, and b_i is the *smallest* of the average dissimilarities between a sample and all samples in *other* clusters (i.e. nearest neighbor cluster) (cluster package; Maechler *et al.*, 2005). Higher average silhouette values across clusters, and across the entire cluster solution, are indicative of cluster distinctness (Kaufman and Rousseeuw, 1990).

Indicator species can be calculated for clusters, in order to characterize the composition of the clusters. One method of classifying species is Dufrêne and Legendre's (1997) Indicator Value algorithm, as implemented in DULEG (labdsv package; Roberts, 2007). Dufrêne and Legendre (1997) define an indicator species as "the most characteristic species of each group, found mostly in a single group of the typology and present in the majority of the sites belonging to that group". Indicator value can be calculated as follows (Dufrêne and Legendre, 1997):

$$INDVAL_{ij} = A_{ij} \text{ x } B_{ij}$$

Where $INDVAL_{ij}$ is the indicator value of species i in sites of cluster j, A_{ij} is the mean abundance of species i in sites of cluster j, and B_{ij} is the frequency of occurrence of species i in sites of cluster j. The formula originally described by Dufrêne and Legendre (1997) involves multiplying A_{ij} and B_{ij} by 100, however, the methods adapted for the DULEG function (labdsv package; Roberts, 2007) do not include this factor.

The Study Area

The Snake River, in Grand Teton National Park, WY, has two large, unregulated tributaries which enter shortly after the Jackson Lake Dam (Figure 2.1). Pacific Creek enters the main river 7.2 km downstream from the dam, and Buffalo Fork enters at 8.1 km. These two rivers contribute substantial flow to the main channel (Schmidt and

Nelson, 2007). Sediment input, particularly from Pacific Creek, plays an important role in the geomorphological processes of the Snake River (Marston *et al.*, 2005). The study area includes the segments of these tributaries from the National Park boundary to the confluence with the main river, a length of 6.7 km for Pacific Creek, and 5.4 km for Buffalo Fork.

Pacific Creek and Buffalo Fork are predominantly braided rivers, with mean braid indices (defined as the ratio of total bankfull channel length, including all secondary channels, to main bankfull channel length; Schmidt and Nelson, 2007) of 2.43 and 2.12, respectively. Pacific Creek is a more graded river, with elevation changes of 28m over the study area (4.2m/ river km), and a resulting large area of active alluvium of 0.65km^2. Buffalo Fork changes only 11m in elevation (2.0m/ river km), and has an active alluvial area of 0.41 km^2. The elevation of the entire study area ranges from 2050 to 2082m.

The riparian forests of Pacific Creek and Buffalo Fork are dominated by the cottonwood species *Populus angustifolia*, and *P. balsamifera* (all species names are based on Dorn, 2001). These species are often indistinguishable when young, and occupy similar habitats, but *P. angustifolia* is clearly dominant in the area. As cottonwoods mature, they typically become co-dominant with *Picea pungens* (blue spruce) and eventually spruce becomes dominant. The mixed *Picea pungens* and *Populus angustifolia* system is not uncommon (Daubenmire, 1972), and a similar succession has been studied along the Red Deer River, in Alberta Canada (Cordes *et al.*, 1997). Other tree species in the study area include *Pinus contorta* (lodgepole pine), which is abundant in the uplands of Grand Teton National Park, and occurs in the riparian

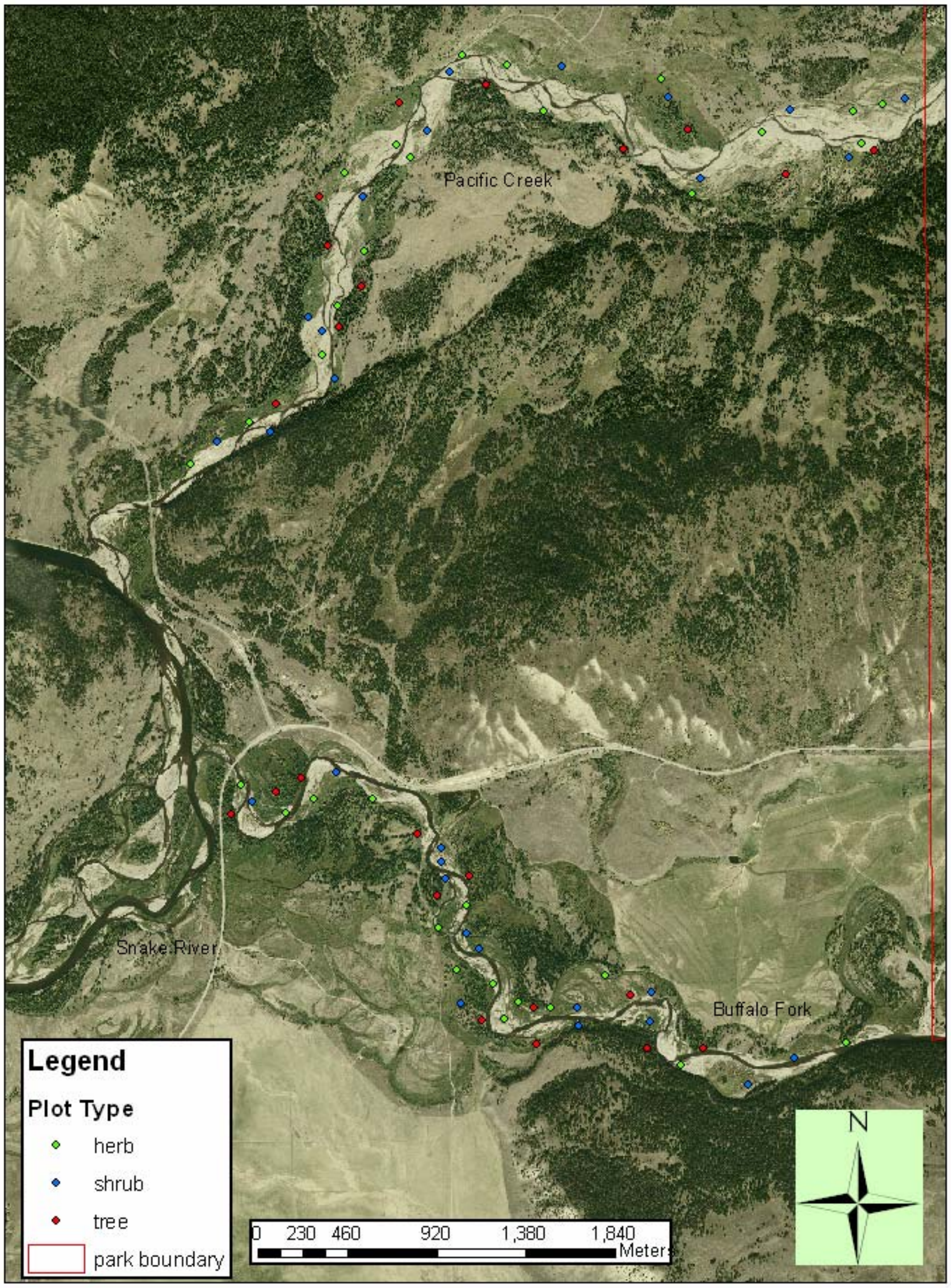

Figure 2.1. Pacific Creek and Buffalo Fork, in Grand Teton National Park. Study plots are displayed, with color indicating vegetation type.

corridor. Willow species, including *Salix boothii, S. exigua, S. lasiandra,* and *S. eriocephala*, all shrubby in growth, are common in the area, as is *Alnus incana*. Dominant wetland species include *Carex utriculata* and *Equisetum sp.*

Methods

During the summer of 2007, 82 plots were established: 42 on Pacific Creek and 40 on Buffalo Fork. Plots were selected by stratifying across all vegetation types and geomorphological landforms. Plot size differed depending on growth form of the tallest vegetation layer: tree plots were 100m^2, shrub plots 25m^2, and herbaceous plots 10m^2. Due to the linear nature of riparian communities, plots were rectangular. Plant community data and environmental data were recorded for each plot.

All vascular plant species were identified to species, based on Dorn (2001), and percent cover was estimated visually using a modified Braun-Blanquet scale (Braun-Blanquet, 1932). Cover classes were assigned as follows: 0.1: *<1% and low frequency*, 0.5: *<1% and frequent,* 1: *1-5%*, 2: *5-25%*, 3: *25-50%*, 4: *50-75%*, 5: *75-100%*. The definition of frequency was dependent on plot size and species growth form. In 10m^2 and 25m^2 plots, low frequency was defined as 1-2 herb individuals, or 1 shrub individual; in 100m^2 plots, it was defined as 1-4 herb individuals, or 1-2 shrub individuals. The two trace categories allowed for a differentiation between common species with low cover, typically due to small plant size (e.g. *Galium sp*.), and those that were rare, or anomalies. Cover was recorded separately for each vegetation layer, so that members of a species growing in the herb layer were considered independently from those of the same species growing in the shrub and tree layers. Herb (H), shrub (S), and tree (T) layers were defined by height (H: *<=0.5m*, S2: *>0.5m-1.5m*, S1: *>1.5-3m*, T2: *>3-10m*, T1: *>10m*)

Environmental data collected for each plot included depth to gravel, elevation above water, distance from water, slope, aspect, local elevation/topography, geomorphological landform, closest water type, and flooding evidence. Depth to gravel increases with soil development, and is indicative of substrate age. Elevation above water and distance to water were collected using survey equipment, after the spring peak in the hydrograph, as flows were approaching base levels. Slope and aspect were measured, where applicable, using an inclinometer and compass. The local elevation (high, intermediate, or low) and topography (concave, convex, undulating >3m, undulating <3m, or flat) were classified for each plot. Geomorphological landform of each plot was classified as a bank (within the active channel), gravelbar (surface dominated by gravel, within the active channel), abandoned gravelbar (gravelbar no longer within active channel) floodplain (inundated only during major flooding events), terrace (abandoned floodplain), or old channel (abandoned channel bed). These definitions are similar to those used by Hupp and Osterkamp (1985), with the addition of "abandoned gravelbar", and "old channel". The closest water type was described as: main channel, secondary channel, secondary ephemeral channel without base flow, or standing water. Recent flooding was recorded as true or false, based on deposited debris, and observations during spring flow.

Additional environmental variables were derived using ARC-GIS (version 9.2, ESRI Inc.), including distance to bankfull channel and braid index. Bankfull channel was defined as predominantly unvegetated, active alluvium, which is flooded annually

(Schmidt and Nelson, 2007) (Figure 2.2). Braid index was defined as the ratio of total bankfull channel length (including all secondary channels) to main bankfull channel length (Schmidt and Nelson, 2007), and was calculated for 7 relatively uniform river segments. Elevation was derived from 2007 LIDAR data, with 15cm vertical accuracy. Y-coordinate, based on UTM (Universal Transverse Mercator) projection system North coordinates, was calculated to measure latitudinal trends. Distance upstream from the confluence with the Snake River was also calculated.

Soil samples were collected from each plot, and the upper soil horizon was analyzed for texture and pH. In 6 cases where the first horizon was less than 5 cm, which was often due to recent sedimentation, the first and second layers were mixed, in masses proportional to their ratio of the first 10cm. Percent cobble (>75mm) and coarse gravel (16-75 mm) were estimated in the field, by volume. Percent fine gravel (2-16mm) was sifted. Soil pH, and soil texture (percent sand, silt and clay) by weight, using the hydrometer method, were measured by the Soils Testing Department at University of Wyoming. Two replicates were averaged for each sample.

All statistical analyses were performed using the program R (R Development Core Team, 2006). The unconstrained ordination technique NMDS (Non-Metric Multidimensional Scaling; Kruskal and Wish, 1978) was applied to plant community data (labdsv package; Roberts, 2007, MASS package; Venables and Ripley, 2002). Vegetation data were used to calculate a Bray-Curtis dissimilarity matrix for this analysis, using the cover classes from 1-5, and trace classes. Environmental variables were evaluated for explanatory value, by two methods. GAMs (generalized additive models, mgcv package; Wood, 2004) were fit to the ordination, and D^2 values of

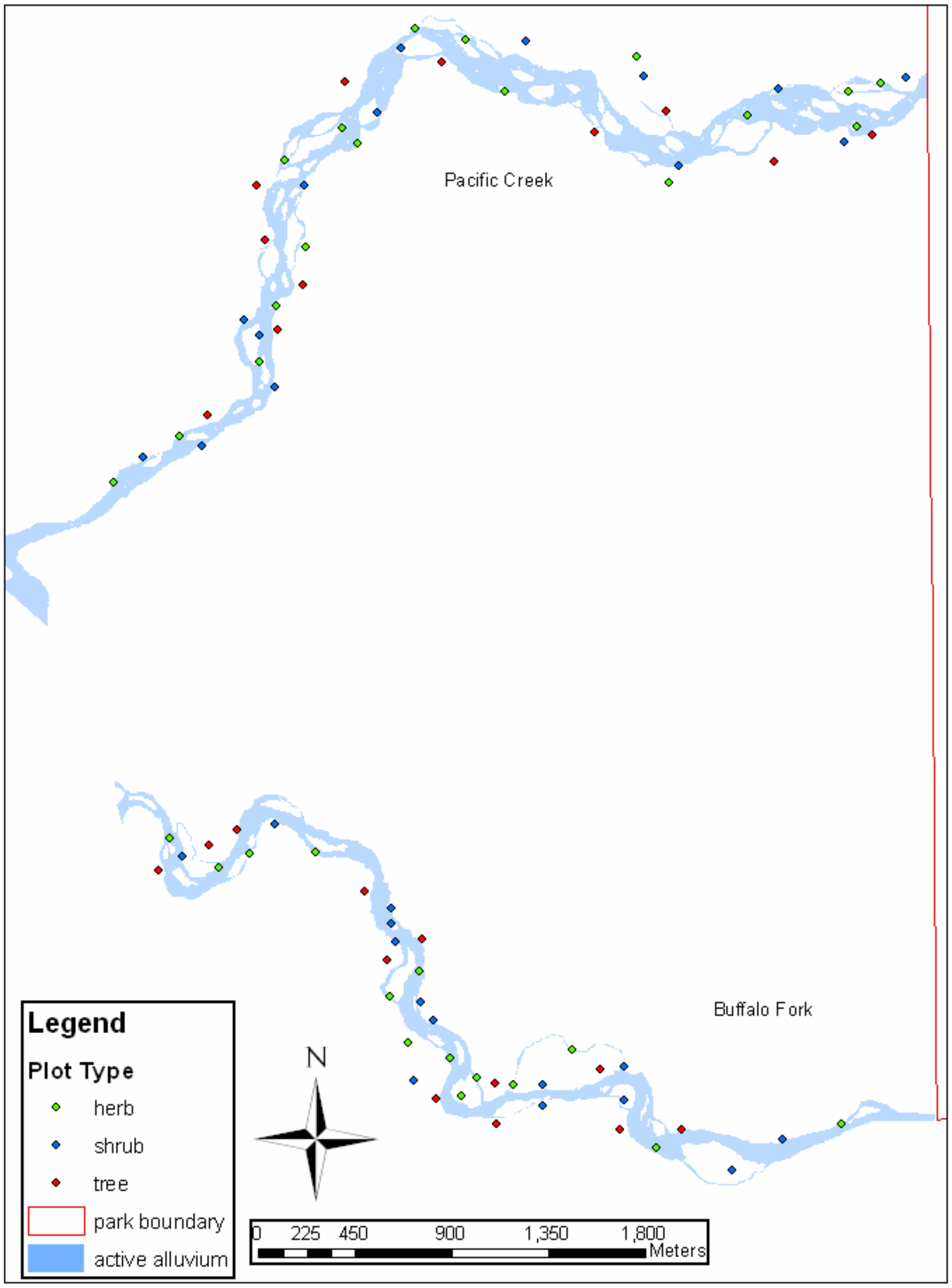

Figure 2.2. Active alluvial area, used to define bankfull channel, on Pacific Creek and Buffalo Fork. Study plots are displayed, with color indicating vegetation type.

deviance explained were calculated. Minimizing residual deviance, or maximizing deviance explained, is a method of evaluating goodness of fit of a GAM, with some parallels to the residual sum of squares in linear modeling (Wood, 2008). The D^2 value of deviance explained was defined as:

$$D^2 = (\text{null deviance} - \text{residual deviance}) / \text{null deviance}.$$

A gamma value of 1.4 was used, which increases the penalty for degrees of freedom, helping avoid overfit GAM models (Wood, 2006). Gaussian models were used, except in the case of 3 variables with a high proportion of zero values, in which case binomial models were used. These variables were percent cobble, fine gravel, and coarse gravel, which were evaluated as present if over 5%, and absent if equal to or less than 5%. Additionally, vectors of variables and corresponding R^2 values with individual axes were calculated using the function ENVFIT (vegan package; Oksanen *et al.*, 2007). The following continuous variables were considered:

- Elevation above water (m)
- Distance to low water channel (m)
- Distance to bankfull channel (m)
- Depth to gravel (cm)
- Braid index
- Elevation (m)
- Y-coordinate (UTM, m)
- Distance from confluence (m)
- Soil PH
- Cobble (% by volume)
- Coarse Gravel (% by volume)
- Fine Gravel (% by volume)
- Sand (% by weight)
- Silt (% by weight)
- Clay (% by weight)

Categorical variables were evaluated using the technique Ordtest (labdsv package; Roberts, 2007), which tests significance in structuring the NMDS ordination. This technique was applied to each categorical variable, and to all factors of that variable. The following variables were evaluated:

- Landform (bank, floodplain/terrace, gravelbar, old channel)
- Topography (concave, convex, undulating >3m, undulating <3m, flat)
- Local Elevation (high, intermediate, low)
- Section (Pacific Creek, Buffalo Fork)
- Closest Water Type (main channel, 2' channel, 2'channel-no baseflow, standing water)
- Recently Flooded (flooded, unflooded)

Cluster analysis was performed using a non-hierarchical reallocation algorithm, based on a pre-determined number of clusters. These techniques employed a Bray-Curtis dissimilarity matrix, using the OPTSIL function in R (optpart package; Roberts, 2008). Two important considerations in selecting a cluster solution were the Partana ratio, which measures the within versus between cluster similarity (Aho *et al.* 2008), and mean Silhouette width, which measures how similar the components of a cluster are to each other, compared to those of the most similar cluster. Silhouette and Partana measure the geometry of a cluster solution. OPTSIL is designed to maximize silhouette width, thereby maximizing within cluster similarity. To consider the ecological implications of a model, a sum of the p-values of all significant indicator species across cluster was calculated, using the DULEG function in R (Dufrêne and Legendre, 1997; labdsv package; Roberts, 2007). This method defines indicator species as the product of the relative frequency and relative average abundance in clusters. Additionally, classification quality was assessed using the TABDEV function, calculating total deviance of all taxa across clusters, using fractional sums by cluster (optpart package; Roberts, 2008). Species that occur in many clusters have high deviance, so an ideal cluster classification should exhibit low deviance. This technique is based on the original vegetation data, rather than the dissimilarity matrix.

Communities were named by the two most abundant species in each cluster that were also significant indicator species. In cases where only one species was highly abundant, only one species was used in naming. Since species were measured separately in herb, shrub and tree layers, all species names include the vegetation layer (H, S1, S2, T1 or T2). Occurrence of each community type was compared across geomorphological landforms.

Results

Vegetation Composition

A total of 229 species was recorded in the study area. Since I considered species growing in different layers separately, the data are composed of 296 unique species/strata entries. Species richness per plot (based on the 296 species/strata) ranges from 3 to 52, with a mean of 30 (Figure 2.3).

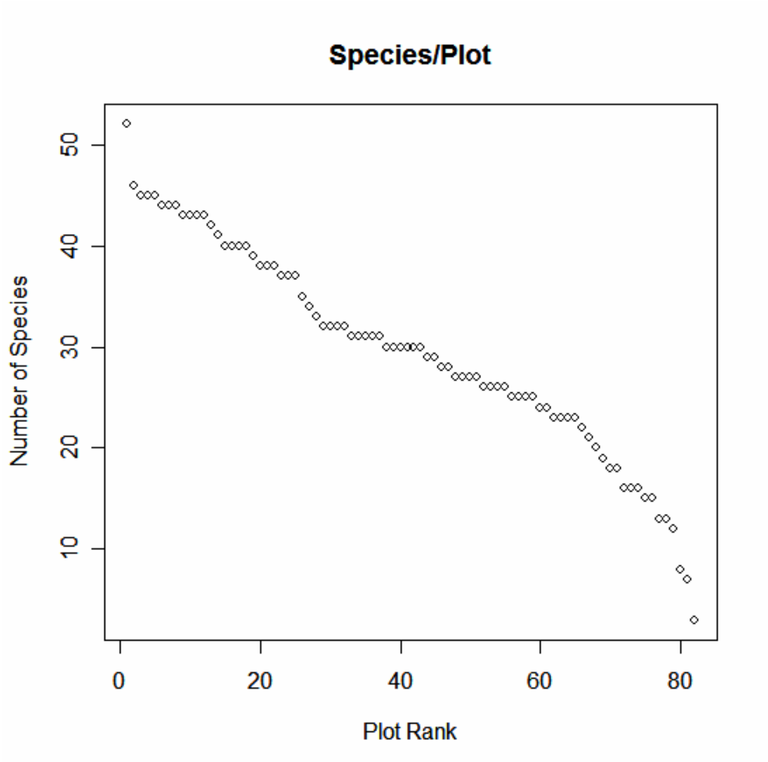

Figure 2.3. Number of species per plot, across all plots.

Mean species richness does not differ significantly between Pacific Creek and Buffalo Fork (means= 29.4 and 29.8, respectively; p=0.86, Welch Two Sample t-test). Of the 229 plant species recorded, 62 occur in only one plot, while several are nearly ubiquitous (Figure 2.4). The species with greatest frequencies across plots are mostly non-native graminoids (ex. *Poa sp.*) and forbs (ex. *Trifolium sp.*), with relatively low mean percent cover (Table 2.1). The species with greatest percent cover, when present, are mostly shrubs and trees, including *Salix boothii, Alnus incana, Populus angustifolia, Pinus contorta,* and *Picea pungens,* as well as *Bromus inermis* and *Carex utriculata* (Table 2.1).

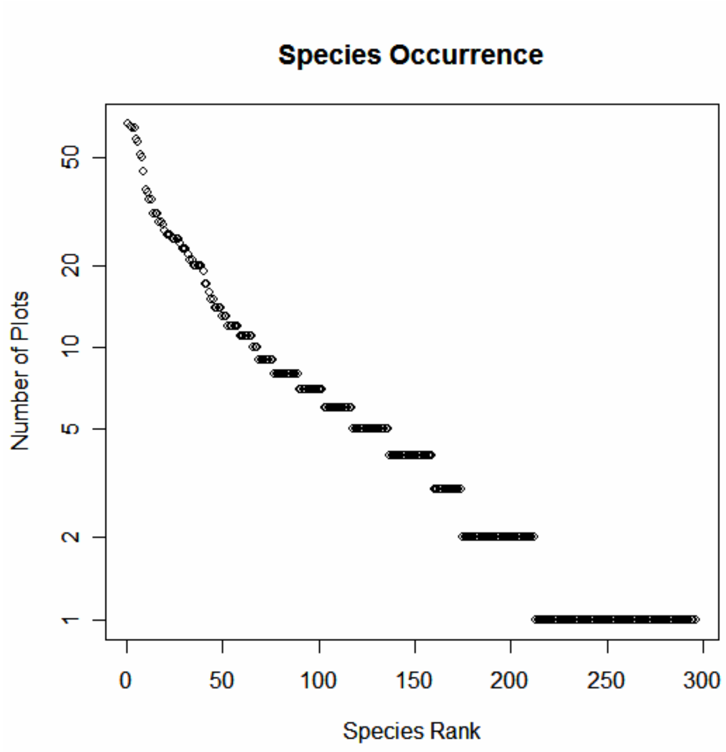

Figure 2.4. Species occurrence on each plot, across all species.

Table 2.1. Mean percent cover (when present) and number of plots occurred in (out of 82), for the 10 most frequent species (most plots occurred in) and the 10 most abundant species (highest percent cover).

Frequent Species	**Mean % Cover**	**# Plots**	**Abundant Species**	**Mean % Cover**	**# Plots**
Trifolium hybridum	4.9	66	*Salix boothii (S1)*	58.8	6
Symphiotrichum lanceolatum	5.0	65	*Picea pungens (T1)*	34.4	12
Taraxacum officinale	1.5	64	*Alnus incana (S1)*	33.8	7
Solidago canadensis	2.0	64	*Populus angustifolia (S1)*	32.5	4
Poa pratensis	2.6	58	*Pinus contorta (T1)*	23.2	5
Agrostis stolonifera	4.5	57	*Carex utriculata*	22.2	11
Equisetum arvense	3.4	51	*Populus angustifolia (T2)*	20.6	4
Poa palustris	2.2	50	*Populus angustifolia (T1)*	18.1	11
Phleum pratense	1.9	44	*Bromus inermis*	17.7	12
Achillea millefolium	0.5	38	*Salix wolfii (S2)*	16.7	1

Non-native species, as described by Shaw (1992), are common in the study area, but typically occur at low densities (Table 2.2). *Bromus inermis* has the greatest mean percent cover, by far, of all non-native species. *Cirsium arvense* is the most frequent and abundant USDA (2008) classified noxious weed in the study area. Three additional USDA (2008) noxious weed species, *Carduus nutans, Isatis tinctoria,* and *Elymus repens,* occur in the study area at low frequencies and densities (Table 2.2). *Lactuca serriola* and *Astragalus cicer* were not described by Shaw (1992), but are classified as introduced by the USDA (2008). These two species were found at low densities in the study area.

Table 2.2. Non-native species in the study area as classified by Shaw (1992), the mean percent cover across plots where present, and number of plots occurring in (out of 82). Stars indicate USDA (2008) listed noxious weeds, † indicates USDA introduced species not described by Shaw (1992), †† indicates *Poa pratensis*, which is classified as non-native by Flora of North America (1993+).

Graminoids:	**Mean % Cover**	**# Plots**		**Mean % Cover**	**# Plots**
Agrostis stolonifera	4.5	57	*Medicago lupulina*	2.3	35
Bromus inermis	17.7	12	*Medicago sativa*	0.5	1
*Elymus repens**	0.5	1	*Melilotus officinalis*	1.2	7
Phleum pratense	1.9	44	*Plantago major*	0.6	24
Poa compressa	1.1	9	*Ranunculus repens*	0.1	1
Poa pratensis ††	2.6	58	*Rumex crispus*	0.3	7
Forbs:			*Silene latifolia*	0.1	1
Astragalus cicer †	1.3	3	*Sonchus uliginosus*	0.8	25
*Carduus nutans**	0.1	1	*Sonschus asper*	0.1	1
Cerastium fontanum	0.4	8	*Taraxacum laevigatum*	2.1	31
*Cirsium arvense**	3.5	31	*Taraxacum officinale*	1.5	64
Cirsium vulgare	0.1	3	*Tragopogon lamottei*	0.3	2
Conyza canadensis	0.7	17	*Trifolium hybridum*	4.9	66
Crepis tectorum	0.1	6	*Trifolium pratense*	0.8	20
*Isatis tinctoria**	0.5	1	*Trifolium repens*	2.5	26
Lactuca serriola †	0.5	1	*Veronica anagallis-aquatica*	0.5	1
Matricaria maritime	0.3	5			

Correlation of Variables

Correlation among environmental variables is generally weak, with the exception of soil texture variables, which are strongly correlated by nature due to a lack of independence (Figures 2.5-2.6). Latitude (Y-coordinate) differs between the tributaries, leading to disjointed correlation plots for this variable. This is most pronounced for elevation and latitude, which have a correlation of 0.75 (Pearson correlation). Similarly, elevation and distance from confluence have a disjointed correlation plot, and a correlation of 0.84. Braid index and latitude have a correlation of 0.54, and distance to low water channel and distance to bankfull channel have a correlation of only 0.33. The sand/silt correlation is -0.99, sand/clay is -0.84, and silt/clay is 0.75. Cobble and coarse gravel have values of zero for 65 of 82 plots, and fine gravel for 45 plots. Correlations between soil texture variables and other environmental variables are weak, and include depth to gravel, which is positively correlated with silt and clay (0.42 and 0.39 respectively), and negatively correlated with cobble (-0.35), coarse gravel (-0.32) and fine gravel (-0.33). Distance to bankfull channel is negatively correlated with sand (-0.41), and positively correlated with silt (0.37) and clay (0.45). Elevation is weakly correlated with cobble (0.31). The variables “slope” and “aspect” were measured in the field, but were not used for any analysis, since slope was zero in 70 of the 82 plots.

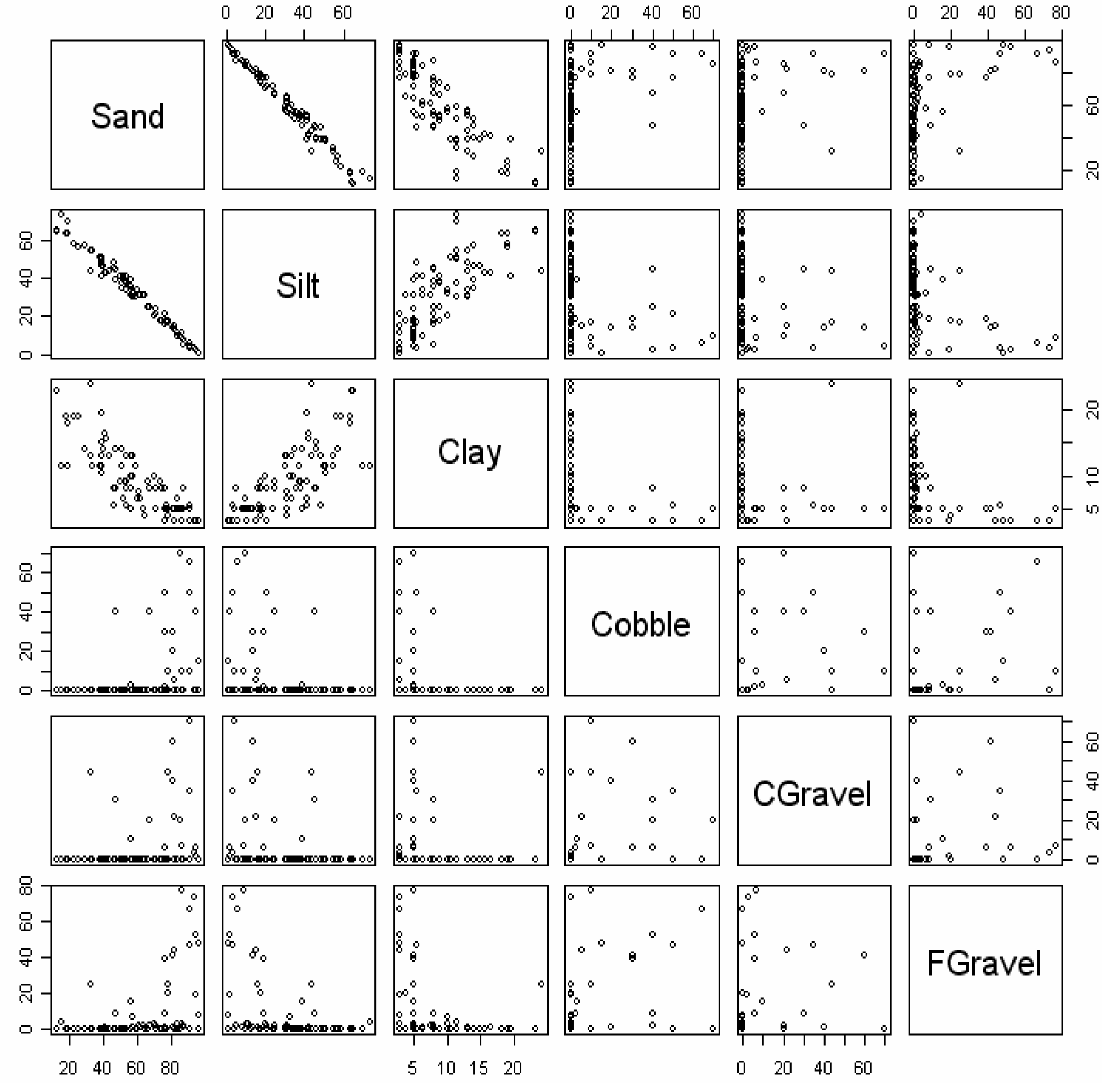

Figure 2.5. Correlations of soil-texture variables: percent sand, silt, clay, cobble, coarse gravel, and fine gravel.

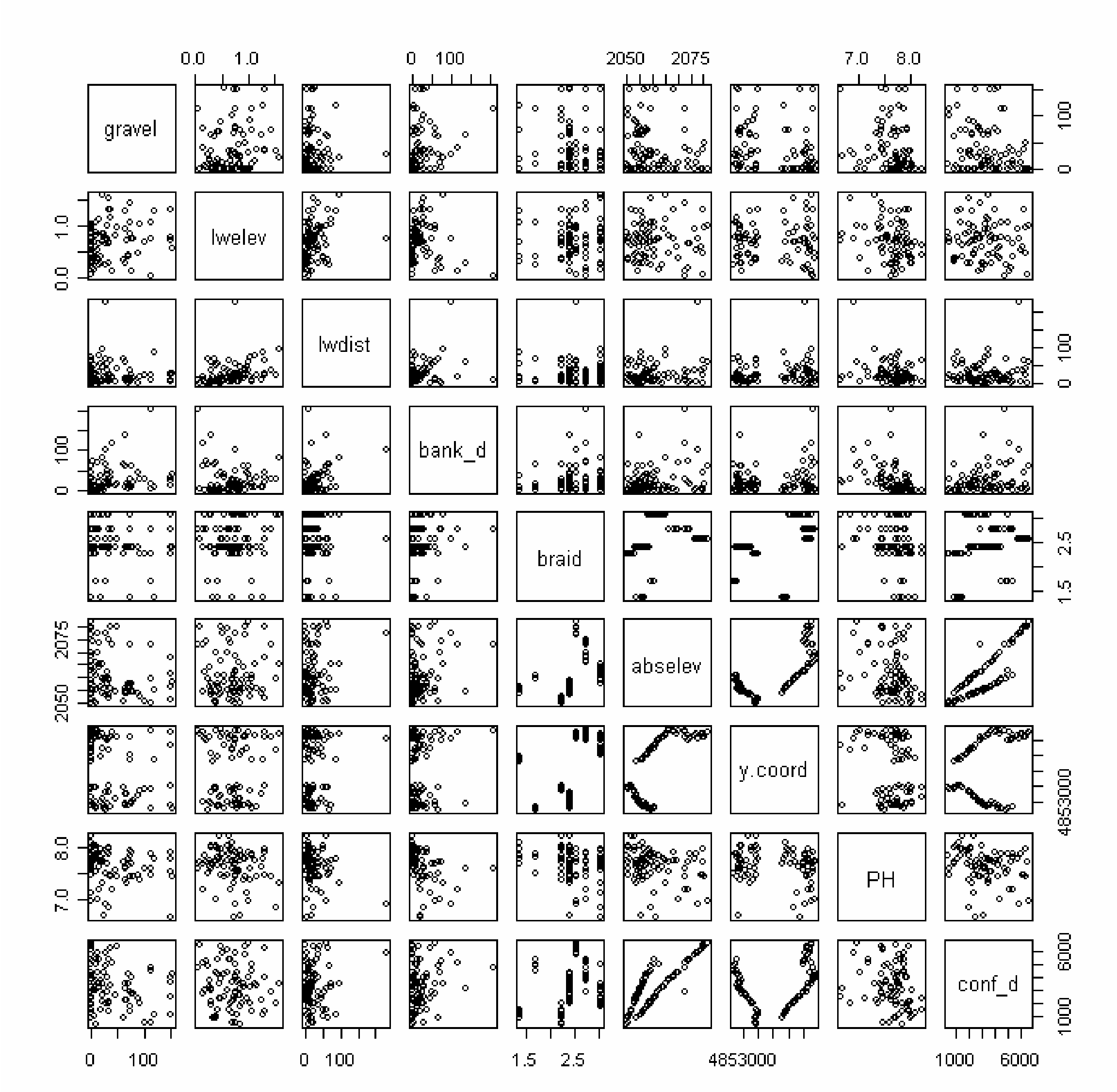

Figure 2.6. Correlations of environmental variables: depth to gravel, elevation above water, distance to low water channel, distance to bankfull channel, braid index, elevation, Y-coordinate (latitude), pH, and distance to confluence.

NMDS Ordination and Evaluation of Environmental Variables

The 2-dimensional NMDS ordination of sample plots has a high r-value (0.86), reflecting a fairly efficient representation of the underlying dissimilarities (Figure 2.7). Depth to gravel (Figure 2.8) and distance to bankfull channel (Figure 2.9) were both logtransformed, due to a high proportion of zero values, and then fit to the ordination coordinates by a GAM. These variables have high D^2 values, as does percent cobble (Figure 2.10), which was modeled as a binomial (<=5 versus >5%). PH is also important (Figure 2.11). GAM contours indicate that relationships are often non-linear. Other important variables with some trend include elevation above water (Figure 2.12), percent sand, silt, and clay, elevation, and distance to confluence (Table 2.3). Latitude and braid index are extremely weak.

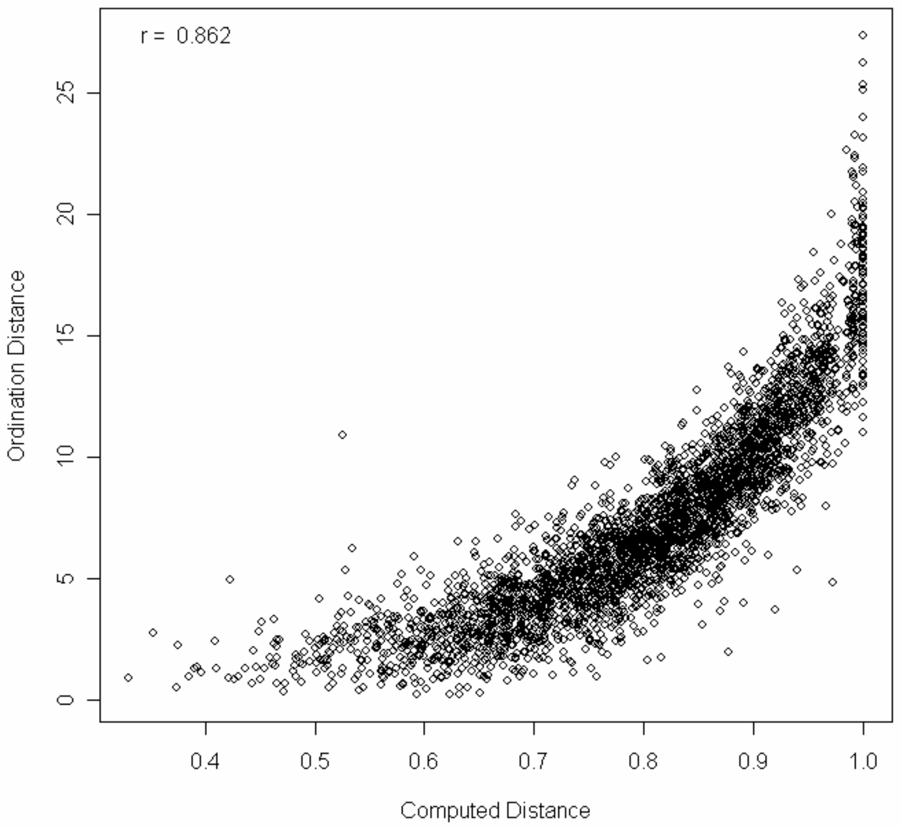

Figure 2.7. Correlation of ordination and computed distances of sample plots, giving an indication of the NMDS ordination quality (r=0.86).

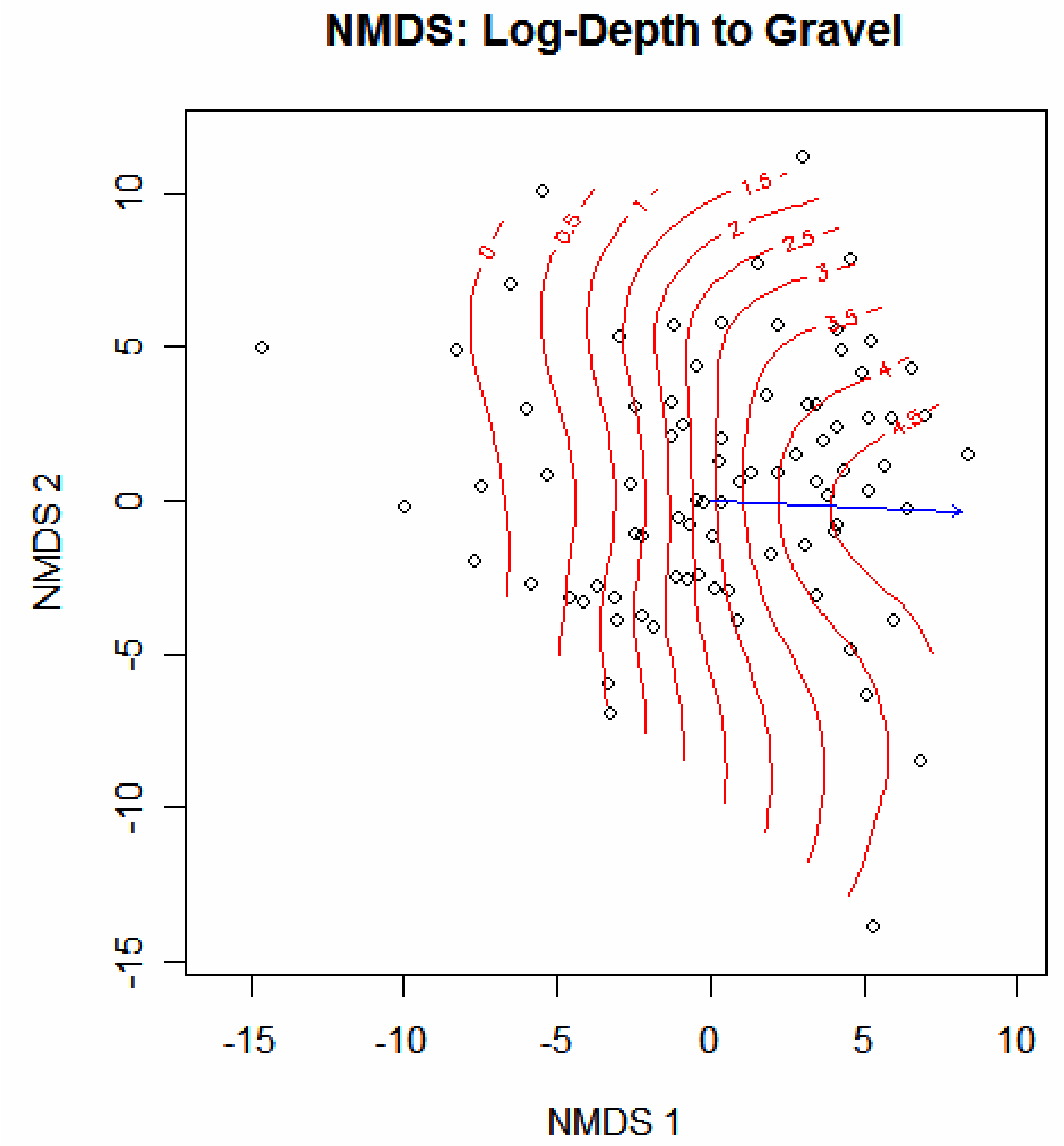

Figure 2.8. NMDS ordination plot, with Gaussian GAM surface (D^2=0.83) and vector (R^2=0.68) for depth to gravel.

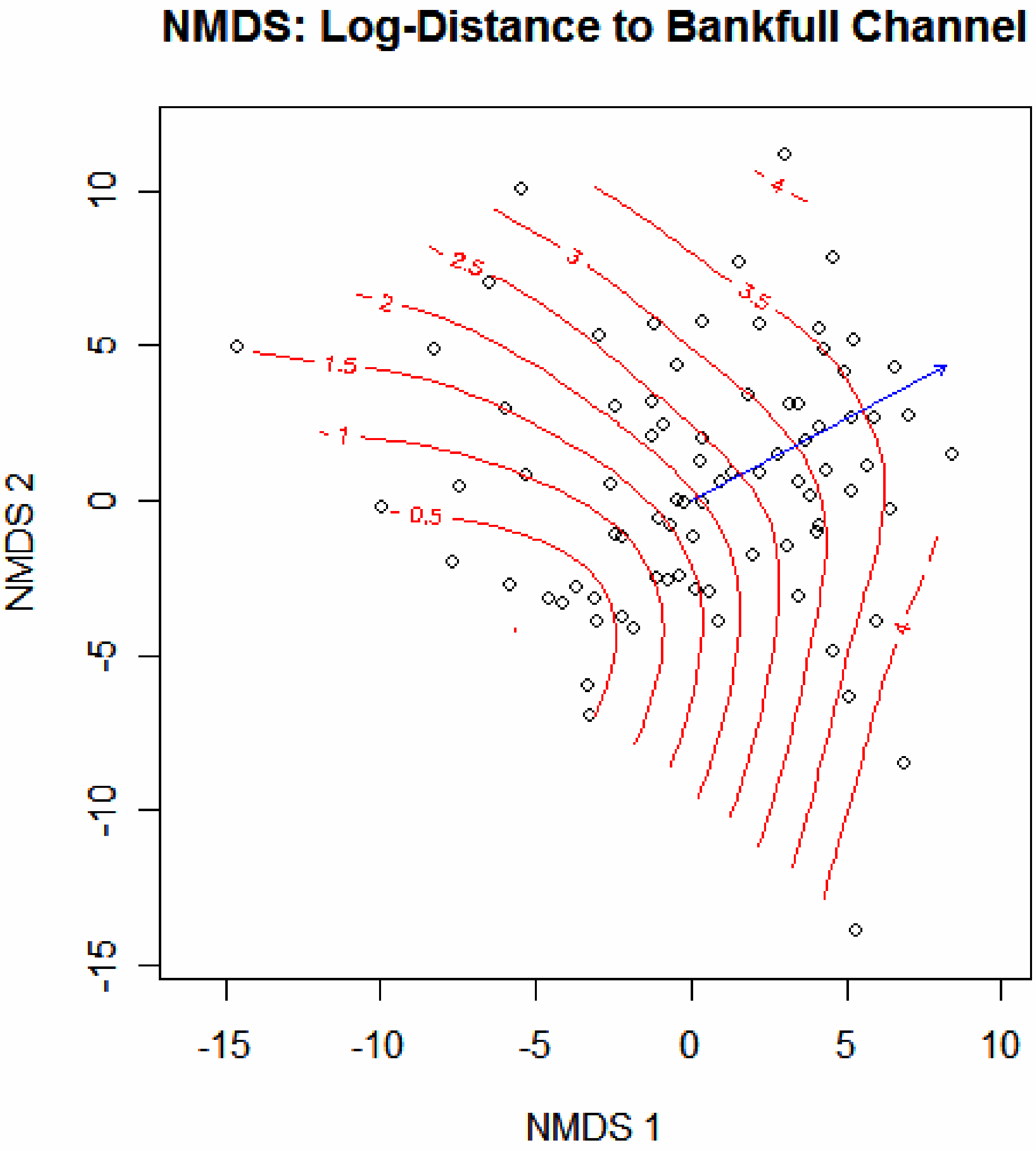

Figure 2.9. NMDS ordination plot, with Gaussian GAM surface (D^2=0.70), and vector (R^2=0.45) for distance to bankfull channel.

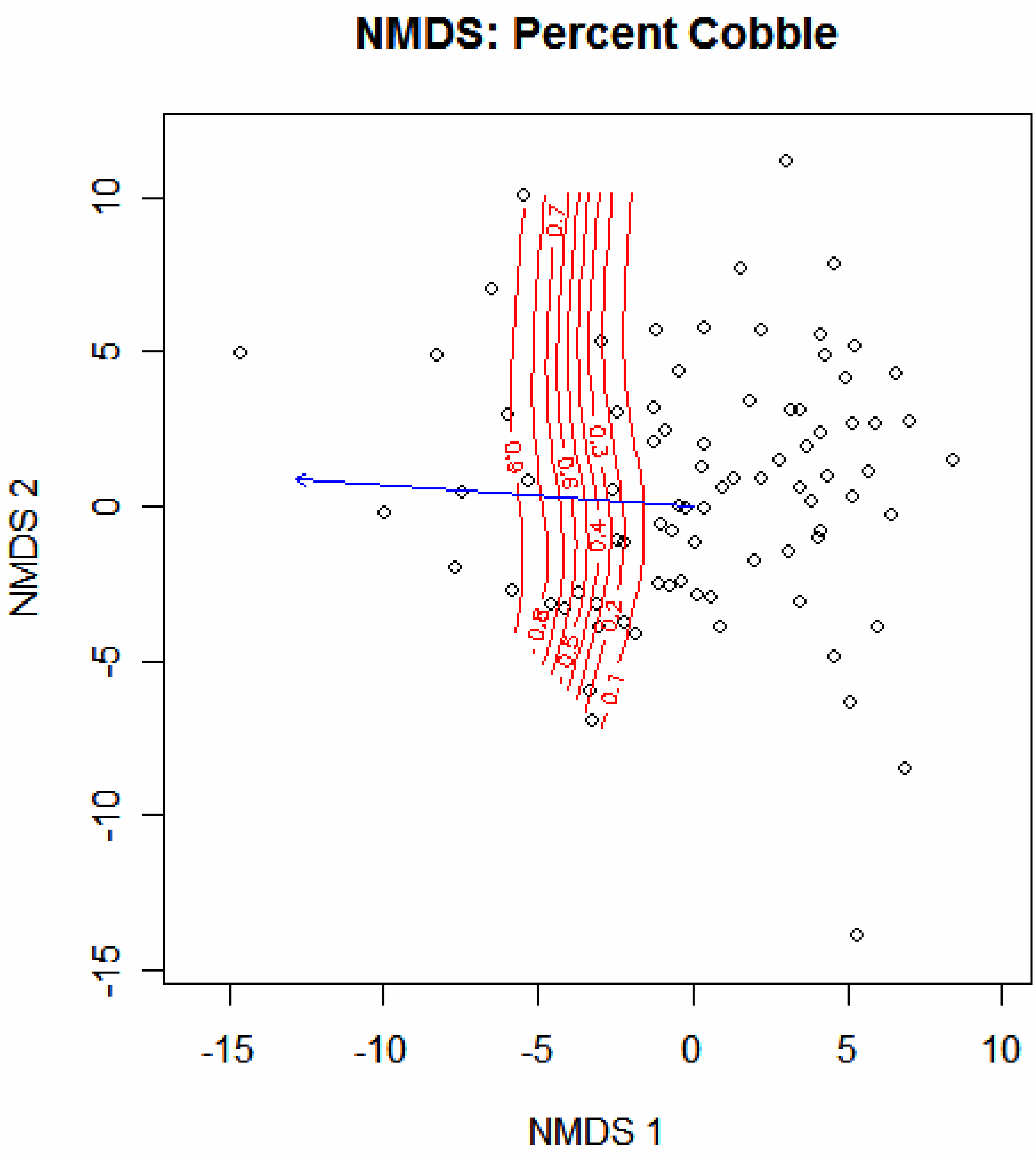

Figure 2.10. NMDS ordination plot, with Binomial GAM surface (D^2=0.71) and vector (R^2=0.49) for percent cobble.

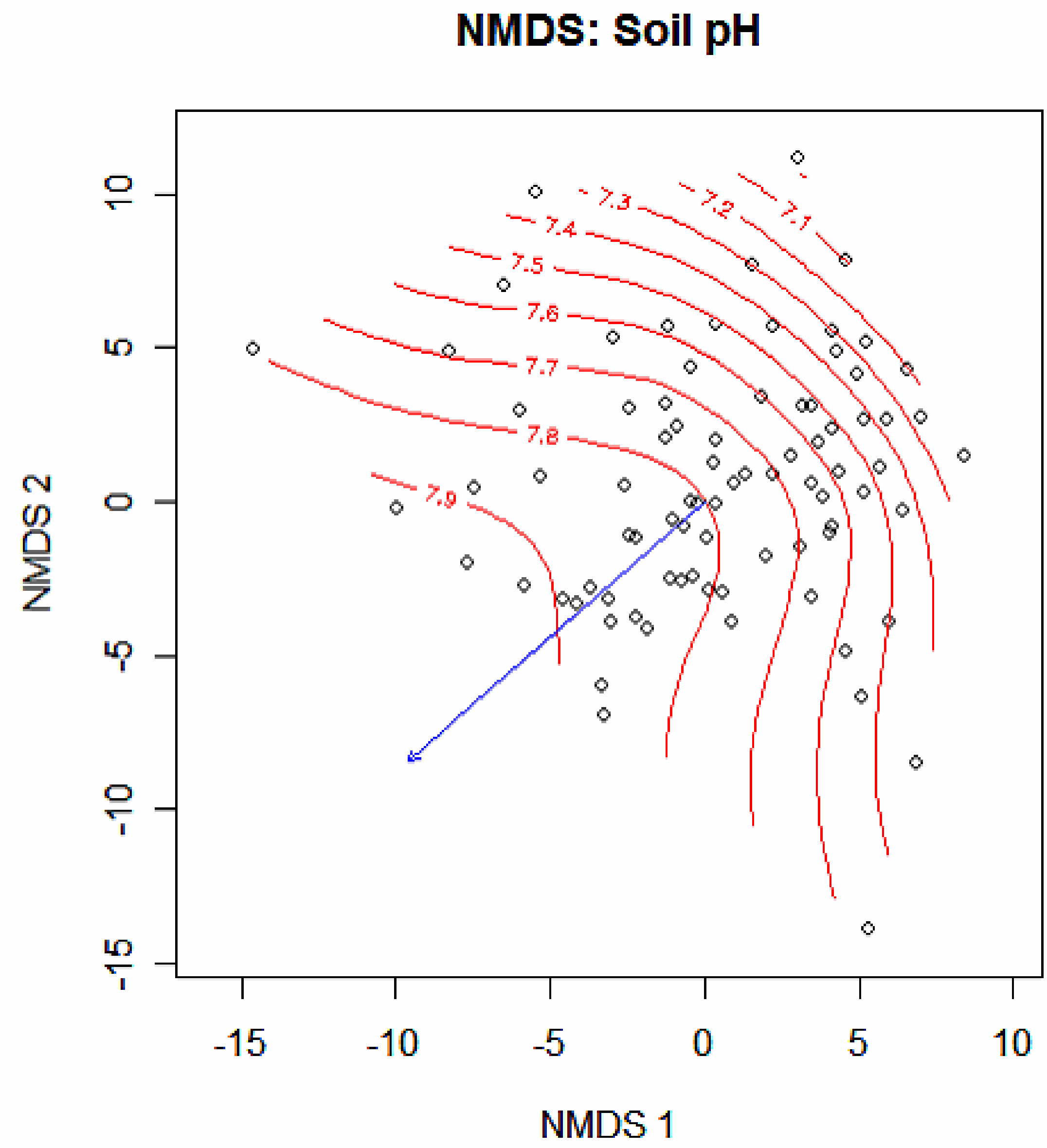

Figure 2.11. NMDS ordination plot, with Gaussian GAM surface (D^2=0.57) and vector (R^2=0.34) for pH.

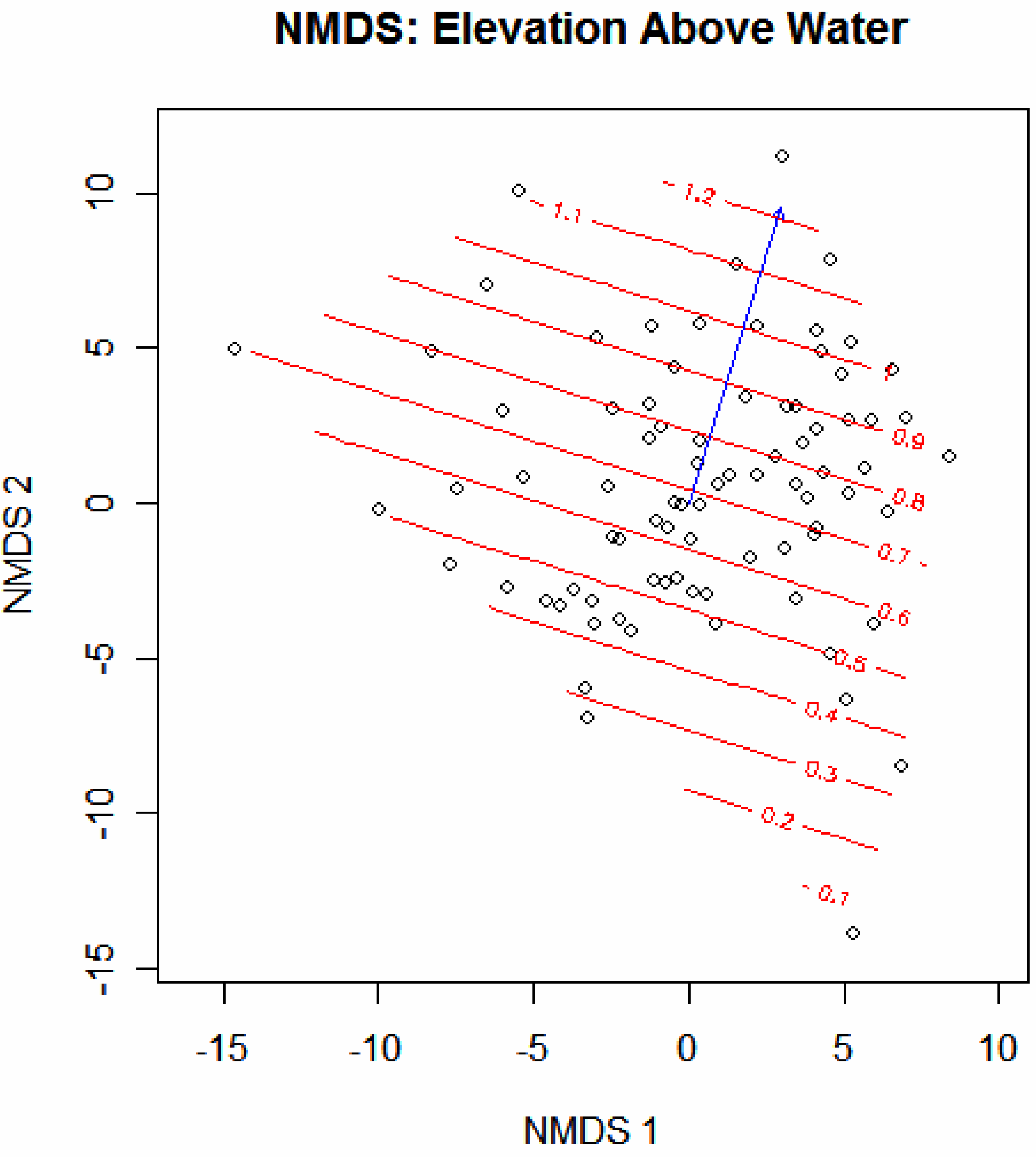

Figure 2.12. NMDS ordination plot, with Gaussian GAM surface (D^2=0.41) and vector (R^2=0.42) for elevation above water.

Table 2.3. D^2 values of GAMs and linear vectors, fit to continuous environmental variables, based on the NMDS ordination. All models are Gaussian, with gamma=1.4, except for percent cobble, coarse gravel, and fine gravel, which are Binomial.

Variable	**GAM D^2**	**Vector R^2**
Elevation	0.21	0.04
Y Coordinate	0.09	0.03
Log-Depth to Gravel	0.83	0.68
Elevation Above Water	0.41	0.41
Distance to Low Water Channel	0.14	0.14
Log-Distance to Bankfull Channel	0.70	0.45
Braid Index	0.01	0.01
Distance to Confluence	0.15	0.03
Cobble >5%	0.71	0.49
Coarse Gravel >5%	0.46	0.29
Fine Gravel > 5%	0.35	0.32
Percent Sand	0.27	0.27
Percent Silt	0.24	0.24
Percent Clay	0.31	0.28
Soil PH	0.57	0.34

Variables were also evaluated by comparing R^2 values of vectors fit to the NMDS axes (Table 2.3). Log-depth to gravel, cobble (> or < 5%), log-distance to bankfull channel, and elevation above water have the strongest linear vectors. Elevation and latitude have extremely weak linear trends. These two variables have modal responses with minimum GAM contours in the center/right of the ordination plot.

Significant categorical variables, determined by ordtest p-values (Table 2.4), include geomorphological landform, particularly the factors “terrace” and “abandoned gravelbar”. The closest water type is also relevant, with the factor “standing water” significantly structuring the NMDS plot. Relative elevation, (high, intermediate, or low) also influences the vegetation, as does the factor “recently flooded” (true or false). Tributary section (Pacific Creek versus Buffalo Fork) is not significant.

Table 2.4. Ordtest p-values based on the NMDS ordination, for categorical environmental variables. Stars indicate significance of variables at the p<0.05 level.

Variable	**Ordtest p-value**	**Category**	**Ordtest p-value**
Section	0.32	PC	0.33
		BF	0.37
Landform*	<0.01	Bank	0.52
		Floodplain	0.13
		Gravelbar	0.40
		Abandoned Gravelbar*	<0.01
		Oldchannel	1.00
		Terrace	0.09
Local Topography	0.55	Concave	0.64
		Convex	0.24
		Undulating <3m	0.70
		Undulating >3m	0.22
		Flat	0.55
Local Elevation*	<0.01	High	0.07
		Intermediate*	0.02
		Low*	0.01
Closest Water Type*	0.05	Main channel	0.13
		2’ Channel	0.21
		2’ Channel (no baseflow)	1.00
		Standing Water*	0.04
Recently Flooded*	<0.01	True*	<0.01
		False*	<0.01

Cluster Analysis of Communities

I selected a 6-cluster OPSIL model to define communities. Samples in each cluster are well classified, as there are very few reversals in the Silhouette plot (Figure 2.13). Reversals, or negative Silhouette widths, occur when a sample is most similar to another cluster. This model also has a high degree of within-cluster similarity, quantified by Partana ratios (Figure 2.14, Table 2.5).

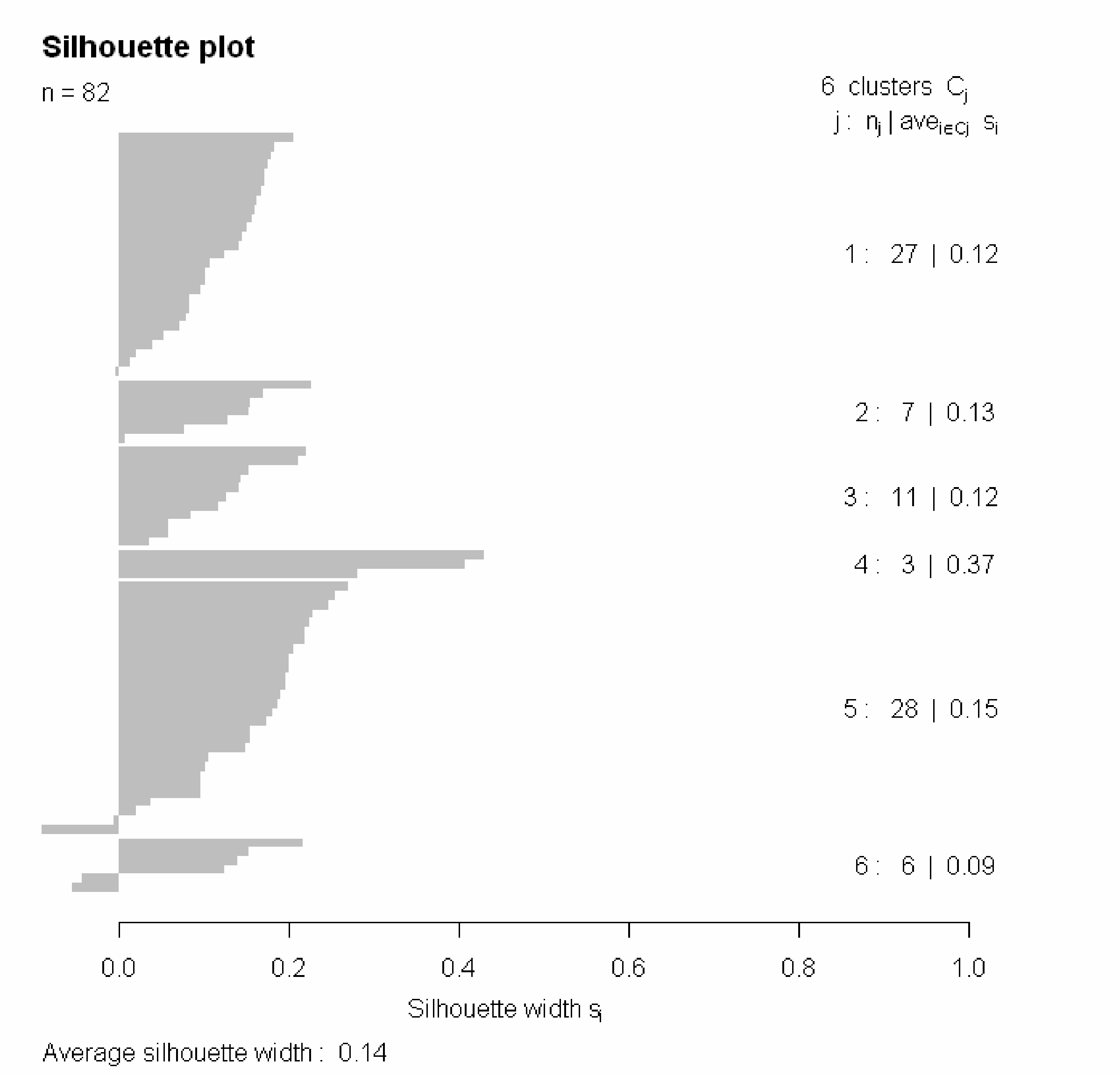

Figure 2.13. Silhouette width plot, indicating within plot similarity for each of 6 clusters. Negative widths indicate poor similarity. Cluster size and Silhouette value are summarized on right of plot.

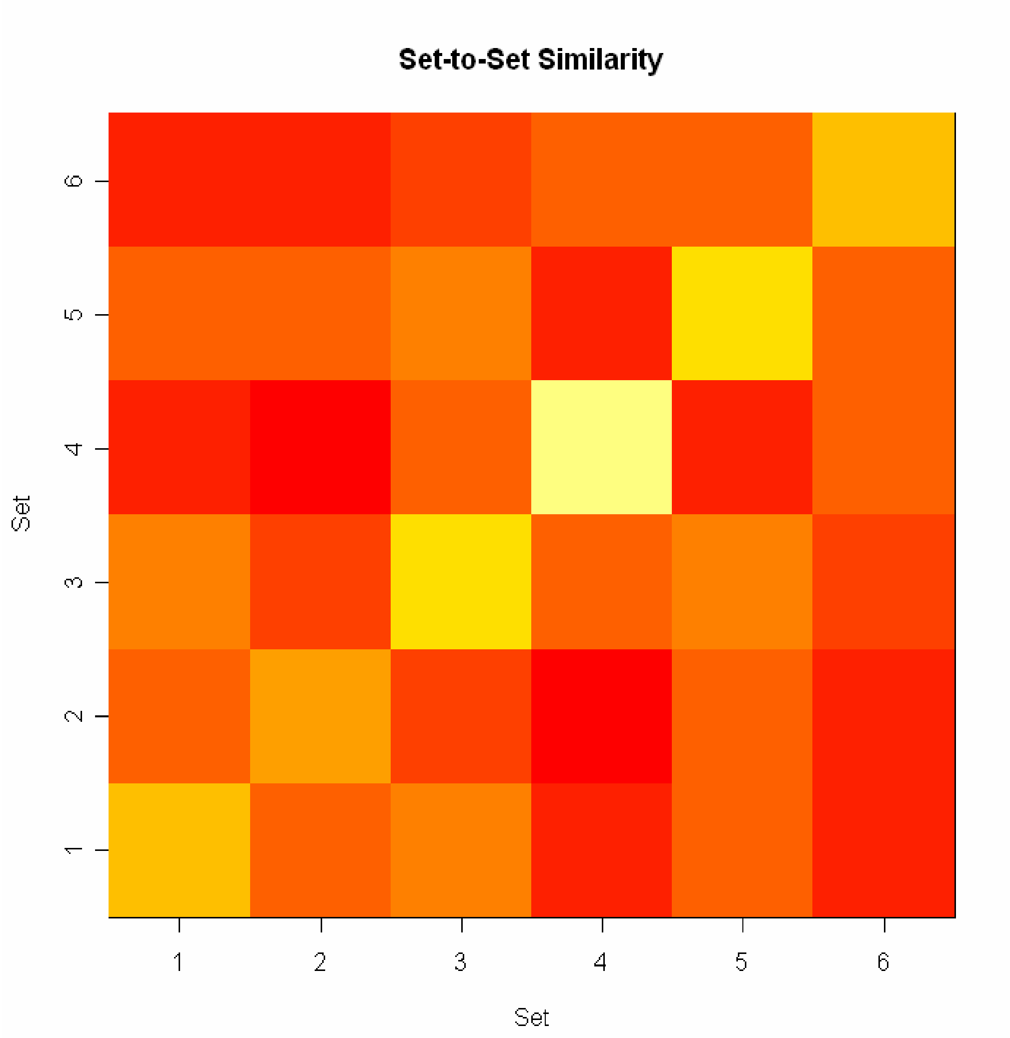

Figure 2.14. Partana plot, showing the similarity of each cluster, compared to each other cluster. Yellow indicates similarity; red indicates a lack of similarity.

Table 2.5. Partana values for each cluster, compared to each other cluster. Higher values indicate greater similarity. Values of greatest similarity for each cluster are highlighted.

Partana Values						
Cluster	**1**	**2**	**3**	**4**	**5**	**6**
1	***0.300***	0.141	0.193	0.062	0.180	0.066
2	0.141	***0.275***	0.098	0.026	0.156	0.049
3	0.193	0.098	***0.325***	0.163	0.202	0.134
4	0.062	0.026	0.163	***0.503***	0.084	0.178
5	0.180	0.156	0.202	0.084	***0.345***	0.157
6	0.066	0.049	0.134	0.178	0.157	***0.287***

Each cluster has the greatest similarity to itself, and low similarity to other clusters, with an overall Partana ratio of 2.06. The 6-cluster OPTSIL solution has a low table deviance of 2509, compared to 3090, 3226, and 3606 for similar 7, 8, and 9 cluster solutions evaluated, respectively. The sum of p-values for indicator species, 96, was slightly higher, but comparable to the values for 7, 8, and 9 cluster solutions (90, 81, and 82 respectively). The larger cluster solutions all had Silhouette values of 1.3, compared to 1.4 for the 6-cluster solution, indicating that within cluster to nearest neighbor ratio was higher (i.e. mathematically superior) for the smaller cluster solution.

Based on the cluster analysis, six community types were identified, and named by the most abundant indicator species (Table 2.6). Cluster 1 is dominated by *Picea pungens* (tree layer) and *Symphyotrichum lanceolatum* (herb layer). The 6th most abundant species in this community is *Populus angustifolia* (T1), indicating that this tree species is co-dominant. I identified a cottonwood-herb community (cluster 6) and a cottonwood-shrub community (cluster 3). In the tree layer, this species is often co-dominant with blue spruce, with spruce being more abundant. Experimenting with additional clusters led to the classification of a separate cottonwood forest community, containing only 3-4 samples. This cluster solution had a lower mean Silhouette value, and was not used in this analysis. Communities not dominated by tree species include a sedge/willow community (cluster 2), dominated by *Carex utriculata*, and *Salix boothii*, a *Lupinus argenteus/ Epilobium suffruticosum* community (cluster 3), and an *Equisetum variegatum/ Agrostis stolonifera* community (cluster 5).

Table 2.6. Cluster number, community type, cluster size, and number of occurrences on each landform type. Vegetation layer (T1-upper tree layer, T2-lower tree layer, S1-upper shrub layer, S2-lower shrub layer or H-herbaceous layer) of each species is indicated.

		Landform Occurrence					
Cluster/Community	size	bank	old channel	gravel-bar	abandoned gravelbar	flood-plain	terrace
1. *Picea pungens* T1 *Symphyotrichum lanceolatum* H *(+ Populus angustifolia* T1)	27	0	1	0	0	20	6
2. *Carex utriculata* H *Salix boothii* S2	7	2	4	0	0	1	0
3. *Populus angustifolia* S2	11	0	0	1	8	0	2
4. *Lupinus argenteus* H *Epilobium suffruticosum* H	3	0	0	0	3	0	0
5. *Equisetum variegatum* H *Agrostis stolonifera* H	28	9	5	9	1	4	0
6. *Populus angustifolia* H	6	0	0	3	3	0	0

Communities occur on significantly distinct geomorphological landforms ($p<0.01$, chi-square test) (Table 2.6). The mixed spruce/cottonwood community (cluster 1) occurs on floodplains and terraces, and the sedge/willow community (cluster 2) occurs on banks and old channels. The lupine community (cluster 4) and the shrubby cottonwood community (cluster 3) occur on abandoned gravelbars, and the herbaceous cottonwood community (cluster 6) occurs on gravelbars, and abandoned gravelbars. The wet-graminoid community (cluster 5) occurs on all sections except terraces, but is particularly abundant on banks and gravelbars.

Communities also occupy distinct regions of the NMDS ordination plot, with no overlap between clusters (Figures 2.15-2.16). While both the ordination and the cluster solution are based on Bray-Curtis dissimilarity matrices, the solutions are independent of each other.

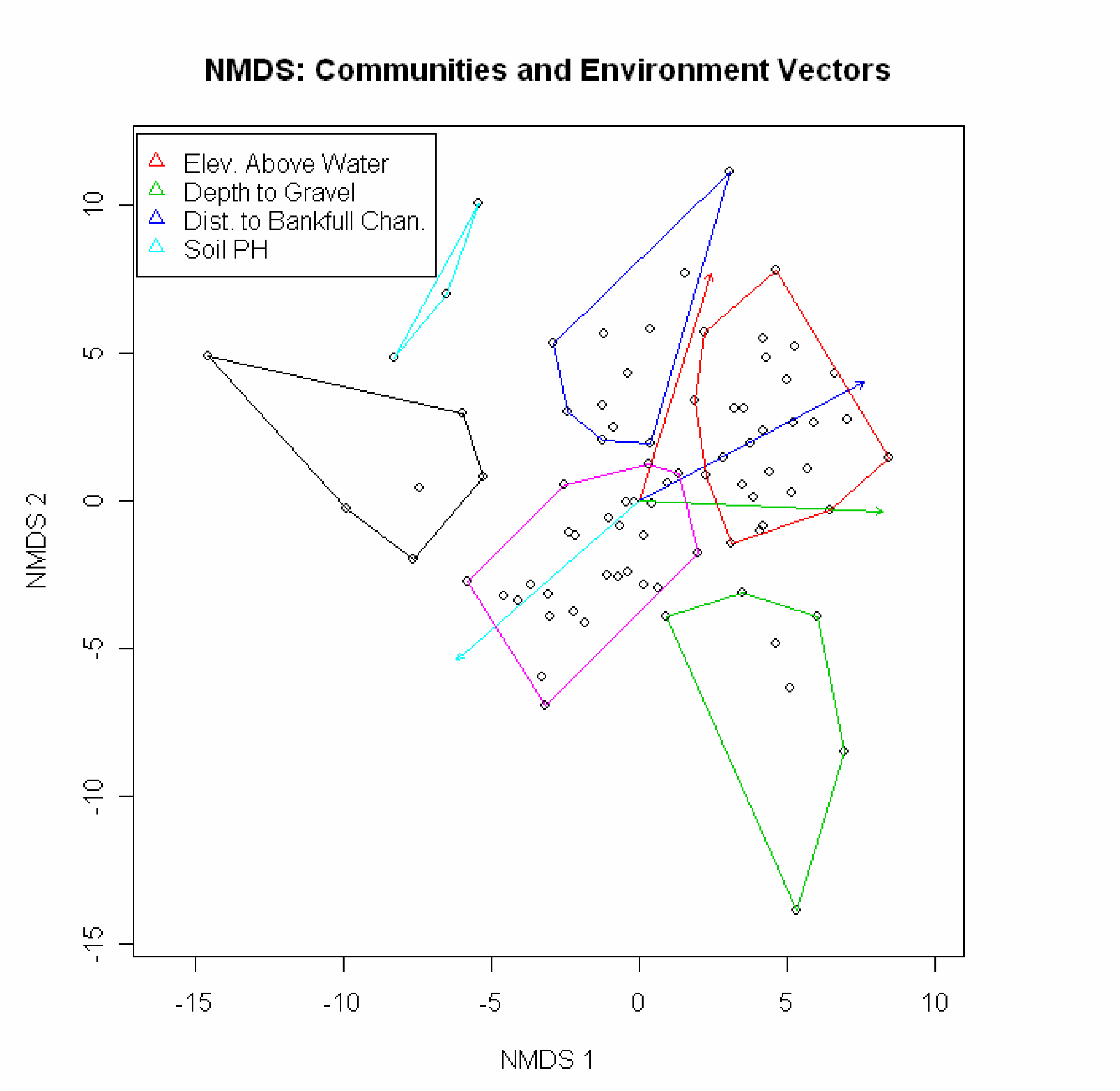

Figure 2.15. NMDS ordination plot with vectors of environmental variables, and community types selected. R^2 values for elevation above water, log-depth to gravel, log-distance to bankfull channel, and soil pH vectors are 0.41, 0.68, 0.45, and 0.34 respectively.

Red: *Picea pungens* T1 / *Symphyotrichum lanceolatum*
(+ *Populus angustifolia* T1)
Green: *Carex utriculata* H / *Salix boothii* S2
Dark Blue: *Populus angustifolia* S2
Light Blue: *Lupinus argenteus* H / *Epilobium suffruticosum* H
Pink: *Equisetum variegatum* H / *Agrostis stolonifera* H
Black: *Populus angustifolia* H

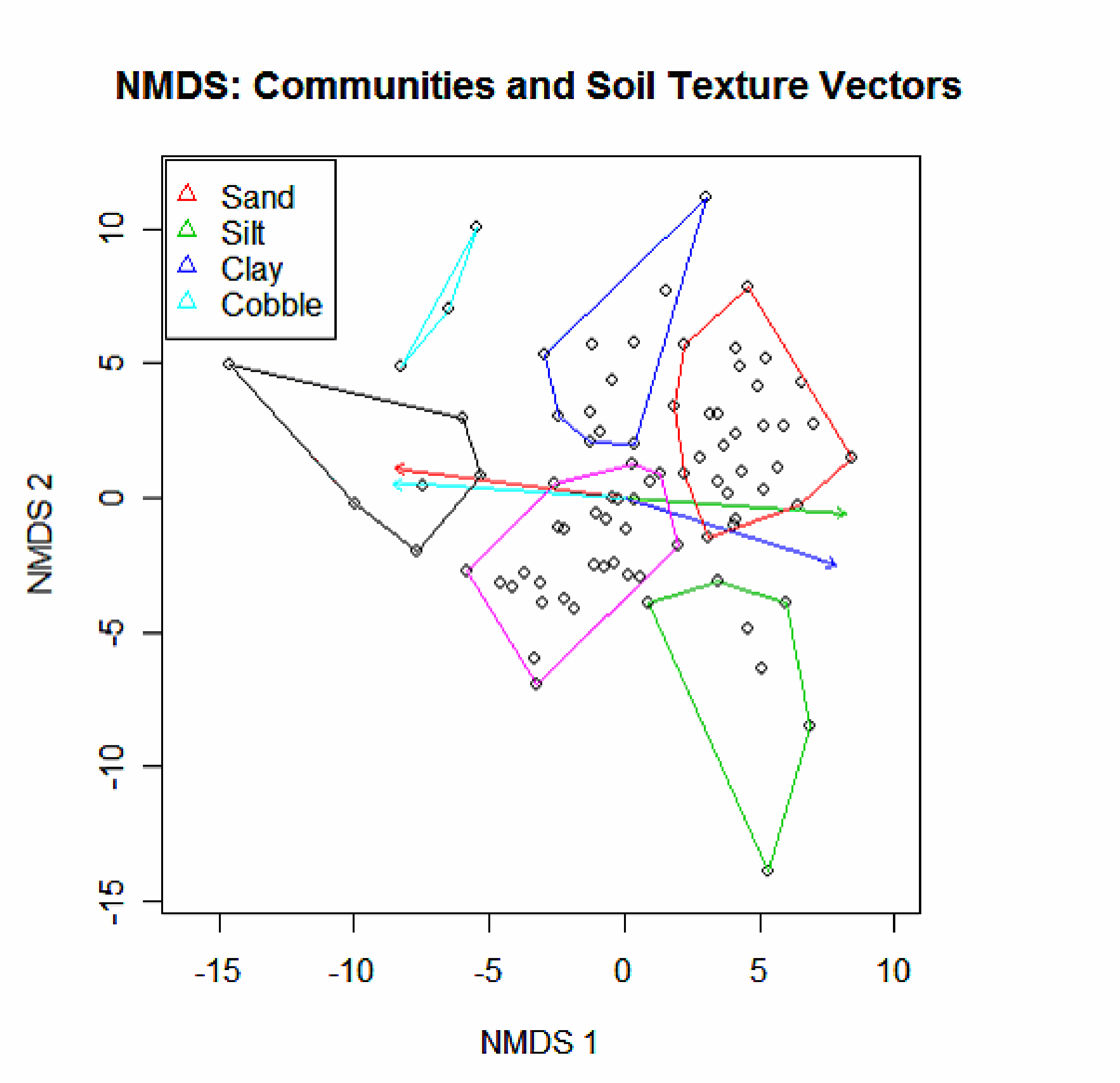

Figure 2.16. NMDS ordination plot with vectors of soil texture variables, and community types selected. R^2 values for probability of cobble, and percent sand, silt, clay are 0.49, 0.27, 0.24, and 0.28 respectively.

Red:	*Picea pungens* T1 / *Symphyotrichum lanceolatum* (+ *Populus angustifolia* T1)
Green:	*Carex utriculata* H / *Salix boothii* S2
Dark Blue:	*Populus angustifolia* S2
Light Blue:	*Lupinus argenteus* H / *Epilobium suffruticosum* H
Pink:	*Equisetum variegatum* H / *Agrostis stolonifera* H
Black:	*Populus angustifolia* H

The shrubby cottonwood community and the mixed forest community both occur on the section of the NMDS plot with high elevation above water, and low pH (Figure 2.15). The mixed forest community occurs at a greater depth to gravel, in soils with higher silt and clay content, further away from the bankfull channel (Figures 2.15-2.16). The sedge/willow community occurs in similar conditions, but at lower elevations from water, and higher pH levels. The herbaceous cottonwood community occurs at low depths to gravel, in sandy, cobbled substrates, close to the bankfull channel. The lupine community occurs similarly, but at higher elevations above water. The variables "elevation" "braid index" and "y-coordinate" have low R^2 values, and are not meaningful to plot linearly. Other variables with marginal R^2 values are also excluded from Figures 2.15-2.16.

Discussion

NMDS Ordination and Evaluation of Environmental Variables

Of the 15 continuous environmental variables I evaluated, depth to gravel, presence of cobble, pH, distance to bankfull channel, and elevation above water describe the greatest deviance in the NMDS ordination, and also have reasonably linear models (Table 2.3). These 5 variables play a large role in structuring the ordination, and are strongly related to riparian vegetation composition in my study area. Additionally, soil texture (percent sand, silt, and clay) appears to influence vegetation.

Distance to bankfull channel is an important variable, while distance to low water channel is not. These variables are only weakly correlated, despite being intuitively similar. This suggests that large-scale hydro-geomorphological processes occurring under high water conditions play a large role in shaping vegetation, while factors linked to low-water channel proximity, such as water availability, are less important. Previous research has emphasized flood regime (Nilsson and Svedark, 2002), and the processes of erosion, deposition, and lateral channel migration as being influential to plants (Naiman and Decamps, 1997). Communities proximal to the active channel tend to be younger, and exposed to a higher frequency, magnitude, and duration of floods (Gregory *et al.*, 1991). Samples on the right side of the NMDS plot tend to have a greater distance from the bankfull channel (Figures 2.9, 2.15), and greater depth to gravel (Figures 2.8, 2.15).

Samples with high elevations above water occur on the upper section of the NMDS plot (Figures 2.12, 2.15), and are not necessarily distant from the bankfull channel. Soil pH varies across samples, with more basic conditions on the lower left of the NMDS plot (Figures 2.11, 2.15). The study area has a high mean pH of 7.6. This is likely due to the largely undeveloped, recently deposited alluvial substrates, as acidification is partially due to decomposition of organic matter (Brady, 1974). Elevation above water and pH have both been previously identified as structuring riparian vegetation (Sagers and Lyon, 1997; Lyon and Sagers, 1998). Elevation above water may reflect water availability as a measure of depth to water table, an important variable structuring vegetation along the Colorado River and tributaries (Busch and Smith, 1995). Alternatively, it may simply reflect flooding likelihood and inundation duration, also recognized to be relevant (Greulich *et al.*, 2007, Gregor *et al.*, 1994). Relative elevation is an important categorical variable (Table 2.4), and despite some overlap with elevation above water, it provides insight on local microenvironments produced by areas surrounding a plot.

The variables elevation and distance from confluence have low D^2 values for GAM models (Table 2.3), and the fitted surfaces appear to be complex. The GAM surfaces for these variables indicate samples with minimum elevation, which are also furthest downstream near the confluence, occur in the center of the ordination plot. While there is a weak trend, it is complex, and these variables have limited value in explaining community structure. The range of these variables is relatively narrow, given the small size of the study area, so strong trends would not be expected.

Soil texture, particularly percent cobble, has explanatory value in the study area. Sediment size class has previously been found to structure plant communities (Hupp and Osterkamp, 1985). The binomial GAM fit to percent cobble ($>5\%$ versus $< 5\%$) has a high D^2 value of 0.71 (Table 2.3), with samples on the left side of the NMDS plot having high cobble (Figures 2.10, 2.16). Percent of fine substrates (sand, silt, and clay) also indicate trends, with the right side of the ordination plot being high in silt and clay, and the left side being high in sand (Figure 2.16). On the Snake River south of Grand Teton National Park, cottonwood forest communities are structured by moisture, and the moisture holding capacity of soil (Merigliano, 2005). This may also be the case in my study area, since texture affects the water holding capacity of soils (Brady, 1974). Along the Mississippi River, the single most important gradient identified was flood inundation, and the resulting soil characteristics (Greulich *et al.*, 2007). Soils of riparian zones are the indirect product of fluvial processes, which determine the flow of substrate and nutrients (Nilsson and Svedmark, 2002).

Cluster Analysis of Communities

Plant community types were classified using a relatively simple, 6-cluster OPTSIL model. This model has the greatest Silhouette width of all models I experimented with, and therefore the greatest ratio of within-cluster to nearest neighbor similarity (Figure 2.13). Ecologically, it may be desirable to identify more communities for management purposes. For my goal, which is to understand how communities respond to environmental gradients related to fluvial processes, this simple model is adequate.

Identifying communities can be done very coarsely, as I have done, or more finely, depending on objectives. Since riparian communities likely occur as a continuum (Sagers and Lyon, 1997), distinctions are somewhat arbitrary. On the Snake River south of Grand Teton National Park, three separate cottonwood forest community types were identified, occurring at varying levels of moisture stress (Merigliano, 2005). These forest communities may exist in my study area, but when all vegetation types are sampled, subtle differences in one type become less prominent.

Given the prevalence of cottonwood communities in the herb and shrub layers, I would expect to also identify a cottonwood forest community (Table 2.6). The natural succession in the area is from cottonwoods to spruce, and the forests are often mixed. While individual stands can be primarily cottonwood or spruce, the overall composition is typically similar. When I increased the number of clusters to 9 community types, I identified a cottonwood forest community, comprising of 4 samples. Lodgepole pine was also abundant in this cluster, suggesting that when cottonwoods grow separately from the spruce communities, they resemble upland forests. I also identified a spruce forest with an *Equisetum arvense* understory, suggesting that when spruce grow independently of cottonwoods, it is in moist habitats. While additional communities may be useful to identify, Partana analysis showed a high degree of similarity between new clusters, and the indicator value of tree species decreased as more forest clusters were added.

The clusters that I have identified occupy completely separate regions of the NMDS ordination plot (Figures 2.15-2.16). Cluster analysis was conducted independently of the NMDS ordination, which increases our confidence in the distinctions of these communities. By plotting vectors of environmental variables, community trends are visible across elevation above water, depth to gravel, distance to bankfull channel, soil pH, and soil texture.

Based on NMDS trends (Figures 2.15-2.16), the shrubby cottonwood community and the mixed forest community both occur at high elevations above water, with the former being closer to the bankfull channel, and more recently influenced by large-scale fluvial processes. The mixed forest community has the most acidic conditions, which is probably related to increased breakdown of organic material in the more established soils (Brady, 1974). Soils of these forests are comparatively deep, with high silt and clay content. The sedge/willow community occurs in similar soil textures, but at lower elevation above water, and higher pH levels. The herbaceous cottonwood community occurs on sandy, cobbled substrates, closest to the bankfull channel. GAM contours indicate that this is less than 20m from the bankfull channel, with a depth to gravel of zero. These trends are consistent with the life history of cottonwoods, requiring recently flooded, newly deposited alluvial substrate in order to germinate (Naiman *et al.*, 2005, Mahoney and Rood, 1998). There is a general trend across the ordination plot, with early successional communities on the left, and late successional communities on the right (Figure 2.15). The lupine community occurs on cobbled substrates, at higher elevations above water than cottonwood. New alluvial surfaces that are colonized by species such as cottonwood tend to accumulate fine sediment (Malanson and Butler, 1990, Francis, 2006, Tabacchi *et al.*, 2000), which explains why shrubby cottonwood communities tend to have less cobble than herbaceous cottonwood communities. Abandoned gravelbars with lupine communities were apparently not colonized by cottonwoods, and did not accumulate sediment, so that they remain cobbled and arid.

Geomorphological landforms support distinct riparian plant communities (Table 2.6), a relationship previously observed by Hupp and Osterkamp (1985). Succession of cottonwood communities follows the progression of landform. Young, herbaceous cottonwoods grow on recently established gravelbars, shrubby communities on abandoned gravelbars no longer flooded annually, and mature cottonwood/spruce forests occur on floodplains and terraces. The lupine community occurs on abandoned gravelbars, and the sedge/willow community on banks and old channels. Landforms are associated with elevation above water (Hupp and Osterkamp, 1985), which is related to the likelihood of flooding. Both elevation above water and flooding are significant variables. Geomorphologic landform incorporates these and other environmental variables that structure vegetation, and is very effective for generalizing where community types will occur.

Conclusions

I evaluated a wide range of environmental variables to determine how they structure vegetation, and community type. Depth to gravel, soil texture, pH, distance to bankfull channel, elevation above water and geomorphologic landform were the most important variables. While these variables influence plants, the relationship is reciprocal, and plants affect many environmental variables. Sedimentation is promoted by plant growth, and erosion hindered, leading to finer substrates, and greater depth to gravel on vegetated surfaces (Malanson and Butler, 1990, Francis, 2006, Tabacchi *et al.*, 2000). As forests mature and organic material accumulates, soils become more acidic (Brady, 1974). Large-scale patterns in landform, including elevation above and distance to water, are less influenced by plant growth. However, landform and vegetation progress together, with mature communities occurring on older, higher surfaces, increasingly distant from the river as the channel migrates laterally (Gregory *et al.*, 1991).

While vegetation and environmental factors are interrelated in riparian zones, the overall trends are clear. Understanding how vegetation relates to specific gradients on these tributaries may help prioritize management on the Snake River, and other regulated rivers. Plant communities are determined by variables linked to large-scale hydro-geomorphological processes. Maintaining these processes through a natural, dynamic flow regime will support the persistence of biodiverse riparian ecosystems.

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CHAPTER 3

RIPARIAN PLANT COMMUNITIES OF TWO UNREGULATED TRIBUTARIES, COMPARED TO THE DAM-REGULATED SNAKE RIVER

Abstract

Riparian ecosystems depend on the dynamic nature of rivers, such that dam-induced changes to the flow regime can have detrimental effects on the plant communities of these diverse areas. To determine whether riparian plant communities of the regulated Snake River in Grand Teton National Park, WY, are impacted by dam operation, I compared the vegetation to that of two unregulated tributaries, Pacific Creek and Buffalo Fork. Species richness per plot is higher on the tributaries than on the Snake River. With the use of NMDS ordination and clustering techniques, I found the composition of the upper section of the Snake River, immediately below the dam, to be distinct. There is no evidence that the dam is influencing the vegetation of lower sections of the river, which suggests the tributaries may have a mitigating effect. Whether trends on the upper section are dam-related is debatable, as this section is naturally more incised. Other important environmental variables structuring the vegetation include elevation above water, depth to gravel, and geomorphological landform.

Introduction

Riparian Ecosystems

Riparian ecosystems are considered to be the most biodiverse of any terrestrial system (Naiman *et al.*, 1993). As ecotones between terrestrial and aquatic systems, riparian zones provide important habitat, produce microclimates, and act as wildlife corridors (Naiman and Decamps, 1997). The diversity of riparian ecosystems is largely influenced by flow regime (Nilsson and Svedmark, 2002, Naiman *et al.*, 1993). The dynamic nature of rivers leads to a high degree of disturbance-related environmental heterogeneity, and subsequently, biodiversity (Nilsson and Svedmark, 2002).

Alterations to the flow regime via damming, particularly the magnitude, frequency, timing and duration of flooding events, can have major implications for the plant communities that depend on the dynamic nature of river systems (Naiman and Decamps, 1997, Poff *et al.*, 1997, Nilsson and Svedmark, 2002). Managed rivers tend to have lower, disrupted peak flows and are often sediment deficient, since dams act as sediment traps (Petts and Gurnell, 2005). This leads to channel degradation, and a lack of alluvial deposits, as a sediment deficit leads to downcutting (Leopold *et al.*, 1964). The processes of erosion, deposition, and lateral channel migration are integral to the dynamic nature of rivers (Naiman and Decamps, 1997) and managed rivers tend to be artificially stable (Merritt and Cooper, 2000).

Riparian forests dominated by cottonwoods have received particular attention in recent years, and the decline of these species in many dammed rivers reflects a strong dependence on the physical processes of rivers (Rood *et al.*, 2003, Johnson, 2000, Rood and Mahoney 1990, Fenner *et al.* 1985, Merritt and Cooper, 2000). Two related explanations for this decline are geomorphological changes involving sedimentation and channel form, and hydrological changes such as flooding (Rood and Mahoney, 1990). Cottonwood seeds, viable for only 1-2 weeks, are wind dispersed in very large numbers and require a moist, fine substrate in order to germinate (Fenner *et al.*, 1985, Naiman *et al.*, 2005, Mahoney and Rood, 1998). The timing of seed dispersal has evolved to coincide with peak floods of early spring, so that germination occurs as water levels recede slowly (Naiman *et al.*, 2005). Dam regulation can reduce the area of suitable substrate and limit cottonwood regeneration, causing a shift to late-successional communities (Marston *et al.*, 2005).

Hydro-geomorphological processes play a large role in structuring riparian plant communities (Hupp and Osterkamp, 1996, Ward, 1998). Geomorphological landforms, including floodplains, terraces, and gravelbars, are associated with distinct plant communities (Bendix and Hupp, 2000, Hupp and Osterkamp, 1985). Landforms have characteristic flooding regimes, substrates, and elevations above water, which are all governed by fluvial processes, and interact to structure vegetation (Bendix and Hupp, 2000, Hupp and Osterkamp, 1985). The link between vegetation and geomorphological processes is complex, as vegetation influences sedimentation and erosion (Francis, 2006, Malanson and Butler, 1990, Tabacchi *et al.*, 2000)

Many important environmental gradients have been identified as influencing riparian vegetation, including inundation duration, (Greulich *et al.*, 2007, Gregor *et al.*, 1994), depth to water, salinity, soil organic content, (Busch and Smith, 1995), height above water, pH, (Sagers and Lyon, 1997), soil moisture (Merigliano, 2005), geomorphic valley type (Harris, 1988) and stream power (Bendix, 1994). In general, these gradients are either directly or indirectly related to hydro-geomorphological processes.

Several mechanisms have been proposed for the high levels of biodiversity in riparian areas. Biotic factors, geomorphology and landscape patterns are all influential (Tabacchi *et al.*, 1996). Flooding disturbance, at intermediate levels, was found to increase diversity in wetland and riparian sites in Alaska (Pollock *et al.*, 1998). This was attributed to plant death by disturbance, thereby slowing competitive exclusion, and increasing diversity. In addition to flood frequency, high levels of spatial variation of flood frequencies were also correlated with species richness (Pollock *et al.*, 1998).

Dispersal is another important mechanism related to flooding, and affecting species richness and composition. Flooded plots in Northern Sweden had 40-200% more colonizing species than unflooded plots, leading to higher richness (Jansson *et al.*, 2005). Richness was found to be lower on tributaries than on a main river in Sweden (Nilsson *et al.*, 1994). This could be due to more effective species dispersal through hydrochory on the larger river, or, alternatively, upstream richness in the entire region may be reflected in the downstream riparian zone (Nilsson *et al.*, 1994).

Compositional differences exist between the regulated Yampa River and the unregulated Green River in Colorado, and have been attributed to the progression to late-successional, less diverse stands on the Yampa River (Uowolo *et al.*, 2005). On the lower segment of the Snake River, species diversity has decreased, as river regulation through the Palisades Dam has caused a decline in early-successional cottonwood regeneration, and an increase in late-successional spruce communities (Marston *et al.*, 2005). The expansion of spruce forests has also been observed below the Jackson Lake Dam (Marston *et al.*, 2005).

In the present study, I compared riparian plant communities of the dam-regulated Snake River to two unregulated tributaries. Previous studies of regulated versus naturally flowing rivers have been successful along the Green and Yampa Rivers in Colorado (Merritt and Cooper, 2000, Uowolo *et al.*, 2005), and have concluded differences in vegetation to be linked to regulation. Impacts due to regulation tend to be most severe directly below dams, before tributaries can enter (Rood *et al.*, 2005).

The purpose of this study was to determine whether riparian community structure along the Snake River and tributaries is related to river regulation, and to examine relevant hydro-geomorphological factors in these systems. I hypothesized that unregulated river sections would consist of early successional, disturbance-associated communities compared to regulated sections, and that differences would be most pronounced immediately below the dam. I compared species richness and community composition across these sections. I used ordination and clustering techniques to model composition, and determined the role of river section, and of various hydro-geomorphological factors in structuring vegetation.

Multivariate Techniques

Several multivariate techniques were used in this thesis, including the unconstrained ordination technique NMDS (Non-Metric Multidimensional Scaling), and OPTSIL, a form of Cluster Analysis. Multivariate statistics were performed in R (R Development Core Team, 2007).

NMDS is an ordination algorithm that is “non-metric” in that functions are calculated on rankings, with values simply ranked from minimum to maximum, rather than on a ratio scale (Kruskal and Wish, 1978). The rank distances of samples in the ordination should reflect the rank distances in the dissimilarity or distance matrix, which is often calculated using a Bray-Curtis dissimilarity index (Bray and Curtis, 1957). NMDS, especially based on a Bray-Curtis dissimilarity matrix, is considered to be one of the more robust ordination techniques (Minchin, 1987, Faith *et al.*, 1987). NMDS models involve an algorithm designed to minimize stress, which is calculated as the square root of a normalized “residual sum of squares” (Kruskal and Wish, 1978).

As with many ordination techniques, data from the dissimilarity matrix are condensed into a few dimensions, and 2-dimensional NMDS plots are often very effective. One problem with an NMDS algorithm is selecting a solution with a local minimum of stress, rather than the global minimum (Kruskal and Wish, 1978). To address this problem, multiple iterations can be used, with independent starting configurations, and the model with the lowest stress selected. The correlation between an ordination and the underlying matrix can also be evaluated by a correlation statistic (labdsv package; Roberts, 2007).

Like NMDS, Cluster Analysis is generally based on a similarity, dissimilarity, or distance matrix (Everitt, 1993). The Bray-Curtis dissimilarity index (Bray and Curtis, 1957) is a common index for evaluating the proximity of samples to each other. Clustering techniques are often hierarchical, and can be represented by a dendrogram, showing sample partitioning (Everitt, 1993). Agglomerative methods involve fusing all samples into groups, and divisive methods separate all samples into progressively finer groupings, until only individuals remain (Everitt, 1993). It is also possible to use optimization algorithms to optimize some criterion, typically by reallocating samples to more suitable clusters (Everitt, 1993). One such method is OPTPART (optpart package for R; Roberts, 2008), which is a reallocation algorithm designed to maximize within versus between cluster dissimilarity (Aho *et al.*, 2008). Ideally, samples in the same cluster should have the least dissimilarity to each other. A similar method is OPTSIL (optpart package for R; Roberts, 2008), which optimizes silhouette width. Silhouette width is a measure of cluster suitability, based on the average dissimilarity of samples in a cluster, compared to samples in the nearest neighbor cluster, and is measured as follows (Kaufman and Rousseeuw, 1990):

$$s_i := (b_i - a_i) / max(a_i, b_i)$$

Where a_i is the average dissimilarity between a sample and all other samples in that cluster, and b_i is the *smallest* of the average dissimilarities between a sample and all samples in *other* clusters (i.e. nearest neighbor cluster) (cluster package; Maechler *et al.*, 2005). Higher average silhouette values across clusters, and across the entire cluster solution, are indicative of cluster distinctness (Kaufman and Rousseeuw, 1990).

Indicator species can be calculated for clusters, in order to characterize the composition of the clusters. One method of classifying species is Dufrêne and Legendre's (1997) Indicator Value algorithm, as implemented in DULEG (labdsv package; Roberts, 2007). Dufrêne and Legendre (1997) define an indicator species as "the most characteristic species of each group, found mostly in a single group of the typology and present in the majority of the sites belonging to that group". Indicator value can be calculated as follows (Dufrêne and Legendre, 1997):

$$INDVAL_{ij} = A_{ij} \, x \, B_{ij}$$

Where $INDVAL_{ij}$ is the indicator value of species i in sites of cluster j, A_{ij} is the mean abundance of species i in sites of cluster j, and B_{ij} is the frequency of occurrence of species i in sites of cluster j. The formula originally described by Dufrêne and Legendre (1997) involves multiplying A_{ij} and B_{ij} by 100, however, the methods adapted for the DULEG function (labdsv package; Roberts, 2007) do not include this factor.

The Study Area

The Snake River, in Grand Teton National Park, WY, has two large, unregulated tributaries that enter shortly below the Jackson Lake Dam (Figure 3.1). Pacific Creek enters the main river 7.2 km downstream from the dam, and Buffalo Fork enters at 8.1 km. There are several other tributaries in the Park, including Spread Creek, Cottonwood Creek, and Ditch Creek, but Pacific Creek and Buffalo Fork are the largest, and are most comparable to the Snake River study area in elevation. These two creeks are unregulated, and contribute substantial flow to the main channel (Schmidt and Nelson, 2007). Sediment input, particularly from Pacific Creek, plays an important role in the geomorphological processes of the Snake River (Marston *et al.*, 2005). The study area includes the segments of these tributaries from the National Park boundary, to the confluence with the main river, a length of 6.7 km for Pacific Creek, and 5.4 km for Buffalo Fork. The Snake River study area extends from the Jackson Lake Dam, to

Deadman's Bar, a length of 33.6 km. Approximately 4.2 km below the dam, there is a large oxbow, with lake-like conditions, which was not sampled for the present study. Areas with obvious anthropogenic disturbance were also excluded.

The study area will be considered in five segments (Figure 3.1): SR1 refers to the 7.2 km, single channel segment of the main Snake River above the tributaries, directly below the dam. SR2 is the 6.3 km predominantly braided area between Pacific Creek and Spread Creek. SR3 is the 20.3 km partially single channel segment from Spread Creek to Deadman's Bar. BF refers to Buffalo Fork, and PC to Pacific Creek. The Snake River and its tributaries are, with the exception of the upper SR1 segment, predominantly braided rivers. The mean braid index (total channel length/main channel length) for Pacific Creek is 2.43, Buffalo Fork is 2.12, and for the Snake River it ranges from 1.0 to 3.14. The elevation of the entire study area ranges from 2012 to 2086m.

Jackson Lake existed before the dam was built in 1908 (and then rebuilt in 1916) and has historically been a sediment trap. The main effect of the dam, therefore, has been to alter flow regime, rather than sediment supply (Schmidt and Nelson, 2007). In 1958, the Palisades dam was built downstream of the National Park boundary. The use of this dam to manage water for agricultural purposes alleviated some of the need to regulate water through the Jackson Lake Dam. Since this time, peak flows have been more natural, occurring in the spring, but overall flood magnitude has been lower than estimated natural levels (Schmidt and Nelson, 2007).

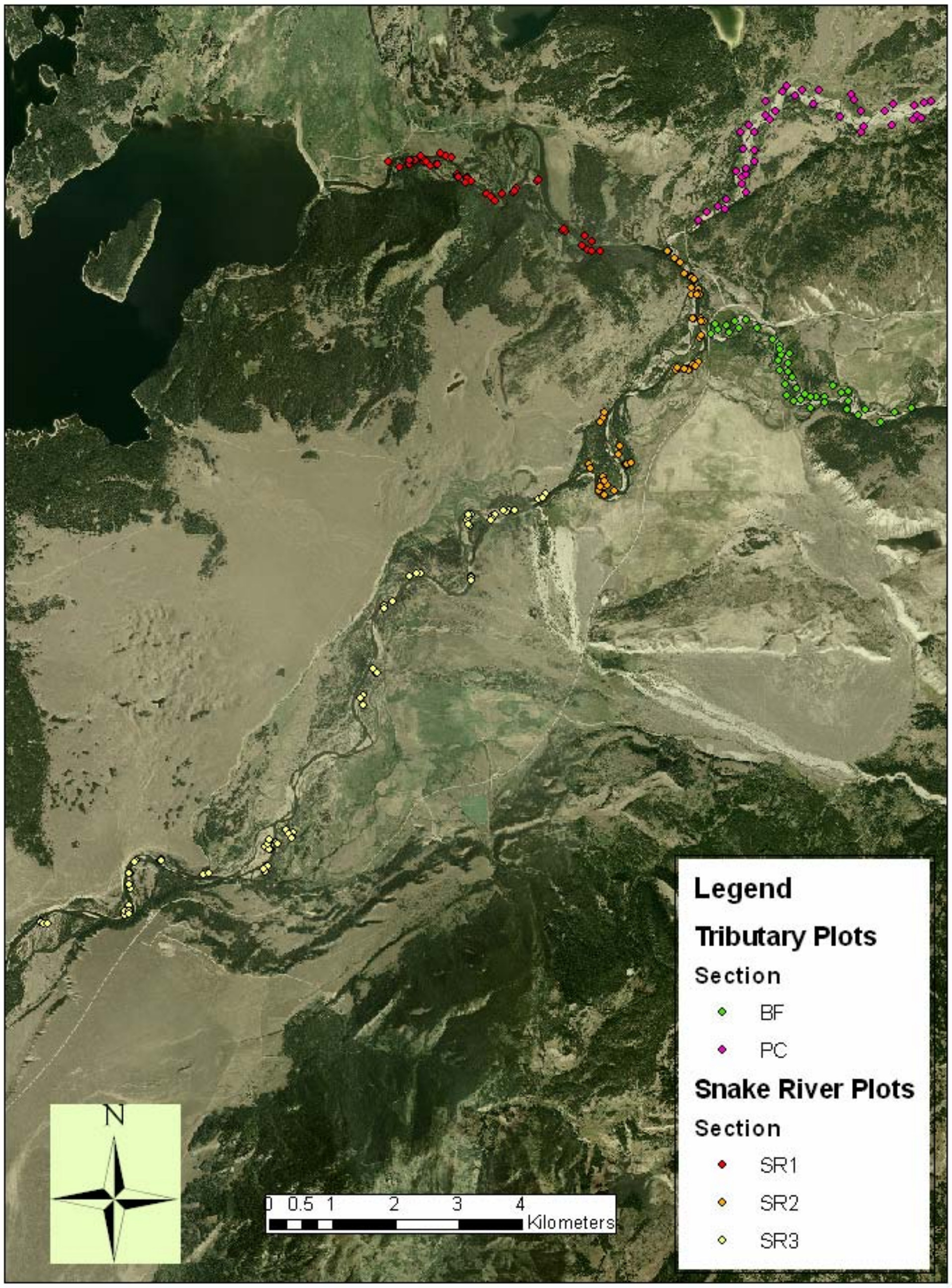

Figure 3.1. The study area, including Jackson Lake, the Snake River from the dam to Deadmans Bar, Pacific Creek and Buffalo Fork. Plots of each river section are displayed in color (BF=Buffalo Fork, PC=Pacific Creek, SR1=Snake River 1, SR2= Snake River 2, SR3= Snake River 3).

Geomorphologically, the Snake River has undergone relatively minor changes since construction of the dam, attributable to two major factors identified by Schmidt and Nelson (2007): First, the tributaries have a mitigating effect on the dam, since they contribute to high flows during the spring, and second, sediment supply has not been significantly altered. The mitigating effect of tributaries has been observed in other river systems, such that riparian areas proximal to dams tend to suffer more negative impacts (Rood *et al.*, 2005). In my study area, the upper SR1 river segment is immediately below the Jackson Lake dam, and may be most impacted.

The riparian forests of the Snake River and tributaries in Grand Teton National Park are dominated by the cottonwood species *Populus angustifolia*, and *Populus balsamifera.* All species names are based on Dorn (2001). These two cottonwood species are often indistinguishable when young, and occupy similar habitats, but *P. angustifolia* is clearly dominant in the area. As cottonwoods mature, they typically become co-dominant with *Picea pungens* (blue spruce) and eventually spruce becomes dominant. The mixed *Picea pungens* and *Populus angustifolia* system is not uncommon (Daubenmire, 1972), and a similar succession has been studied along the Red Deer River, in Alberta Canada (Cordes *et al.*, 1997). Other tree species in the study area include *Pinus contorta* (lodgepole pine), which are abundant in the uplands of Grand Teton National Park, and occur in the riparian corridor. Similarly, *Artemisia tridentata* (sagebrush) is common in the uplands, and occasionally occurs in the riparian corridor. Willow species, including *Salix boothii, S. exigua, S. lasiandra,* and *S. eriocephala*, all shrubby in growth, are common in the area, as is *Alnus incana*. Dominant wetland species include *Carex utriculata, Carex vesicaria,* and *Equisetum sp.* Six broad types of vegetation/landscape have previously been identified, and include: unvegetated channel deposits, grass covered deposits, alder-willow shrub-swampland, low density cottonwood, medium density spruce/cottonwood mix, and high density spruce (Marston *et al.*, 2005).

Below the Palisades dam, riparian plant communities dominated by cottonwood have been studied, and are primarily influenced by moisture, and the moisture holding capacity of soil (Merigliano, 2005). Three important communities, occurring at various moisture levels, are *Populus angustifolia* with *Cornus stolonifera*, *Elaeagnus commutata*, and *Heterotheca villosa* (Merigliano, 2005). Cottonwood forests are declining along this section of the Snake River, with a shift towards late-successional spruce communities as cottonwoods are unable to germinate effectively (Merigliano, 1996). Below the Jackson Lake dam, spruce is predicted to expand, due to a decline in destructive floods, and stabilization of the river (Marston *et al.*, 2005). However, evidence for stabilization was not supported by Schmidt and Nelson (2007).

Methods

During the summers of 2005 and 2006, 174 plots were established on the Snake River: 47 on SR1, 53 on SR2 and 74 on SR3. In 2007, 82 plots were established on Pacific Creek and Buffalo Fork (42 and 40 respectively). Plots were stratified across all vegetation types and geomorphological landforms. Plots size differed depending on growth form of the tallest vegetation layer: tree plots were $100m^2$, shrub plots $25m^2$, and herbaceous plots $10m^2$. To accommodate the linear nature of riparian communities, plots were rectangular. Plant community data and environmental data were recorded for each plot.

All vascular plant species were identified to species based on Dorn (2001), and percent cover was estimated visually using a modified Braun-Blanquet scale (Braun-Blanquet, 1932). Cover classes between one and five were assigned, and a trace category of 0.5 was included for species with less than 1% cover (0.5: *<1%*, 1: *1-5%*, 2: *5-25%*, 3: *25-50%*, 4: *50-75%*, 5: *75-100%*). Cover was recorded separately for each vegetation layer, so that members of a species growing in the herb layer were considered independently from those of the same species growing in the shrub and tree layers. Herb (H), shrub (S), and tree (T) layers were defined by height (H: *<=0.5m*, S2: *>0.5m-1.5m*, S1: *>1.5-3m*, T2: *>3-10m*, T1: *>10m*).

Environmental data collected for each plot included: elevation above water, distance from water, depth to gravel, slope, aspect, local elevation, topography, geomorphological landform, and flooding evidence. Elevation above water and distance to water were collected using surveying equipment after hydrographs had peaked, and were approaching base flow levels. Depth to gravel was recorded as a surrogate for substrate age. On 36 plots, gravel was not reached within 1 m. Depth to gravel for these plots was assigned as 150cm, corresponding to the deepest gravel measured (except in the case of GAMs fit to NMDS, where they were entered as ‘no data’ to avoid problems with normality). Slope and aspect were measured using an inclinometer and compass on the 55 plots with slope. The local elevation relative to surrounding areas (high, intermediate, low) and topography (concave, convex, undulating >3m, undulating <3m, flat) were classified for each plot. Geomorphological landform of each plot was classified as a bank (within the active channel), gravelbar (surface dominated by gravel within the active channel), floodplain/terrace (inundated only during major flooding events/abandoned floodplain), or old channel (abandoned channel bed).

Additional environmental variables were derived using ARC-GIS (version 9.2, ESRI Inc.), including distance to bankfull channel and braid index. Bankfull channel was defined as predominantly unvegetated, active alluvium, which is flooded annually (Schmidt and Nelson, 2007). I mapped tributary bankfull channel based on the methods and channel maps of the Snake River provided by Schmidt and Nelson (2007). Braid index was defined as the ratio of total bankfull channel length (including all secondary channels) to main bankfull channel length (Schmidt and Nelson, 2007), and was calculated for 18 relatively uniform river segments. Elevation was derived from 2007 LIDAR data, with 15cm vertical accuracy. Y-coordinate, based on UTM (Universal Transverse Mercator) projection system North coordinates, was calculated to measure latitudinal trends.

All statistical analyses were performed using the program R (R Development Core Team, 2006). Species richness, defined as the number of species occurring in each plot, was calculated. Mean species richness was compared across all landforms, river sections, and for the Snake River versus tributaries. Welsh two-sample t-tests and ANOVA were used to determine whether differences were significant.

Indicator species were identified for each river section, using the technique Murdoch (optpart package; Roberts, 2008), which calculates species positively and negatively associated with a factor. Murdoch, originally used to quantify prey preference, is calculated as the proportion of species associated with a factor, multiplied by the proportion in the environment (Krebs, 1999). Species that occurred predominantly in one river section were considered positive indicators for that section, and those that rarely occurred were negative indicators. Percent cover of taxa across sections were used to calculate a Murdoch value. Species with Murdoch values greater than 1.0 were considered as descriptive of river sections, and those with values less than -1.0 were considered negative indicators. A minimum abundance value of 1% cover and a minimum occurrence value of 10 plots were used, so that only dominant species were used for characterizing river sections.

Species composition across river sections was explored using Partana (Partition Analysis), which evaluates the within versus between group similarities (optpart package; Roberts, 2008). Using this technique, a plot can be created, displaying which group is compositionally most similar to each other group. Meaningful groups should have the greatest similarity to themselves.

The unconstrained ordination technique NMDS (Non-Metric Multidimensional Scaling; Kruskal and Wish, 1978) was applied to plant community data, using the NMDS function in R (labdsv package; Roberts, 2007, MASS package; Venables and Ripley, 2002), with a Bray-Curtis dissimilarity matrix. Based on the NMDS ordination, environmental variables were evaluated for explanatory value. This was achieved by fitting Gaussian GAMs (generalized additive models, mgcv package; Wood, 2004), and calculating D^2 values of deviance explained. Minimizing residual deviance, or maximizing deviance explained, is a method of evaluating goodness of fit of a GAM, with some parallels to the residual sum of squares in linear modeling (Wood, 2008). The D^2 value of deviance explained was defined as:

$$D^2 = (\text{null deviance} - \text{residual deviance}) / \text{null deviance}.$$

A gamma value of 1.4 was used, which increases the penalty for degrees of freedom, simplifying overfit GAM models (Wood, 2006).

The following continuous variables were considered:

- Elevation above water (m)
- Distance to low water channel (m)
- Distance to bankfull channel (m)
- Depth to gravel (cm)
- Braid index
- Elevation (m)
- Y-coordinate (UTM, m)

Categorical variables were evaluated using Ordtest (labdsv package; Roberts, 2007), to test the significance (p-value) of the correlation between a category and the NMDS ordination. This technique was applied to the categorical variables, and to each factor of the variable. The following categorical variables were evaluated:

- Landform (bank, floodplain/terrace, gravelbar, old channel)
- Topography (concave, convex, undulating >3m, undulating <3m, flat)
- Local Elevation (high, intermediate, low)
- Section (SR1, SR2, SR3, PC, BF)

Cluster analysis was performed using a non-hierarchical reallocation algorithm, involving non-permanent allocation of samples, based on a pre-determined number of clusters. These techniques were based on a Bray-Curtis dissimilarity matrix, using the OPTSIL function in R (optpart package; Roberts, 2008). Two important considerations in selecting a cluster solution were Partana, which measures the within versus between cluster similarity (Aho *et al.* 2008), and mean Silhouette width, which measures how similar the components of a cluster are to each other, compared to those of the most similar cluster. Reversals occur when a sample would be best classified in another cluster. Silhouette and Partana measure the geometry of a cluster solution. OPTSIL is designed to maximize silhouette width, thereby maximizing within cluster similarity. To consider the ecological implications of a model, a sum of the p-values of all significant indicator species across cluster was calculated, using the DULEG function in R (Dufrêne and Legendre, 1997; labdsv package; Roberts, 2007). This method defines indicator species as the product of the relative frequency and relative average abundance in clusters. Additionally, classification quality was assessed using the TABDEV function, calculating total deviance of all taxa across clusters, using fractional sums by cluster (optpart package; Roberts, 2008). Species that occur in many clusters have high deviance, so an ideal cluster classification should exhibit low deviance. This technique is based on the original vegetation data, rather than the dissimilarity matrix.

Communities were named based on the two most abundant species in each cluster that were also significant indicator species (as defined by Dufrêne and Legendre, 1997). In cases where only one species was highly abundant, one species was used in naming. Since species were measured separately in herb, shrub and tree layers, all species names include the vegetation layer (H, S1, S2, T1 or T2). Occurrence of each community type was compared across river sections, environmental variables, and geomorphological landform.

Results

Richness and Indicator Species of River Sections

Richness per plot (α-diversity) is significantly higher on the tributaries than on the Snake River, across all sizes of plots, and across each section as a whole (Table 3.1). The range of richness is 3-52 on the tributaries, and 2-51 on the Snake River. The total number of species sampled was 291 on the Snake River, and 229 on the tributaries.

Table 3.1. Mean species richness per plot for the Snake River and Tributaries, for the three different plot sizes, and for all plots combined. P-values are given, based on a Welsh 2- sample t-test.

Plot Size (m^2)	**Richness**		**P-Value**
	Tributaries	**Snake River**	
10	23.4	17.5	0.0087
25	28.9	22.6	<0.01
100	38.7	30.6	<0.01
All Plots	29.6	23.8	<0.01

Indicator species (based on Murdoch values; optpart package; Roberts, 2008) include *Pinus contorta* (upper tree layer), which is positively associated with SR1, and negatively associated with BF, SR2 and SR3 (Table 3.2). *Populus angustifolia*, in all vegetation layers but the upper shrub layer, is negatively associated with SR1, and positively associated with SR3 in the lower tree layer. *Elaegnus commutata* is also associated with SR3, and *Carex utriculata* is negatively associated with this section. SR1 has the most indicator species, the majority of which are negative. BF, PC, and SR2 have no abundant positive indicator species with Murdoch values >1.

Table 3.2. Indicator species, defined by Murdoch value, for each section. Minimum mean cover class is 1, minimum occurrence is 10 plots, and Murdoch values are >+1 or <-1. Species are shown for each section, and are followed by a letter representing the vegetation layer (Tree, Herb, or Shrub)

Section	**Positive Indicator Species**	**Negative Indicator Species**
BF	NA	*Pinus contorta* T1 *Salix boothii* S1
PC	NA	*Elaegnus commutata* S2
SR1	*Pinus contorta* T1 *Carex vesicaria* H *Calamagrostis canadensis* H	*Elaegnus commutata* S2 *Alnus incana* S1 *Picea pungens* T1 *Picea pungens* T2 *Populus angustifolia* H *Populus angustifolia* S2 *Populus angustifolia* T2 *Populus angustifolia* T1 *Equisetum variegatum* H *Medicago lupulina* H
SR2	NA	*Pinus contorta* T1 *Carex vesicaria* H
SR3	*Populus angustifolia* T2 *Elaeagnus commutata* S2	*Pinus contorta* T1 *Carex utriculata* H

Partana analysis (Figure 3.2, Table 3.3) does not indicate close compositional similarity either within, or between sections. BF is the most homogeneous section, but it is not easily distinguishable from the other river sections, since all clusters have the highest values of similarity to BF. SR1 is the most heterogeneous, with the lowest value of within-cluster similarity. The tributaries are somewhat distinct from the main river.

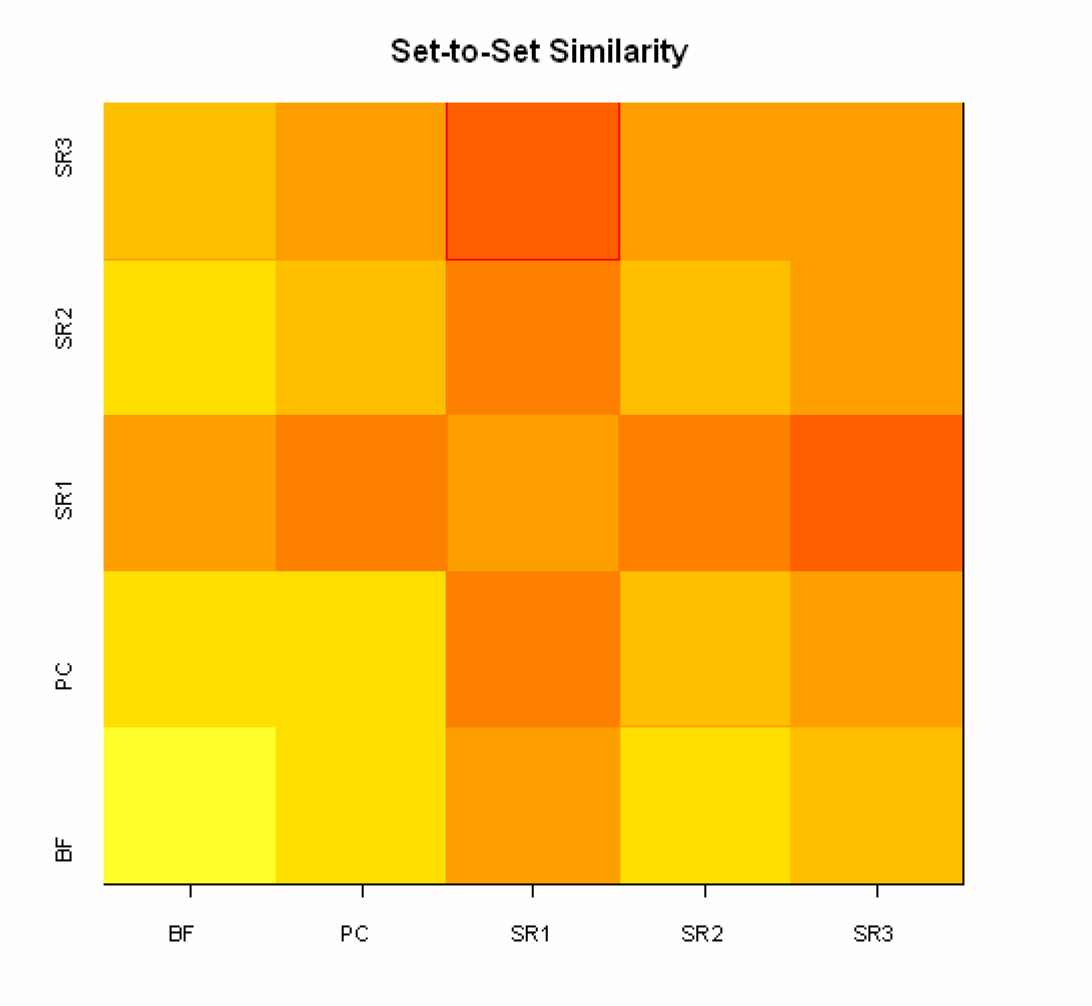

Figure 3.2. Partana plot of vegetation composition similarity of each river section, compared to all other sections. Yellow indicates similarity; red indicates a lack of similarity.

Table 3.3. Partana values for each section, compared to each other section. Higher values indicate greater similarity. Values of greatest similarity for each section are highlighted. Overall Partana ratio is 1.15.

Section	BF	PC	SR1	SR2	SR3
BF	**0.26**	0.21	0.15	0.20	0.19
PC	**0.21**	0.20	0.13	0.17	0.15
SR1	**0.15**	0.13	**0.15**	0.13	0.11
SR2	**0.20**	0.17	0.13	0.18	0.16
SR3	**0.19**	0.15	0.11	0.16	0.17

Correlation of Variables

While slope and aspect were measured in the field, these variables were not used for any analysis, since slope was zero in 201 of the 256 plots. Correlation is generally weak between continuous variables (Figure 3.3). “Braid index” and “elevation” have a correlation of $r=0.47$ (Pearson correlation), so that channels of high elevation tend to be more braided. “Elevation” and “Y-coordinate” are correlated, with more northern plots being higher in elevation. “Distance to low water channel” and “distance to bankfull channel” have a correlation of only 0.55, reflecting major seasonal variation. Landform is significantly non-random across river sections ($p<0.01$, chi-square), such that floodplains/terraces are correlated with SR1, and gravelbars are negatively correlated with this section. Banks were sampled most on the BF section. Compared to other sections, SR1 has the highest mean elevation above water ($p=0.051$, Welsh 2-sample t-test) and the greatest mean depth to gravel ($p<0.01$).

NMDS Ordination and Evaluation of Environmental Variables

The NMDS ordination has a correlation of 0.82 with the Bray-Curtis dissimilarity matrix, and is a 2-dimensional model (Figure 3.4). Including a third dimension only increased the r-value to 0.86. Several general trends are visible on the ordination diagram, including the location of samples from the SR1 section (Figure 3.5). These samples tend to occur on the left side of the ordination plot. No other trend in section is easily visible. The landform types “gravelbar” and “floodplain” occupy separate areas of the ordination (Figure 3.6).

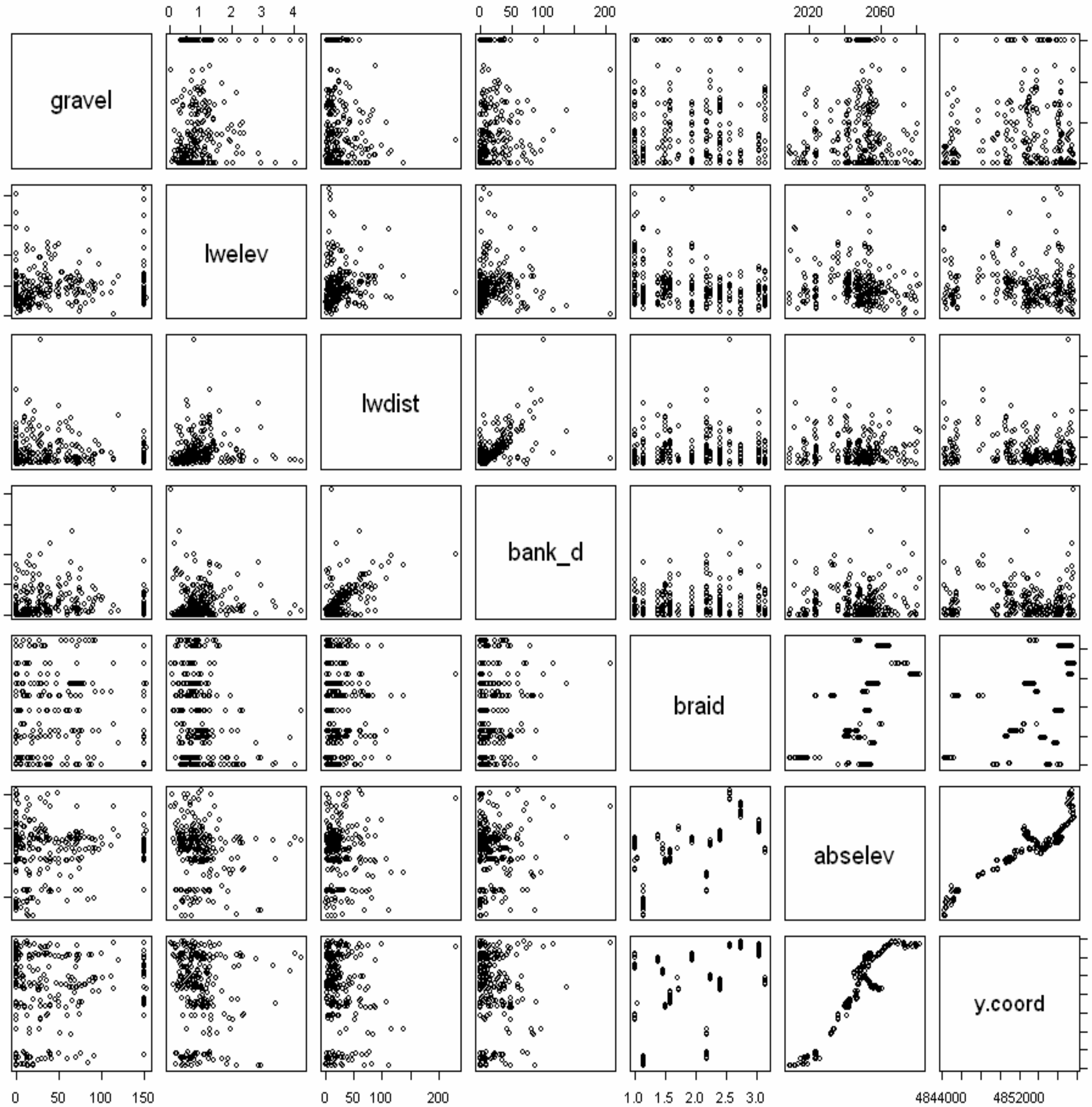

Figure 3.3. Correlations of the continuous variables depth to gravel, elevation above water, distance to low water channel, distance to bankfull channel, braid index, elevation, and y- coordinate.

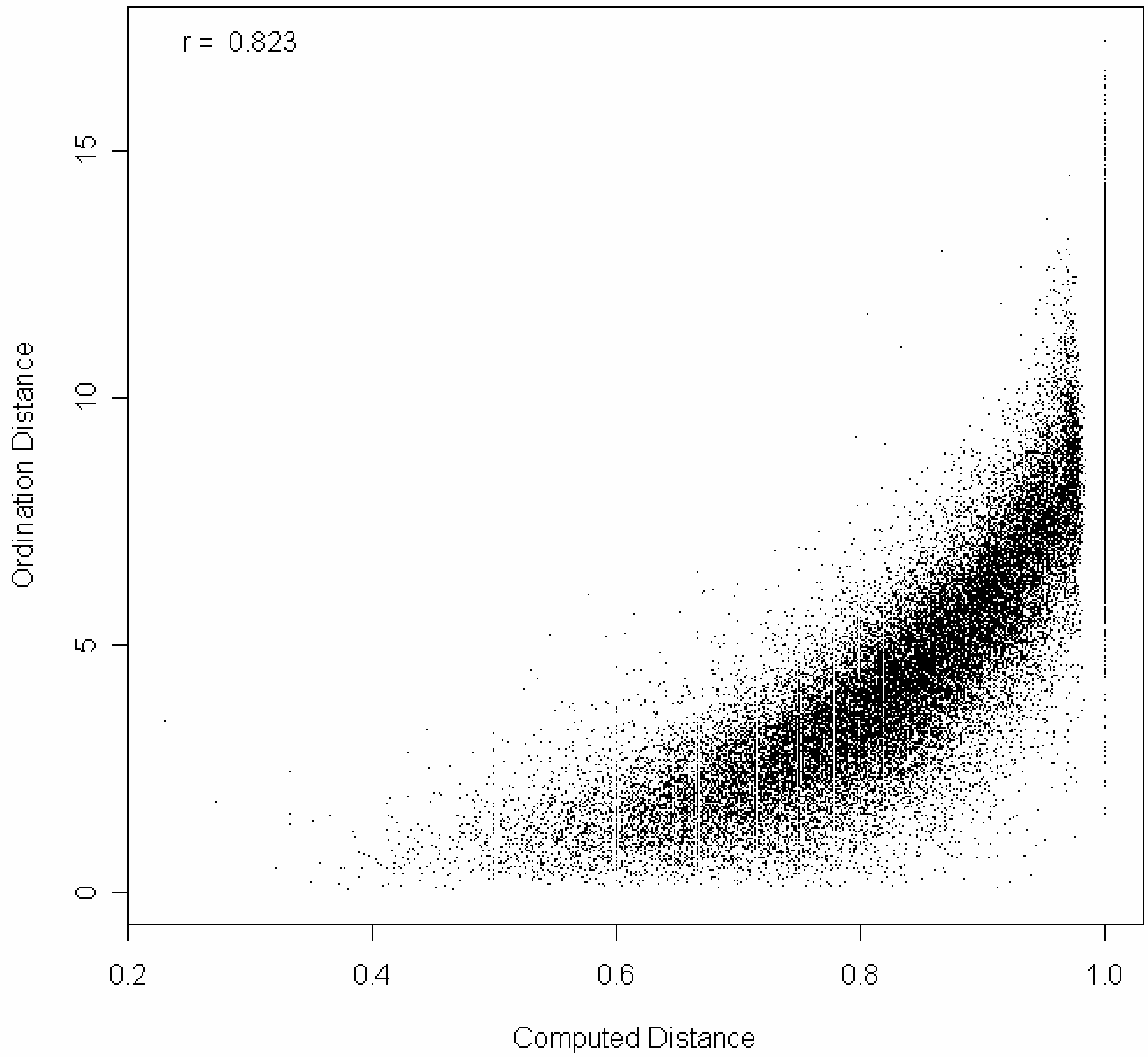

Figure 3.4. Correlation of ordination and computed distances of sample plots, giving an indication of the NMDS ordination quality (r=0.82).

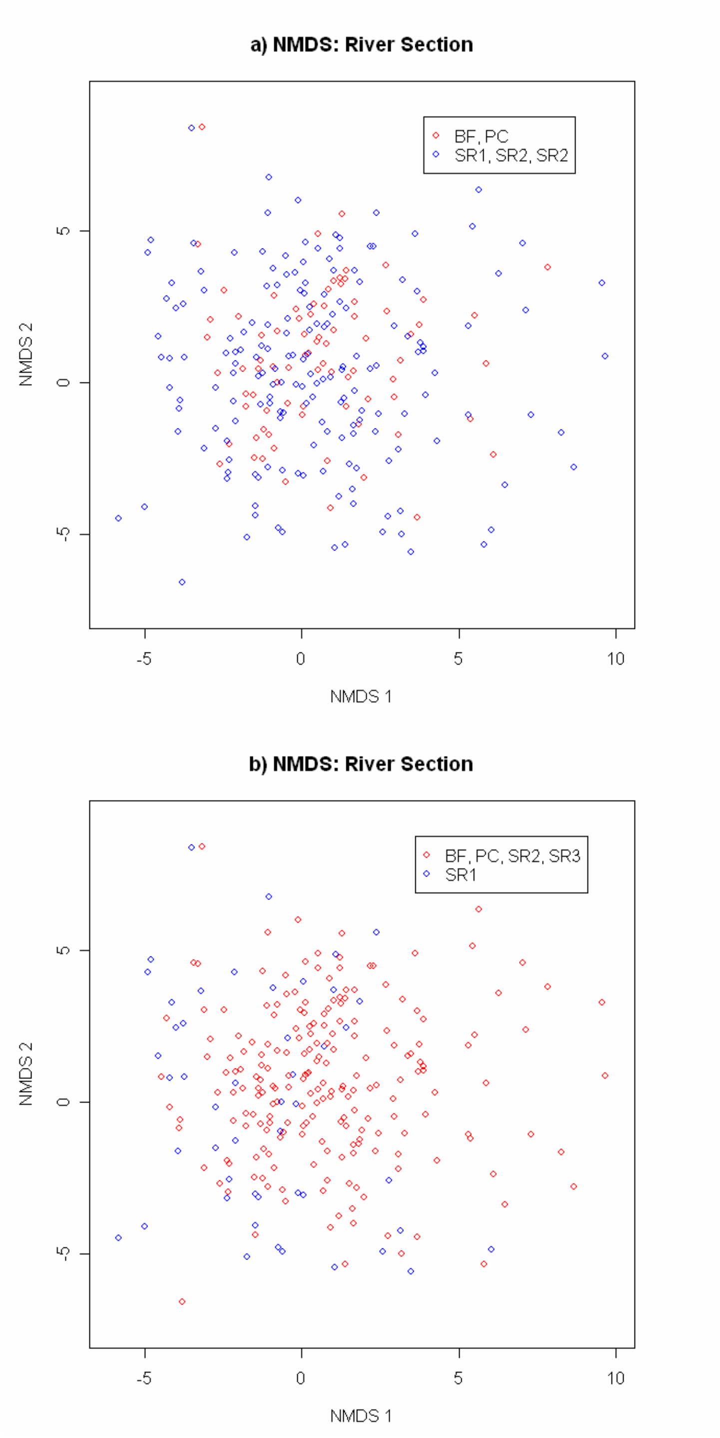

Figure 3.5. NMDS ordination plot, with river sections highlighted (SR1-Upper Snake River, SR2-Middle Snake River, SR3-Lower Snake River, PC-Pacific Creek, BF-Buffalo Fork) a) Tributary samples are red, Snake River samples are blue. b) SR1 samples are blue, all other samples are red.

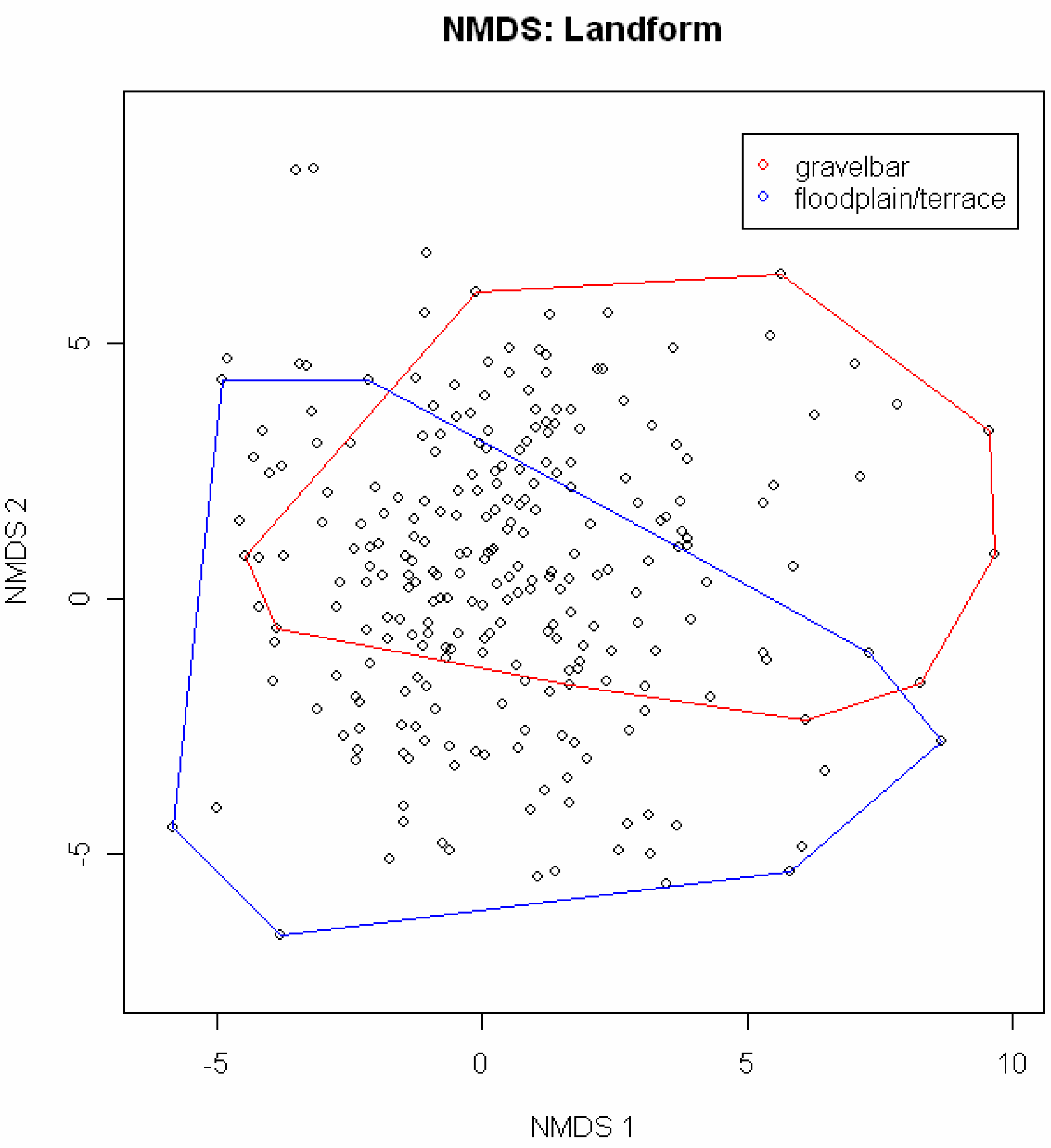

Figure 3.6. NMDS ordination plot, with landforms selected. Gravelbar samples are indicated by red, floodplain/terrace samples by blue.

Based on the D^2 values of GAM surfaces fit to the NMDS ordination (Table 3.4), the variables “depth to gravel” (Figure 3.7) and “elevation above water” (Figure 3.8) best explain deviation in the vegetation composition. The variables “distance to bankfull channel”, “distance to low water channel”, and “Y-coordinate” have limited explanatory value, and “braid index” and “elevation” are not meaningful (Table 3.4). Samples on the lower portion of the NMDS plot have greatest elevation above water (Figure 3.8), and samples on the lower left portion have greatest depths to gravel (Figure 3.7).

Table 3.4. D^2 values of Gaussian GAMs, with gamma=1.4, fit to continuous environmental variables, based on the NMDS ordination.

Variable	**D^2**
Elevation Above Water	.67
Distance to Low Water Channel	.17
Distance to Bankfull Channel	.47
Y Coordinate	.11
Depth to Gravel	.73
Elevation	.04
Braid Index	.04

Of the categorical variables considered, “section”, “landform”, and “local elevation” are significantly correlated with the structure of the NMDS ordination (Ordtest statistics) (Table 3.5). Individual factors that are significant at the 0.01 level include: “SR1”, “SR3”, “gravelbar”, “floodplain”, “intermediate”, and “low”. “Concave” and “high” are marginally significant.

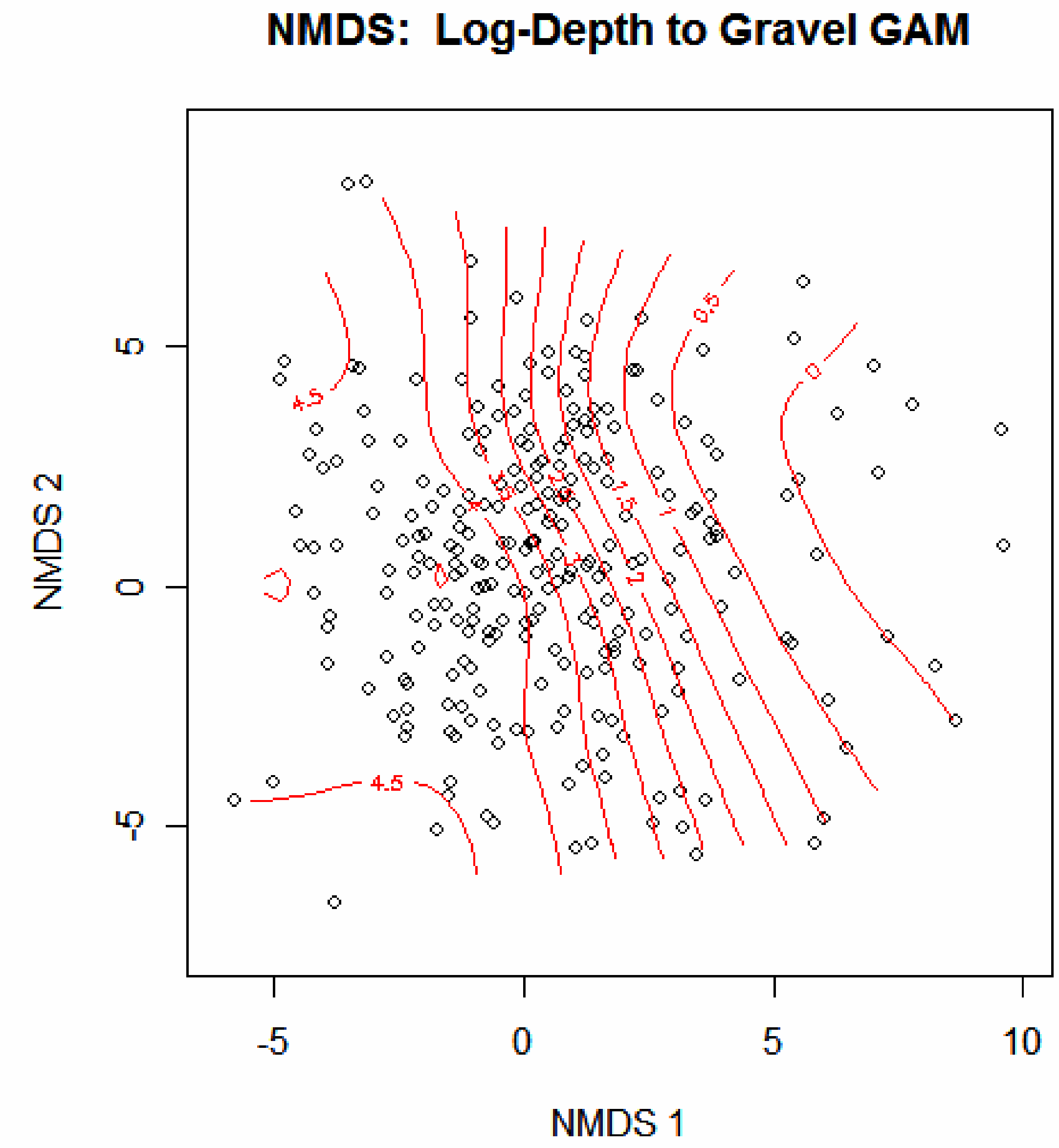

Figure 3.7. NMDS ordination plot, with Gaussian GAM surface of log-depth to gravel. D^2=0.73.

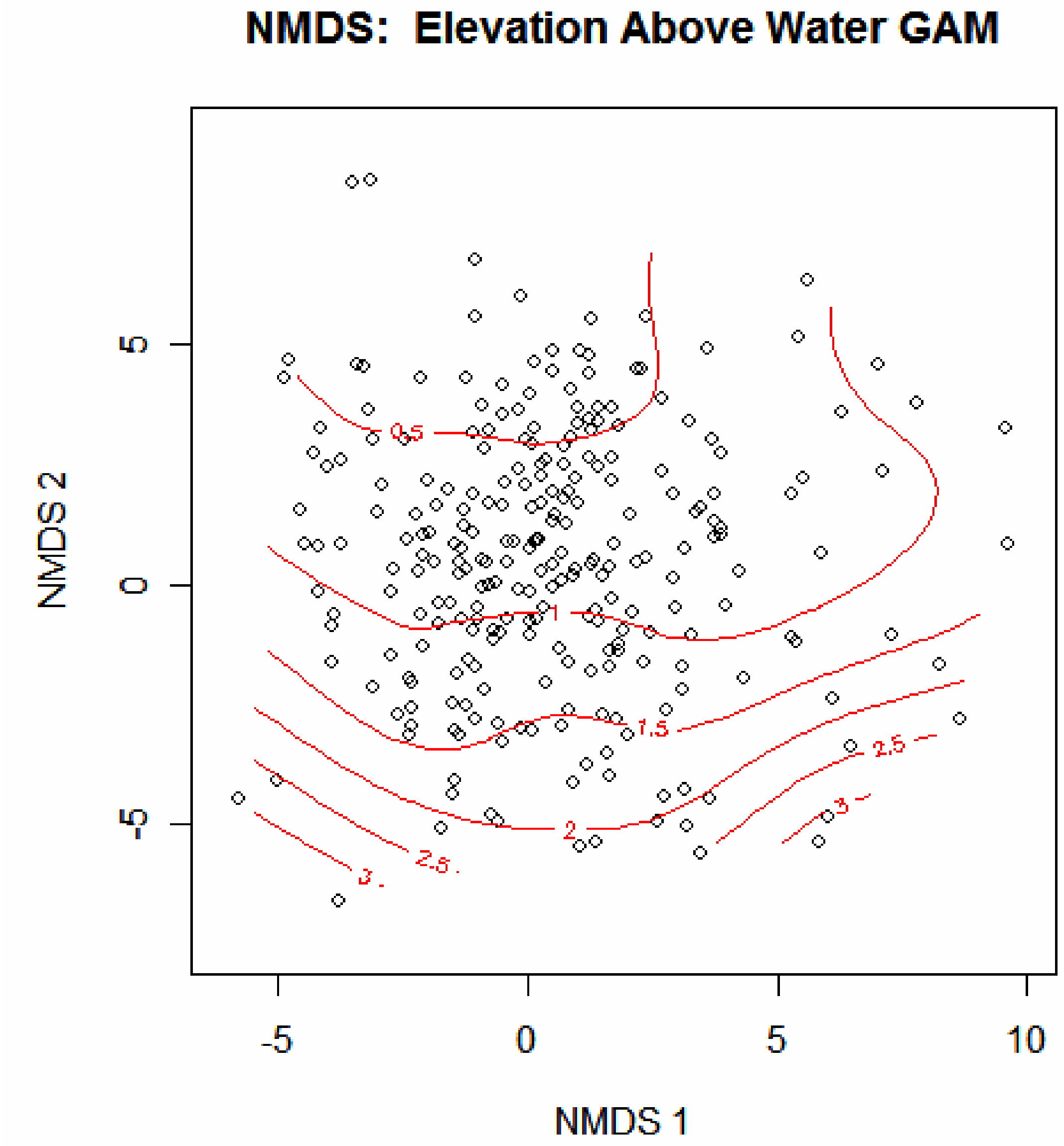

Figure 3.8. NMDS ordination plot, with Gaussian GAM surface of elevation above water. D^2=0.67.

Table 3.5. Ordtest p-values, based on the NMDS ordination, for categorical environmental variables. Stars indicate significance of variables at the p<0.01 level.

Variable	**Ordtest p-value**	**Category**	**Ordtest p-value**
Section*	<0.01	SR1*	<0.01
		SR2	0.72
		SR3*	0.02
		PC	0.64
		BF	1.00
Landform*	<0.01	Bank	0.50
		Floodplain*	<0.01
		Gravelbar*	<0.01
		Oldchannel	0.42
Local Topography	0.87	Concave	0.69
		Convex	0.07
		Undulating <3m	1.00
		Undulating >3m	0.39
		Flat	0.91
Local Elevation*	<0.01	High	0.08
		Intermediate*	<0.01
		Low*	<0.01

Cluster Analysis: Coarse Communities

One effective cluster solution for comparing river sections is a 7-cluster OPTSIL model. Compared to similar cluster solutions (*see Cluster Analysis: Fine Communities*), it has a low sum of p-values (95) and low table deviance (10,678). The Silhouette (Figure 3.9) and Partana (Figure 3.10, Table 3.6) plots indicate that within-cluster similarity is high, with a Partana ratio of 2.19. This solution has very few reversals in the Silhouette plot, which would indicate poor classification.

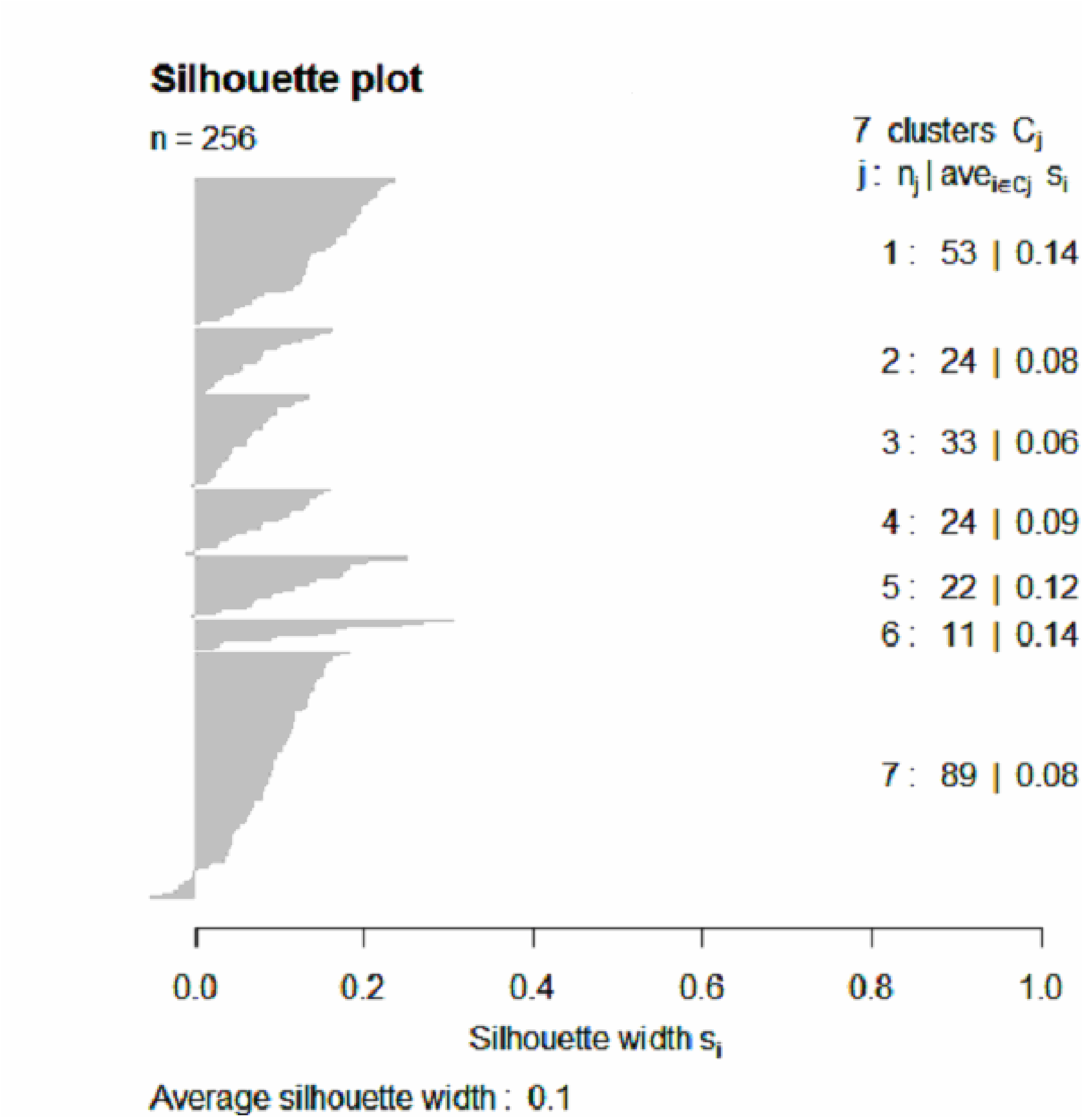

Figure 3.9. Silhouette width plot, indicating within plot similarity for each of 7 clusters. Negative widths indicate poor similarity. Cluster size and silhouette value are summarized on right of plot.

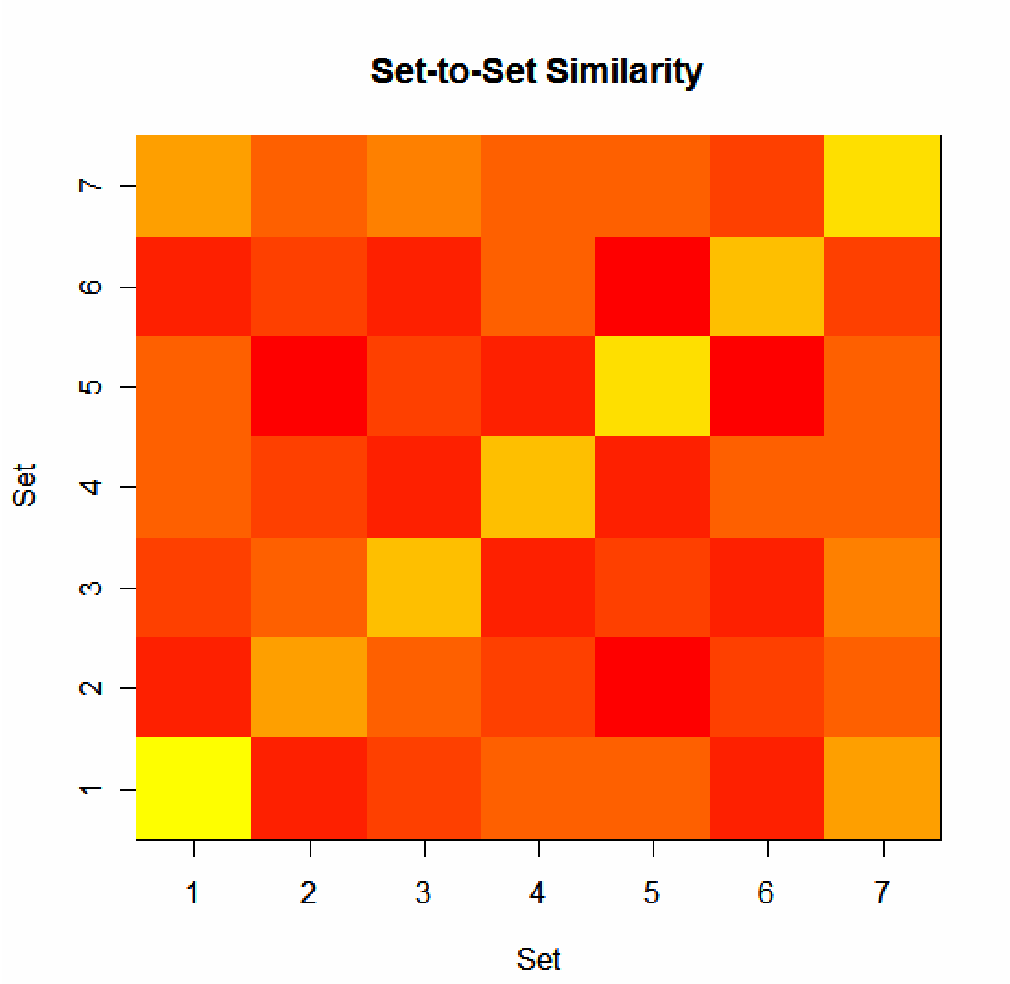

Figure 3.10. Partana plots, showing the similarity of each cluster to each other cluster. Yellow indicates similarity; red indicates a lack of similarity.

Table 3.6. Partana values for each cluster, compared to each other cluster. Higher values indicate greater similarity. Values of greatest similarity for each cluster are bolded. Overall Partana ratio is 2.19.

Cluster	1	2	3	4	5	6	7
1	**0.32**	0.07	0.09	0.15	0.14	0.07	0.20
2	0.07	**0.22**	0.14	0.10	0.03	0.08	0.13
3	0.09	0.14	**0.23**	0.07	0.10	0.04	0.17
4	0.15	0.10	0.07	**0.24**	0.05	0.12	0.13
5	0.14	0.03	0.10	0.05	**0.26**	0.03	0.14
6	0.07	0.08	0.04	0.12	0.03	**0.25**	0.08
7	0.20	0.13	0.17	0.13	0.14	0.08	**0.29**

The seven community types resulting from this cluster solution are named by the most abundant indicator species (as defined by Dufrêne and Legendre, 1997) in each cluster (Table 3.7). In all but one case (cluster 7), the most abundant species were also indicator species. The *Trifolium hybridum/ Solidago canadensis* type was sampled most in the study area. These two herbaceous species are very common, and the community is better reflected by the high abundance of the willow species *Salix boothii.* This species is the sixth most abundant species in this cluster, preceded by the common herbaceous species *Symphyotrichum lanceolatum*, *Agrostis stolonifera*, and *Poa pratensis. Salix boothii* is a significant indicator species, as are several other willow species, including *S. lasiandra, S. eriocephala, and S. exigua*. *Alnus incana* is also a significant indicator species in this cluster.

The *Carex vesicaria/ C. utriculata* community type was sampled most on the SR1 section, as was the *Pinus contorta/ Picea pungens/Equisetum arvense* community (Table 3.7). The *Populus angustifolia* S2/H community was not sampled on the SR1 section. The mature *Populus angustifolia/ Poa pratensis* was sampled most on the SR3 section. The *Epilobium suffruticosum* community was not sampled on BF or on SR1, and the *Carex utriculata/ C. vesicaria* community was not sampled on SR3. Communities occur on distinct sections of the NMDS plot, with little overlap (Figure 3.11).

Table 3.7. Cluster number, community type, occurrence (% of plots) in each river section, and size of each cluster, for the 7 cluster solution. Vegetation layer (T1-upper tree layer, T2-lower tree layer, S1-upper shrub layer, S2-lower shrub layer or H-herbaceous layer) of each species is indicated. Communities are ordered roughly by succession.

Cluster #	**Community Type**	**Section Occurrence (% of Plots)**					**Cluster Size**
		BF	**PC**	**SR1**	**SR2**	**SR3**	
4	*Populus angustifolia* H *Populus angustifolia* S2	10	7	0	11	15	24
1	*Agrostis stolonifera* H *Equisetum variegatum* H	25	24	11	21	23	53
7	*Trifolium hybridum* H *Solidago canadensis* H *(+ Salix boothii* & *Salix* sp.)	50	26	15	45	36	89
5	*Carex utriculata* H *Carex vesicaria* H	8	7	28	6	0	22
6	*Epilobium suffruticosum* H	0	12	0	4	5	11
2	*Populus angustifolia* T1 *Poa pratensis* H	3	5	15	2	18	24
3	*Picea pungens* T1 OR *Pinus contorta* T1 *Equisetum arvense* H	5	19	32	11	3	33
Total Plots		40	42	47	53	74	256

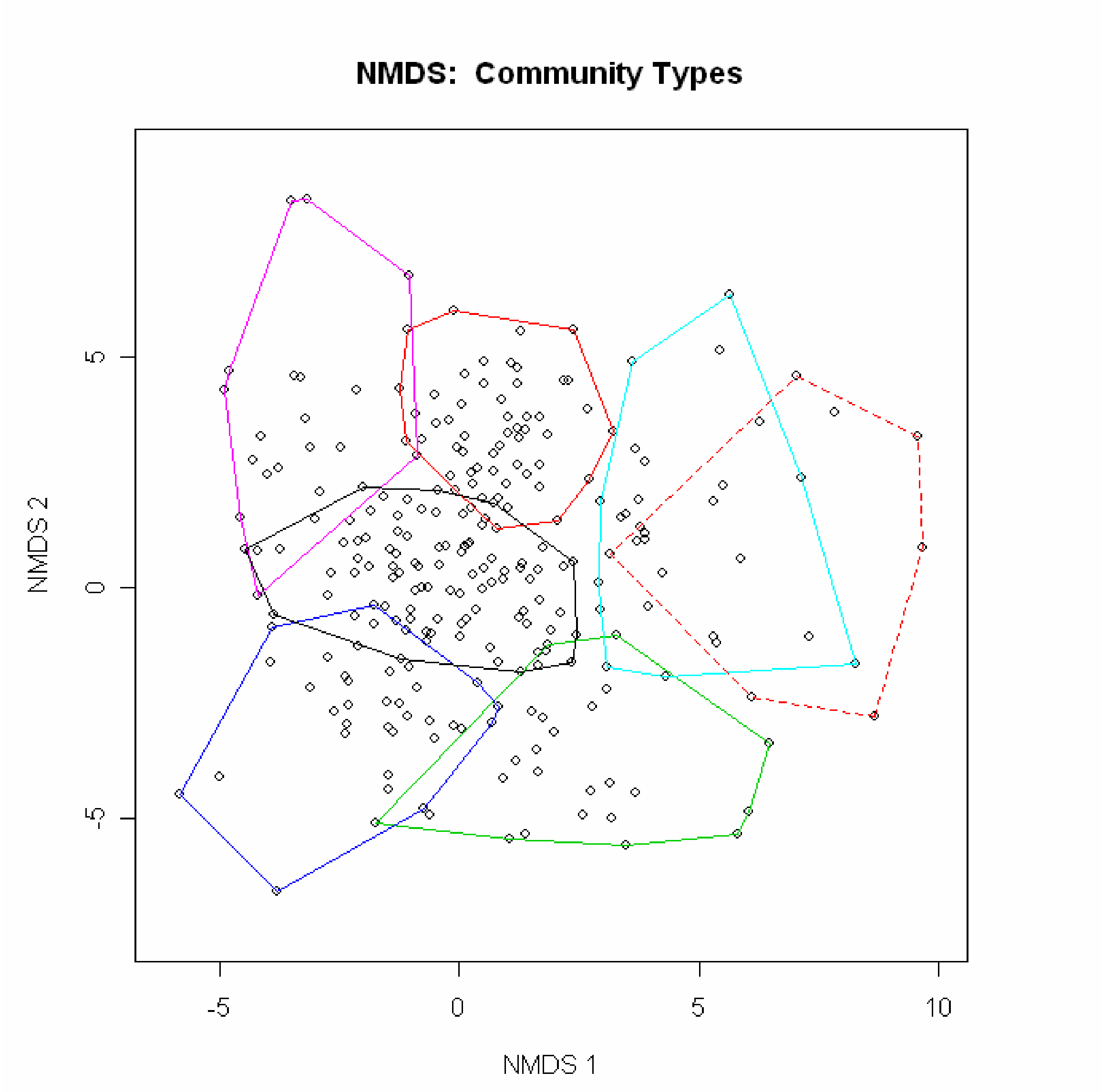

Figure 3.11. NMDS ordination plot, with community types selected.

Community Type	**Color**
Populus angustifolia S2/ *Populus angustifolia* H	Light blue
Agrostis stolonifera H/ *Equisetum variegatum* H	Red
Trifolium hybridum H/ *Solidago canadensis* H *(+ Salix boothii & Salix* sp.)	Black
Carex utriculata H/ *Carex vesicaria* H	Pink
Epilobium suffruticosum H	Red dashed
Populus angustifolia T1/ *Poa pratensis* H	Green
Picea pungens T1/ *Pinus contorta* T1 / *Equisetum arvense* H	Dark blue

Cluster Analysis: Fine Communities

The 14-cluster solution is a second mathematically valid model. The Silhouette (Figure 3.12) and Partana (Figure 3.13, Table 3.8) values are actually slightly higher (i.e. better) than the 7- cluster solution, being 0.11 and 2.33. The table deviance is 15,641 and the sum of p-values for indicator species is 110, which are both slightly higher, and therefore poorer than values of the 7-cluster solution. As with the 7-cluster solution, communities were named by the most abundant indicator species.

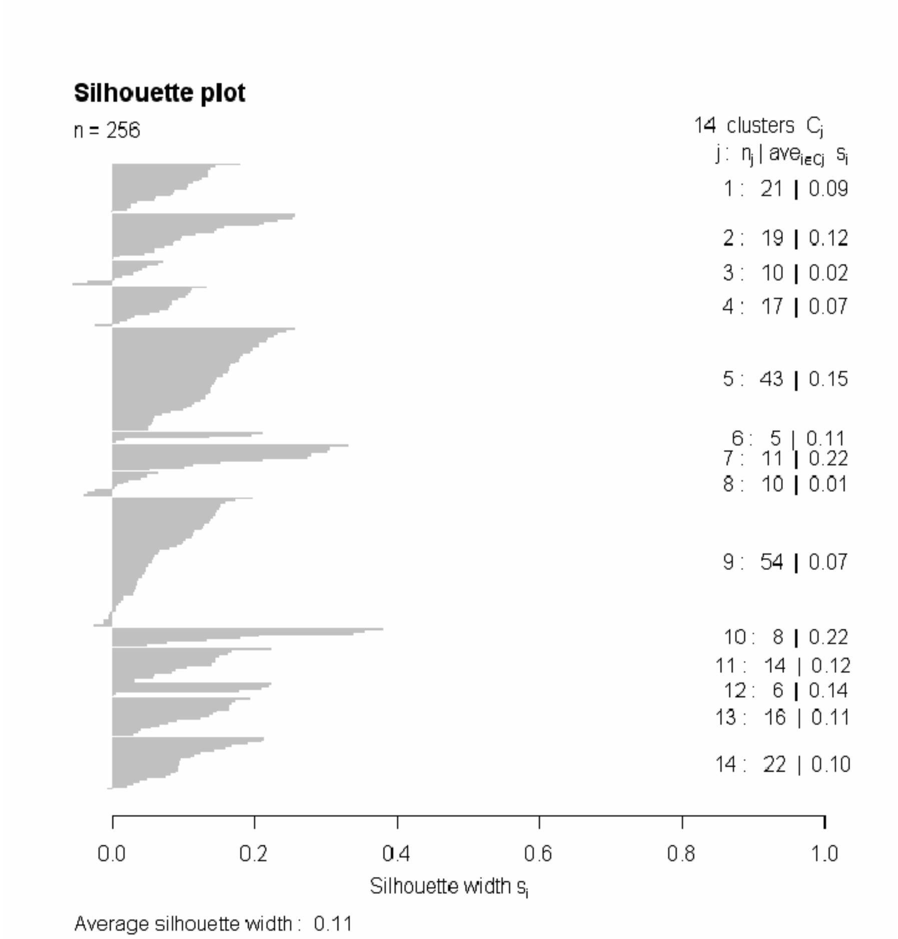

Figure 3.12. Silhouette width plot, indicating within plot similarity for each of 14 clusters. Negative widths indicate poor similarity. Cluster size and silhouette value are summarized on right of plot.

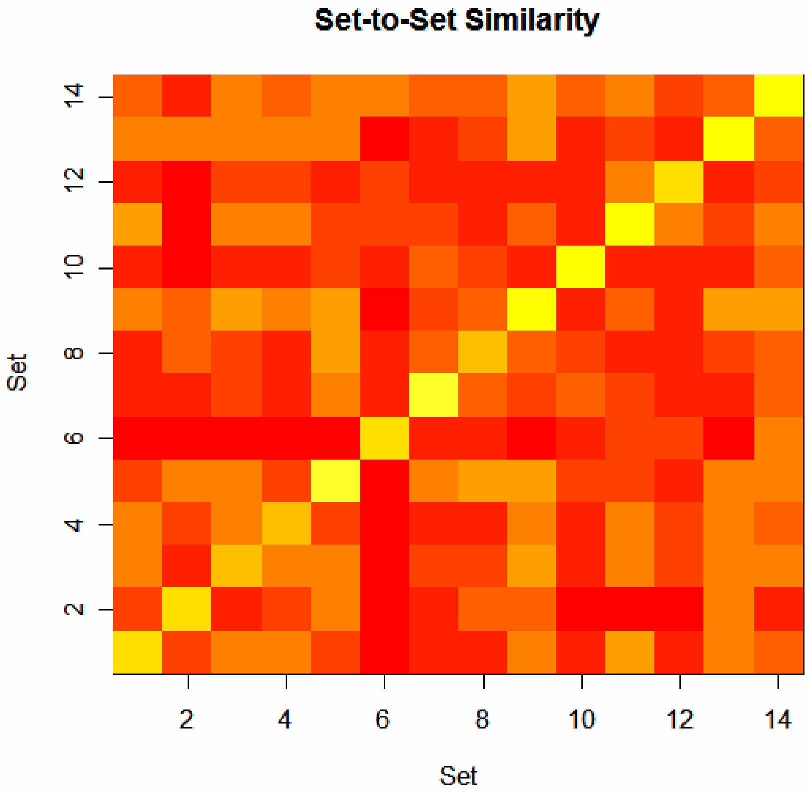

Figure 3.13. Partana plot, showing the similarity of each cluster to each other cluster. Yellow indicates similarity; red indicates a lack of similarity.

Table 3.8. Partana values for each cluster, compared to each other cluster. Higher values indicate greater similarity. Values of greatest similarity for each cluster are highlighted. Overall Partana ratio is 2.33.

Cluster	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	**0.30**	0.09	0.16	0.18	0.12	0.01	0.07	0.07	0.19	0.05	0.20	0.07	0.17	0.13
2	0.09	**0.30**	0.08	0.09	0.17	0.01	0.06	0.12	0.15	0.03	0.04	0.02	0.16	0.07
3	0.16	0.08	**0.25**	0.17	0.16	0.02	0.10	0.11	0.22	0.07	0.18	0.11	0.16	0.19
4	0.18	0.09	0.17	**0.26**	0.10	0.01	0.06	0.07	0.18	0.04	0.17	0.09	0.17	0.12
5	0.12	0.17	0.16	0.10	**0.36**	0.03	0.18	0.21	0.23	0.08	0.08	0.05	0.16	0.17
6	0.01	0.01	0.02	0.01	0.03	**0.28**	0.07	0.05	0.04	0.06	0.11	0.09	0.01	0.18
7	0.07	0.06	0.10	0.06	0.18	0.07	**0.37**	0.15	0.11	0.13	0.08	0.06	0.07	0.15
8	0.07	0.12	0.11	0.07	0.21	0.05	0.15	**0.24**	0.14	0.09	0.06	0.05	0.11	0.13
9	0.19	0.15	0.22	0.18	0.23	0.04	0.11	0.14	**0.33**	0.07	0.15	0.07	0.23	0.23
10	0.05	0.03	0.07	0.04	0.08	0.06	0.13	0.09	0.07	**0.34**	0.08	0.06	0.05	0.12
11	0.20	0.04	0.18	0.17	0.08	0.11	0.08	0.06	0.15	0.08	**0.32**	0.16	0.10	0.18
12	0.07	0.02	0.11	0.09	0.05	0.09	0.06	0.05	0.07	0.06	0.16	**0.29**	0.05	0.10
13	0.17	0.16	0.16	0.17	0.16	0.01	0.07	0.11	0.23	0.05	0.10	0.05	**0.33**	0.13
14	0.13	0.07	0.19	0.12	0.17	0.18	0.15	0.13	0.23	0.12	0.18	0.10	0.13	**0.34**

Clustering of these two communities can be compared in Table 3.9. In the 7-cluster solution, the two tree species *Picea pungens* and *Pinus contorta* compose a community type. While these species only occurred together in 3 sampled plots, they seem to contain similar understory communities. In the 14-cluster solution, there are two separate coniferous communities: *Pinus contorta/Phleum pratense*, and *Picea pungens/ Equisetum arvense*. In the larger model, *Populus angustifolia* S2 and H layers were classified as separate communities, with *Salix melanopsis* S2 co-occurring with shrubby cottonwoods. There was also a *Salix boothii* S1/ *Alnus incana* S1 community, which is distinct from the *S. boothii* S2/*Trifolium hybridum* community, being in the taller S1 layer. A community dominated by *Artemisia tridentata* was also identified in this solution. These plots were grouped with *Populus angustifolia* T1/ *Poa pratensis* in the 7-cluster OPTSIL model.

New clusters in the 14-cluster solution include several herbaceous communities, most of which were included in the *Trifolium hybridum/ Solidago canadensis/ Salix sp.* community in the 7-cluster model (Table 3.9). A *Medicago lupulina/ Trifolium repens* community, with the non-native grasses *Agrostis stolonifera, Phleum pratense, and Poa pratensis* occurring in high abundances, was frequenctly sampled. There is also a herbaceous *Potentilla norvegica*/ *Crepis tectorum* community. A *Selaginella densa*/*Hetherotheca depressa* community was identified, which was grouped with *Populus angustifolia* T1/ *Poa pratensis* in the 7-cluster model. The *Carex utriculata/ Carex vesicaria* community, and the *Epilobium suffruticosum/Lupinus argenteus* community are very similar in both cluster solutions.

Table 3.9. Distibution of the 174 sample plots in the 7-cluster, versus the 14-cluster solution. Values ≥5 are bolded. Communities are ordered roughly by succession.

Community Type	*Populus angustifolia* H *Populus angustifolia* S2	*Agrostis stolonifera* H *Equisetum variegatum* H	*Trifolium hybridum* H *Solidago canadensis* H (+ *Salix boothii* & *Salix sp.*)	*Carex utriculata* H *Carex vesicaria* H	*Epilobium suffruticosum* H	*Populus angustifolia* T1 *Poa pratensis* H	*Picea pungens* T1 OR *Pinus contorta* T1 *Equisetum arvense* H
Populus angustifolia H	**10**	1	0	0	0	0	0
Potentilla norvegica H *Crepis tectorum* H	2	**6**	0	1	1	0	0
Equisetum variegatum H *Agrostis stolonifera* H	0	**42**	1	0	0	0	0
Medicago lupulina H *Trifolium repens* H	0	0	**8**	0	0	2	0
Carex utriculata H *Carex vesicaria* H	0	3	0	**16**	0	0	0
Epilobium suffruticosum H *Lupinus argenteus* H	0	0	0	0	**8**	0	0
Selaginella densa H *Hetherotheca depressa* H	3	0	0	0	1	1	0
Populus angustifolia S2 *Salix melanopsis* S2	**9**	0	**11**	0	1	1	0
Salix boothii S2 *Trifolium hybridum* H	0	1	**53**	0	0	0	0
Salix boothii S1 *Alnus incana* S1 *Poa palustris* H	0	0	**9**	**5**	0	0	2
Artemisia tridentata S2 *Hesperostipa comata* H	0	0	0	0	0	**6**	0
Populus angustifolia T1 *Poa pratensis* H +*Sheperdia canadensis* S2	0	0	0	0	0	**13**	1
Picea pungens T1 *Equisetum arvense* H	0	0	**5**	0	0	0	**16**
Pinus contorta T1 *Phleum pratense* H	0	0	2	0	0	1	**14**

Communities of the 14-cluster solution show some patterns across river sections (Table 3.10). The *Pinus contorta/Phleum pratense* community occurs predominantly on the SR1 section, while both the herbaceous and shrubby cottonwood communities were not sampled here. The *Equisetum variegatum/ Agrostis stolonifera* community was rarely sampled on this section. The sagebrush community (*Artemisia tridentata* S2/*Hesperostipa comata* H) was only sampled on SR1 and SR3. Three herbaceous communities (*Medicago lupulina/ Trifolium repens, Selaginella densa*/*Hetherotheca depressa,* and *Potentilla norvegica*/ *Crepis tectorum*) were not sampled on the tributaries.

Table 3.10. Vegetation type, community type, cluster number, percent of occurrences in each river section, and size of each cluster, for the 14 cluster solution. Vegetation layer (T1-upper tree layer, T2-lower tree layer, S1-upper shrub layer, S2-lower shrub layer or H-herbaceous layer) of each species is indicated.

	Community Type	**Cluster Number**	**Section Occurrence (% of Plots)**					**Cluster Size**
			BF	**PC**	**SR1**	**SR2**	**SR3**	
Herbaceous	*Populus angustifolia* H	1	5	5	0	4	7	11
	Potentilla norvegica H *Crepis tectorum* H	8	0	0	11	9	0	10
	Equisetum variegatum H *Agrostis stolonifera* H	5	25	24	2	13	20	43
	Medicago lupulina H *Trifolium repens* H	3	0	0	4	4	8	10
	Carex utriculata H *Carex vesicaria* H	2	8	7	17	6	3	19
	Epilobium suffruticosum H *Lupinus argenteus* H	10	0	10	0	2	4	8
	Selaginella densa H *Hetherotheca depressa* H	6	0	0	0	2	5	5
Shrub	*Populus angustifolia* S2 *Salix melanopsis* S2	14	13	7	0	8	14	22
	Salix boothii S2 *Trifolium hybridum* H	9	30	21	9	28	19	54
	Salix boothii S1 *Alnus incana* S1 *Poa palustris* H	13	3	7	9	9	4	16
	Artemisia tridentata S2 *Hesperostipa comata* H	12	0	0	6	0	4	6
Tree	*Populus angustifolia* T1 *Poa pratensis* H +*Sheperdia canadensis* S2	11	3	7	4	2	10	14
	Picea pungens T1 *Equisetum arvense* H	1	15	10	4	13	3	21
	Pinus contorta H *Phleum pratense* H	17	0	2	34	0	0	17
	n=		40	42	47	53	74	256

Environmental Trends of 14 Communities

Trends in community distributions occur across depth to gravel, elevation above water, distance to bankfull channel, and geomorphological landform, for the 14-cluster communities (Figure 3.14, Table 3.11). Trends also exist for the 7-cluster community model, but since many of these are simply coarser versions of the 14-cluster model, I am only considering environmental details of the latter.

Several communities occur at depths to gravel of virtually zero (i.e. gravelbars), which are *Populus angustifolia* H, *Potentilla novegica/Crepis tectorum, Epilobium suffruticosum/Lupinus argenteus,* and *Selaginella densa/ Hetherotheca depressa.* Deep soils occur with the spruce and lodgepole forest communities, the 2 *Salix boothii* communities, and the *Carex utriculata/ Carex vesicaria* community. Most communities occur at relatively low to intermediate elevations above water (means of approximately 1m). The sagebrush community typically occurs at elevations between 2 and 4m above water, but at a very close distance from bankfull channel. The communities *Populus angustifolia* H, *Potentilla norvegica/Crepis tectorum, Equisetum variegatum/Agrostis stolonifera,* and *Epilobium suffruticosum/Lupinus argenteus* also occur in close proximity to the bankfull channel. Several communities are associated with a low braid index; these include *Potentilla norvegica/Crepis tectorum, Medicago lupulina/ Trifolium repens, Selaginella densa*/*Hetherotheca*, as well as the sagebrush community.

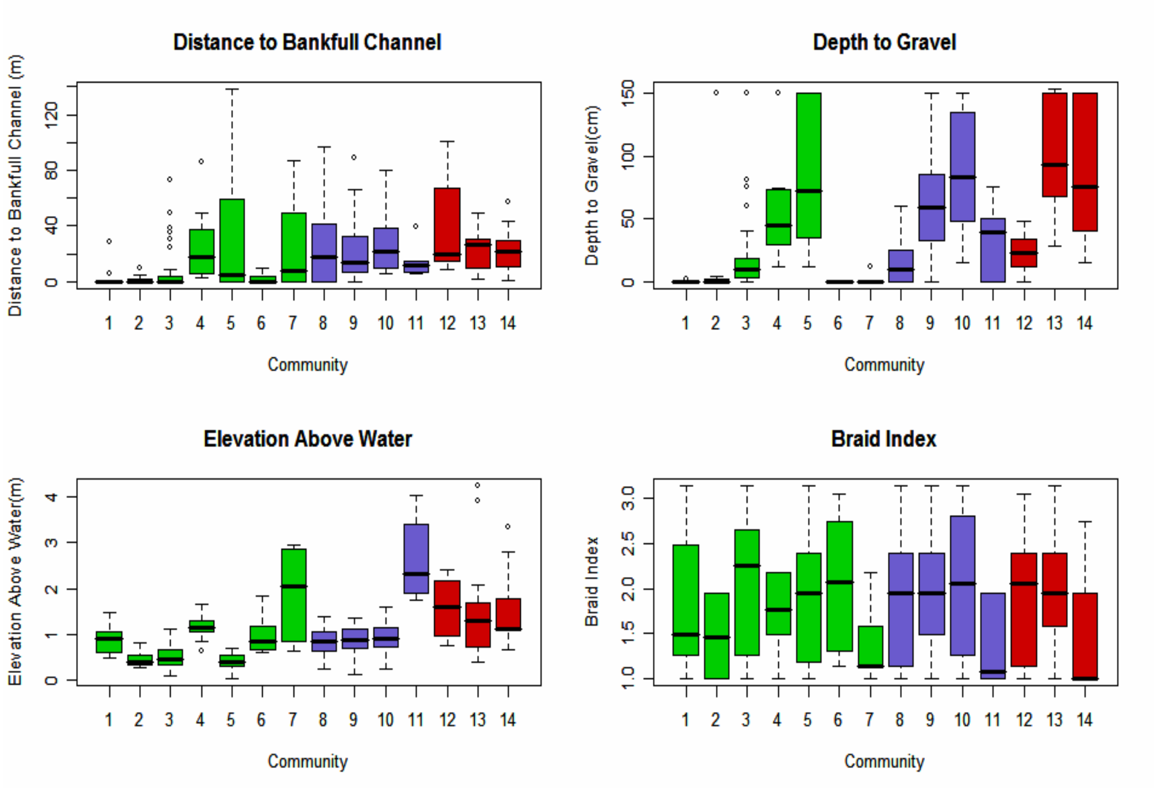

Figure 3.14. Environmental trends of the 14-cluster community. Herbaceous communities are green, shrubby communities are blue, and tree communities are red.

#	**Community Type**
1	*Populus angustifolia* H
2	*Potentilla norvegica* H/ *Crepis tectorum* H
3	*Equisetum variegatum* H/ *Agrostis stolonifera* H
4	*Medicago lupulina* H/ *Trifolium repens* H
5	*Carex utriculata* H/ *Carex vesicaria* H
6	*Epilobium suffruticosum* H/ *Lupinus argenteus* H
7	*Selaginella densa* H/ *Hetherotheca depressa* H
8	*Populus angustifolia* S2/ *Salix melanopsis* S2
9	*Salix boothii* S2/ *Trifolium hybridum* H
10	*Salix boothii* S1/ *Alnus incana* S1/ *Poa palustris* H
11	*Artemisia tridentata* S2 /*Hesperostipa comata* H
12	*Populus angustifolia* T1/ *Poa pratensis* H +*Sheperdia canadensis* S2
13	*Picea pungens* T1/ *Equisetum arvense* H
14	*Pinus contorta* H/ *Phleum pratense* H

Table 3.11. Percent occurrence geomorphological landforms across communities, for the 14-cluster community.

		Geomorphological Landform			
	Community	Bank %	Oldchannel %	Gravelbar %	Floodplain/ Terrace %
Herbaceous	*Populus angustifolia* H	4	0	14	0
	Potentilla norvegica H *Crepis tectorum* H	0	6	11	0
	Equisetum variegatum H *Agrostis stolonifera* H	69	27	21	1
	Medicago lupulina H *Trifolium repens* H	4	3	1	6
	Carex utriculata H *Carex vesicaria* H	15	21	1	6
	Epilobium suffruticosum H *Lupinus argenteus* H	0	0	11	0
	Selaginella densa H *Hetherotheca depressa* H	0	0	3	2
Shrub	*Populus angustifolia* S2 *Salix melanopsis* S2	0	6	20	5
	Salix boothii S2 *Trifolium hybridum* H	4	15	14	30
	Salix boothii S1 *Alnus incana* S1 *Poa palustris* H	0	12	1	9
	Artemisia tridentata S2 *Hesperostipa comata* H	0	3	0	4
Tree	*Populus angustifolia* T1 *Poa pratensis* H +*Sheperdia canadensis* S2	4	0	0	10
	Picea pungens T1 *Equisetum arvense* H	0	3	0	16
	Pinus contorta H *Phleum pratense* H	0	3	0	13
	n=	26	33	70	127

Discussion

Richness and Indicator Species of River Sections

Species richness, measured as number of species per plot (α-diversity), is lower on the Snake River than on the tributaries (Table 3.1). These findings are consistent with low species richness being associated with river regulation, due to a shift towards less diverse, late-successional stands (Uowolo *et al.*, 2005, Marston *et al.*, 2005), and a lack of disturbance related heterogeneity (Pollock *et al.*, 1998). Conversely, Nilsson *et al.* (1994) observed higher richness on a main river than on tributaries, potentially due to higher discharge and subsequent species dispersal. The overall richness of the Snake River (β-diversity) is actually higher than the tributaries, which is consistent with this dispersal related hypothesis. Alternatively, the richness may be a result of a longer environmental gradient on the Snake River, due to the larger study area.

Dam regulation could be responsible for lower richness per plot (α-diversity) found on the Snake River, by some combination of the following mechanisms: i) decreased environmental heterogeneity due to lower flooding disturbance, ii) decreased dispersal via floods, or iii) a shift to late-successional communities as cottonwoods decline. However, the higher overall richness (β –diversity) of the Snake River contradicts this hypothesis. A more likely explanation involves patch sizes of tributary communities, which seem to be smaller than for the Snake River (personal observation). This could lead to a greater number of edge species in the tributary plots, which would inflate richness. Flood induced environmental heterogeneity promotes richness (Pollock *et al.*, 1998), which is closely related to this hypothesis. Spatial modeling would be necessary to determine quantitative differences in community sizes in the study area. Differences could potentially be attributed to flooding related heterogeneity, or simply to the size discrepancy in the rivers, with larger systems consisting of larger community patches.

Many of the Murdoch-derived indicator species (optpart package; Roberts, 2008) for river sections (Table 3.2) correspond to those used in naming community types, which were based on Dufrêne and Legendre (1997) (Table 3.7, Table 3.9). *Pinus contorta* is an indicator species for the upper Snake River section. Cottonwood trees, in all vegetation layers but the upper shrub layer, are negatively associated with this section, as are spruce trees. These findings are consistent with those of Chapter 4, and suggest that the typical cottonwood-spruce riparian forests are absent from this section, with the common upland species, *Pinus contorta*, occurring in close proximity to the river. On the lower Snake River section, *Populus angustifolia* in the lower tree level, as well as the shrub *Elaeagnus commutata*, are indicator species. *E. commutata*, in combination with *Populus angustifolia,* constitutes one of three cottonwood communities identified by Merigliano (2005) on the Snake River below the Palisades Dam. It has been described as particularly abundant near Moose, WY, downstream from my study area (Shaw, 1992). Although common on all sections of the study area, this species seems to be most prevalent along the lower Snake River.

As a means for classifying plant composition, river section alone does not explain trends. Partana analysis indicates that within-section similarity is low, so that vegetation composition of each section is not consistent (Figure 3.2, Table 3.3). Buffalo Fork is the only section with a high within-cluster similarity, but all other sections are also similar to it. The upper section of the Snake River has the least within-cluster similarity, and does not resemble any other sections. This suggests that the vegetation on this section is somehow unique, yet heterogeneous. Samples corresponding to the upper section occur on the left side of the NMDS plot (Figure 3.5), and, based on Ordtest (Table 3.5), have vegetation that is significantly related to this factor. The factor “SR3” is also significant in structuring the vegetation. The combined methods of NMDS and Ordtest indicate that the upper and lower sections of the Snake River are different from the tributaries, and provide some indication that vegetation may be related to dam regulation. However, the middle section is not different from the tributaries, which is contradictory to this theory, and suggests differences on the lower section are independent of the dam. Spatially, the middle section of the Snake River is closest to the tributaries, and has similar levels of braiding. The effects of the tributaries on the main river, particularly sediment input, may decrease further downstream as deposition occurs. Compositional similarities between the middle Snake River and the tributaries may be due to similar environmental/hydro-geomorphological factors.

NMDS Ordination and Evaluation of Environmental Variables

Elevation above water explains the most deviance of environmental variables (Table 3.4). This variable has been identified as structuring vegetation in other riparian areas (Sagers and Lyon, 1997), and reflects likelihood of flooding, substrate age, and water availability. The importance of this variable is reinforced by the significance of the categorical variable, local elevation (Table 3.5). Local elevation is not simply a broader measure of elevation above water; it contains information on microenvironments created by the landform surrounding a plot.

Depth to gravel is also an important variable (Table 3.4), and is not correlated with elevation above water (Figure 3.3). While GAMs have a tendency to be overfit, this does not seem to be the issue for the variable “depth to gravel”. Samples with deepest soils occur on the bottom left side of the NMDS plot (Figure 3.7). This area corresponds to the coniferous forest and willow/common herb communities (Figure 3.11), both of which tend to occur on relatively deep soils. The elevation above water GAM (Figure 3.8) indicates that these samples occur at approximately 1m above water.

Geomorphological landform, particularly the factors “gravelbar” and “floodplain/terrace”, plays a significant role in structuring the vegetation of the study area (Table 3.5). This is consistent with previous research, describing characteristic plant communities on each landform (Bendix and Hupp, 2000, Hupp and Osterkamp, 1985).

Cluster Analysis of Communities

Cluster analysis, as a method to classify community types, requires an evaluation of both mathematical and ecological factors. I experimented with several models that split communities at varying levels of coarseness, and identified two models with a high degree of within-cluster similarity. Identifying fewer or more communities may be beneficial, depending on research goals. The community types derived from the 7-cluster model occupy different regions of the NMDS ordination plot (Figure 3.11). There is very little overlap, which supports the distinctness of these communities. The most overlap occurs between the *Populus angustifolia* S2/H and the *Epilobium suffruticosum* communities. These communities both occur at depths to gravel of 0-10 cm (i.e. gravelbars) based on the GAM contours for this variable (Figure 3.7), and seem to share some species.

The 14-cluster solution is a more descriptive model, but has higher deviance and a higher p-value sum for significant indicator species. While this is partially an artifact of increased cluster number, the added complexity provides some modeling difficulties. For instance, these communities do not occupy distinct regions of the NMDS ordination, suggesting they are less distinct than the clusters of the smaller model. The 14-cluster solution would be most interesting to Grand Teton National Park to more fully describe the communities of the area. For broader management, and to understand general vegetation trends and the relationship to hydrogeomorphology, the smaller model is more practical.

Occurrence of community types across river sections suggests that a late-successional trend exists on the upper section of the Snake River. The lodgepole pine communities were sampled most along this section, and herbaceous and shrubby cottonwood communities were not sampled at all (Table 3.7, 3.10). The new alluvial surfaces and flooding conditions necessary for these young cottonwood communities may be insufficient on the upper Snake River, since gravelbars are negatively correlated with this section, and floodplains/terraces are positively correlated. Young cottonwood communities occur at low depths to gravel, while lodgepole communities occur on deep soils, with intermediate/high elevations above water (Figure 3.14). While these results support previous research linking dam regulation to late-successional trends (Marston *et al.*, 2005, Fierke and Kauffman, 2006), particularly in close proximity to dams (Rood *et al.*, 2005), the upper Snake River may be inherently different. This section of the river is more incised and less braided than other sections, resulting in fewer gravelbars, and more floodplains/terraces with deep soils, and high elevations above water. While incision can be caused by dam regulation (Leopold *et al.*, 1964), the Snake River has undergone very few dam-related geomorphological changes (Schmidt and Nelson, 2007). It is possible that the upland species, *Pinus contorta,* is more abundant in this incised section simply because the riparian corridor is narrower, and upland species growing on the floodplains and terraces are in closer proximity to the river.

The sagebrush community, identified in the 14-cluster model, was sampled on the upper and the lower sections of the Snake River, but not on the middle section or the tributaries. As with lodgepole pine, the narrow nature of the riparian corridor may lead to this upland species being located in close proximity to the river. The sagebrush community was sampled most at high elevations above water, on less braided sections, so that distance to bankfull chanel was low. The river has several single-channel segments in the lower section. However, there were no lodgepole pine communities sampled on this lower section, which suggests there may be other factors involved besides river incision in explaining the distribution of upland species near the Snake River.

The *Carex utriculata/ Carex vesicaria* community was identified in both cluster solutions, and sampled most on the upper Snake River (Table 3.7). *C. vesicaria* is also an indicator species for this section. This wetland community occurs at low elevations above water, and on deep soils (Figure 3.14). The increased frequency of this community on the upper section of the river may be the result of more stable conditions, which promote fine substrate deposition and wetland conditions. The herbaceous community *Equisetum variegatum/ Agrostis stolonifera* was rarely sampled on this section, suggesting that low-lying areas are most likely to develop into sedge communities in this section.

There were several herbaceous communities identified in the 14-cluster solution that were only found on the Snake River. The *Selaginalla densa/Hetherotheca depressa* community was not sampled on the tributaries. *Selaginella densa* has been described as growing in exposed rocky sites in the valley, and sometimes extending above tree line (Shaw, 1992). This community occurred mainly at high elevations above water, on primarily single channel sections. As with the sagebrush community, this upland community may have occurred along the tributaries at higher elevations above water, which were distant from the riparian corridor, and therefore not sampled.

Medicago lupulina and *Trifolium repens*, as well as the non-native grasses *Agrostis stolonifera, Phleum pratense, and Poa pratensis*, compose a community in the 14-cluster solution. While these species are all abundant on the tributaries, they typically occur in the understory of shrub and forest communities. On the Snake River, they comprise their own community. This may be due to the larger patch sizes of communities noted on the Snake River. Patches of common grasses and forbs on the tributaries growing near the edges of other communities were too small to sample. However, on the Snake, it seems that these edge/transition communities were more extensive.

The species *Potentilla norvegica* was only sampled once on the tributaries. This species, along with *Crepis tectorum*, compose a community in the 14-cluster model, which commonly occurs along the upper Snake River. *P. norvegica* is commonly associated with disturbed areas along the Snake River, and *C. tectorum* is a non-native species of concern (Shaw, 1992). The prevalence of these weedy species on the Snake may be due to greater disturbance along the larger river, or due to sites of introduction.

The two largest communities are *Salix boothii/ Trifolium hybridum* and *Agrostis stolonifera/Equisetum variegatum*, which were identified in both cluster solutions (Tables

3.7, 3.10). These two clusters incorporate many diverse shrubby and herbaceous assemblages with no single species being abundant. Intuitively, these assemblages were considered distinct "communities" in the field. While the clustering methods used in this analysis were successful overall, assemblages lacking dominant species were difficult to distinguish.

Conclusions

The primary purpose of this study was to explore riparian plant community composition of the dam-regulated Snake River, using the unregulated tributaries as a control. Additionally, I identified several important variables that are related to vegetation composition, including elevation above water, depth to gravel, and geomorphological landform. Plots on the tributaries have a greater α-diversity than the Snake River, despite the higher β-diversity of the main river. This may be related to dam regulation, but is more likely due to differences in community patch sizes. I found the upper section of the Snake River to be distinct from the tributaries, supported by NMDS and Ordtest statistics, indicator species, and community occurrence. The upper section has more lodgepole pine communities, more wetland sedge communities, and fewer young cottonwood communities. These trends could be due to dam-related river incision, stabilization, or flood regime changes. Major changes to the geomorphology of the river have not been supported, however, there has been a decrease in the magnitude of flows (Schmidt and Nelson, 2007). While the tributaries seem to mitigate this effect on the mid and lower section of the Snake River, the community trends on the upper section may be related to a lack of flood-related disturbance, which could create gravelbar habitat for young cottonwood communities, and inhibit development of sedge community habitat. However, since sediment is trapped by Jackson Lake, gravel-bar formation, even in the absence of the dam, would be impeded in this section. Upland lodgepole pine may be more prevalent due to the naturally narrow riparian corridor. The lower section of the Snake River is distinct from the tributaries, and from the upper section, with sagebrush communities being more abundant. There are several communities that were only sampled on the Snake River, which may be due to incision, low sediment, and larger patch sizes of communities. The middle section of the Snake River does not differ significantly from the tributaries, which suggests that the dam is not responsible for differences on the lower sections.

Geomorphologically, the Jackson Lake dam has had relatively little impact on the Snake River, due to the mitigating effect of the tributaries, and the fact that the lake historically existed as a sediment trap (Schmidt and Nelson, 2007). In general, the vegetation seems to follow this trend, and I have no direct evidence to suggest that the dam influences plant communities below the tributaries. Above the tributaries, plant communities are distinct. This may be due to dam-related changes in the flood regime, or it may be due to the incised, single channel nature of this section. Overall, riparian vegetation along the Snake River in Grand Teton National Park seems to be exempt from many of the dam-induced problems facing other regulated rivers.

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CHAPTER 4

RIPARIAN FOREST STRUCTURE OF TWO UNREGULATED TRIBUTARIES, COMPARED TO THE SNAKE RIVER

Abstract

Across western North America, the detrimental effects of dams on riparian forests have included a decline in cottonwood regeneration, and a shift towards late successional species. To determine how riparian forests of the dam-regulated Snake River in Grand Teton National Park, WY, are impacted, I compared these forests to those of two unregulated tributaries: Pacific Creek and Buffalo Fork. I analyzed the age class and species distributions across river sections and landforms, to estimate the influence of hydro-geomorphological factors on these forests. There was no trend toward late successional spruce forests in the regulated river segments, nor did cottonwood recruitment appear to have been interrupted historically by flow regime changes. I did not find direct evidence for cottonwood decline in the study area. This is consistent with the relatively minor hydro-geomorphological changes this system has undergone in the past century. Age classes of spruce and cottonwood were associated with specific geomorphological landforms. Forest structure was also influenced by browsing, which leads to multi-stemmed growth of cottonwoods through root coppicing. A variety of cottonwood age/diameter classes should promote overall biodiversity, based on generalized linear models (GAMs) fit to an ordination of understory vegetation.

Introduction

Riparian Forests

The negative impacts of dams on riparian forests, particularly those dominated by cottonwoods, have been well documented in the past two decades (Rood *et al.*, 2003a, Johnson, 2000, Rood and Mahoney 1990, Fenner *et al.* 1985, Merritt and Cooper, 2000). The development of cottonwood forests reflects a strong dependence on the physical processes of rivers, and the decline of these species is related to altered flow regime in dam regulated rivers (Rood and Mahoney, 1990). Two explanations for this decline are geomorphological changes involving sedimentation and channel form, and hydrological changes such as flooding (Rood and Mahoney, 1990). Managed rivers tend to be sediment deficient, since dams act as sediment traps, and have lower, disrupted flows (Petts and Gurnell, 2005). This often leads to degradation, as this sediment deficit leads to downcutting (Leopold *et al.*, 1964). The processes of erosion, deposition, and lateral channel migration are integral to the dynamic nature of rivers (Naiman and Decamps, 1997) and managed rivers tend to be artificially stable (Merritt and Cooper, 2000).

The relationship between flooding and cottonwoods is intricate and extensive, and involves not only the magnitude of peak flows, but also the timing, duration and frequency of floods (Poff *et al.*, 1997). The formation of newly deposited, damp, alluvial surfaces as a result of natural geomorphological processes such as sedimentation is crucial for cottonwood establishment (Johnson, 2000, Mahoney and Rood, 1998). The life history strategy of cottonwoods depends on hydro-geomorphological processes, reflecting the evolution of this species in naturally dynamic river systems.

Cottonwood seeds, viable for only 1-2 weeks, are wind dispersed in very large numbers, and require a moist, fine substrate for successful germination (Fenner *et al.*, 1985, Naiman *et al.*, 2005, Mahoney and Rood, 1998). The timing of seed dispersal has evolved to coincide with peak floods in early spring, so that germination occurs as water levels recede slowly (Naiman *et al.*, 2005), at a maximum of 2.5cm per day (Mahoney and Rood, 1998). The presence of new alluvial surfaces is important for these early colonizers, and the narrow strip of suitable germination substrate must be both unvegetated and recently flooded or moist (Johnson, 2000), ideally 60-150cm above base flow level (Mahoney and Rood, 1998). While cottonwoods are capable of germinating in vegetated areas, establishment in these areas is typically unsuccessful (Johnson, 2000) and cottonwood stands are generally single cohort (Dykaar and Wigington, 2000, Baker, 1990). Although diameter is variable within a stand, most trees are within 4-5 years of age, with colonization corresponding to a large flooding event (Merigliano, 1996). Relatively large floods, in the 5 to 10 year recurrence interval, seem to be most effective at distributing cottonwood seedlings in the ideal recruitment zone, which is low enough to prevent drought, and high enough to avoid scouring (Mahoney and Rood, 1998).

Clonal reproduction of cottonwoods and other members of the *Salicaceae* family is common, and is thought to be influenced by flooding events, such that large floods encourage seed regeneration, while smaller floods lead to vegetative growth (Karrenberg *et al.*, 2002, Barsoum, 2002). In California, willow species were more heavily reliant on clonal growth than cottonwoods in early years (McBride and Strahan, 1984), suggesting that cottonwoods invest more heavily in seed production. This seems to be the case on the Snake River in Idaho, where, despite being abundant, sucker shoots rarely reached maturity (Merigliano, 1996), indicating that clonal growth plays a lesser role in overall reproduction in this area. The extremely large numbers of seeds dispersed by cottonwoods lead to dense patterns of single cohort stands, eventually thinning such that an estimated one in a billion seeds becomes a mature adult (Dykaar and Wigington, 2000).

While the process of cottonwood regeneration is heavily reliant on hydro-geomorphological processes, mature cottonwoods may also suffer directly from drought in some managed rivers (Rood *et al.*, 2003a). Dam induced drought and flooding can both have major physiological consequences for riparian trees (Kozlowski, 2002). In many rivers, however, the effect is simply a higher proportion of mature forests as regeneration is halted due to a lack of new alluvial substrate (Marston *et al.*, 2005). Specific responses to river management differ across systems, and must be studied for each ecosystem of interest (Rood *et al.*, 2005).

Snake River History

The Snake River, in Grand Teton National Park, WY, is regulated by a dam on the East side of Jackson Lake. Jackson Lake existed before the dam was constructed in 1908 (and then rebuilt in 1916) and has historically been a sediment trap. The main effect of the dam, therefore, has been to alter flow regime, rather than to decrease sediment supply (Nelson and Schmidt, 2008, in review). As a result, geomorphological changes to channels have been minimal (Nelson and Schmidt, 2008, in review). In 1958, the Palisades dam was built downstream of the National Park boundary. The use of this dam to manage water for agricultural purposes alleviated some of the need to regulate water through the Jackson Lake Dam. Between 1916 and 1957, the timing of peak flows was disrupted, occurring an average of 45 days later than the estimated natural peak flow of early June (Nelson and Schmidt, 2008, in review). Since 1958, the timing of peak flows has been more natural, occurring in the spring, but overall flood magnitude has been 45% lower than estimated natural levels, and 37% lower than for 1916-1957 (Nelson and Schmidt, 2008, in review). However, due to tributary input, the overall magnitude of floods on the Snake River has remained relatively natural, except for immediately below the dam (Nelson and Schmidt, 2008, in review). For instance, below Pacific Creek and Buffalo Fork, the magnitude of the 2-year recurrence annual maximum daily mean discharge was only 11% lower than for 1944-1957 (Nelson and Schmidt, 2008, in review). Late summer flows remain unnaturally high, but to a lesser degree than during the pre-1957 regime (Nelson and Schmidt, 2008, in review).

Geomorphologically, the Snake River has undergone relatively minor changes since construction of the dam, attributable to two major factors identified by Schmidt and Nelson (2007): First, the tributaries mitigate effects of the dam, since they contribute to high flows during the spring, and second, sediment supply has not been significantly altered. The mitigating effect of tributaries has been observed in other river systems, such that riparian areas proximal to dams tend to suffer more negative impacts (Rood *et al.*, 2005).

Riparian forest shifts along the Snake River have been previously studied below the Palisades dam, and include a reduced area of young cottonwood patches (Merigliano, 1996). This has been attributed to the decrease in peak flow, leading to decreased channel migration, erosion, and deposition of new gravel bar islands (Merigliano, 1996).

By altering these hydro-geomorphological processes, the extent of area suitable for cottonwood growth has declined in this section of the Snake River (Merigliano, 1996). Within the park boundaries, Marston *et al.* (2005) concluded an expansion of spruce forests, with cottonwood forests becoming less prevalent. This late successional trend was attributed to the Jackson Lake Dam, and resulting changes to channel morphology (Marston *et al*., 2005). However, changes to channel morphology were not supported by Nelson and Schmidt, (2008, in review).

Objectives

In the present study of the regulated Snake River and two of its unregulated tributaries, I explored how hydro-geomorphological processes of this system influence riparian forests. By using the unregulated tributaries as a control, I compared the forest structure of these otherwise similar systems. Previous studies of regulated versus naturally flowing rivers have been successful along the Green and Yampa rivers in Colorado (Merritt and Cooper, 2000, Uowolo *et al.*, 2005), and have concluded differences in vegetation to be linked to regulation.

There were several objectives to this study, the first of which was to relate forest structure to geomorphology. Riparian vegetation is closely tied to geomorphological landform and flooding (Bendix and Hupp, 2000, Hupp and Osterkamp, 1996, Hupp and Osterkamp, 1985), and understanding this relationship is a crucial first step in describing the dynamics of cottonwood forests.

Additionally, I examined potential differences in cottonwood forest structure on the dam-regulated Snake River, compared to the unregulated tributaries. I compared age class distributions for regulated and unregulated segments of the study area, and determined whether regeneration is occurring in regulated areas, and whether cottonwood regeneration was limited in years of more unnatural flow regimes (1916-1957). Previous research has suggested that river regulation can produce these results (Rood *et al.*, 2003b, Petts and Gurnell, 2005, Johnson, 2000, Rood and Mahoney 1990, Fenner *et al.* 1985, Merritt and Cooper, 2000), and that impacts are most severe directly downstream from dams, before tributaries enter (Rood *et al.*, 2005). Additionally, I examined whether a trend towards late successional spruce stands is evident, as suggested by Marston *et al.* (2005).

Based on these studies, and the work of Nelson and Schmidt (2008, in review), I had two hypotheses regarding cottonwood regeneration on the Snake River. First, I expected that cottonwood regeneration has historically been impacted by the dam, with recruitment inhibited between the years of 1916 and 1957 when peak flows occurred late in the spring. During these years, floods did not correspond with the release of cottonwood seeds, and new seedlings would have been scoured. As a result, trees between the ages of 50 and 90 should be sparse. My second hypothesis was that age gaps and possible trends towards late succession should be most prevalent in the sections of the Snake River immediately below the dam, where the tributaries have not had a mitigating effect on the magnitude of peak flows.

A further aspect of this research was to explore the relationship between cottonwood age classes, and understory communities. Natural riparian forests are mosaics of different tree sizes, each patch supporting unique flora (Fierke and Kauffman, 2005) and fauna (Hansen and Rotella, 2003), and contributing to the overall biodiversity of the ecosystem. I used the ordination technique NMDS (Non-metric multidimensional scaling), coupled with GAMs (Generalized Additive Models) to examine the relationship between tree size/age and understory vegetation in the unregulated segments of the study area.

Finally, to gain a more complete understanding of the various influences to forest structure, I observed the effects of browsing by beavers and ungulates on cottonwood growth form. Beavers play an important role in many riparian ecosystems, altering the structure of forests through tree removal, as well as creating wetland habitat and changing hydrology via damming (Naiman *et al.*, 1988). I examined how beavers and ungulates influence forest structure through root coppicing and multi-stemmed shrubby growth of browsed cottonwoods. Root coppicing occurs when a dominant stem is damaged, and multiple new shoots form below the damaged point (Barsoum, 2002). The extent to which beavers and ungulates stimulate this type of growth is of interest, and may affect the long term forest structure.

By analyzing the various hydro-geomorphological factors influencing the structure and composition of riparian forests, as well as how growth is impacted by browsing, I elucidated the dynamics of these forests on unregulated and regulated river segments.

The Study Area

The Snake River, in Grand Teton National Park, WY, has two large, unregulated tributaries which enter shortly after the Jackson Lake Dam (Figure 4.1). Pacific Creek enters the main river 7.2 km downstream from the dam, and Buffalo Fork enters at 8.1

km. There are several other tributaries in the Park, including Spread Creek, Cottonwood Creek, and Ditch Creek, but Pacific Creek and Buffalo Fork are most comparable to the Snake River study area in elevation, and size. These two creeks contribute significant sediment to the main channel, as well as 27% of the mean annual flow measured downstream in Moose, WY (Nelson and Schmidt, 2008, in review). The study area includes the segments of these tributaries from the National Park boundary, to the confluence with the main river, a length of 16.4 km for Pacific Creek, and 12.7 km for Buffalo Fork. The Snake River study area extends from the Jackson Lake Dam, to Deadman's Bar, a length of 33.6 km. Approximately 4.2 km below the dam, there is a large oxbow, with lake-like conditions, which was not sampled for the present study. Areas with obvious anthropogenic disturbance were also excluded.

The study area was considered in five segments (Table 4.1): SR1 refers to the segment of the main Snake River above the tributaries, directly below the dam. SR2 is the predominantly braided area between Pacific Creek and Spread Creek, with a length of 6.3 km. SR3 is the 20.3 km partially single channel segment from Spread Creek to Deadman's Bar. BF refers to Buffalo Fork, and PC to Pacific Creek.

Table 4.1. Number of plots, section length, and area description for each section of the study area.

Section	**# Plots**	**Length (km)**	**Description**
BF	40	5.4	Buffalo Fork
PC	42	6.7	Pacific Creek
SR1	48	7.2	Upper Snake River
SR2	53	6.3	Mid Snake River
SR3	74	20.3	Lower Snake River

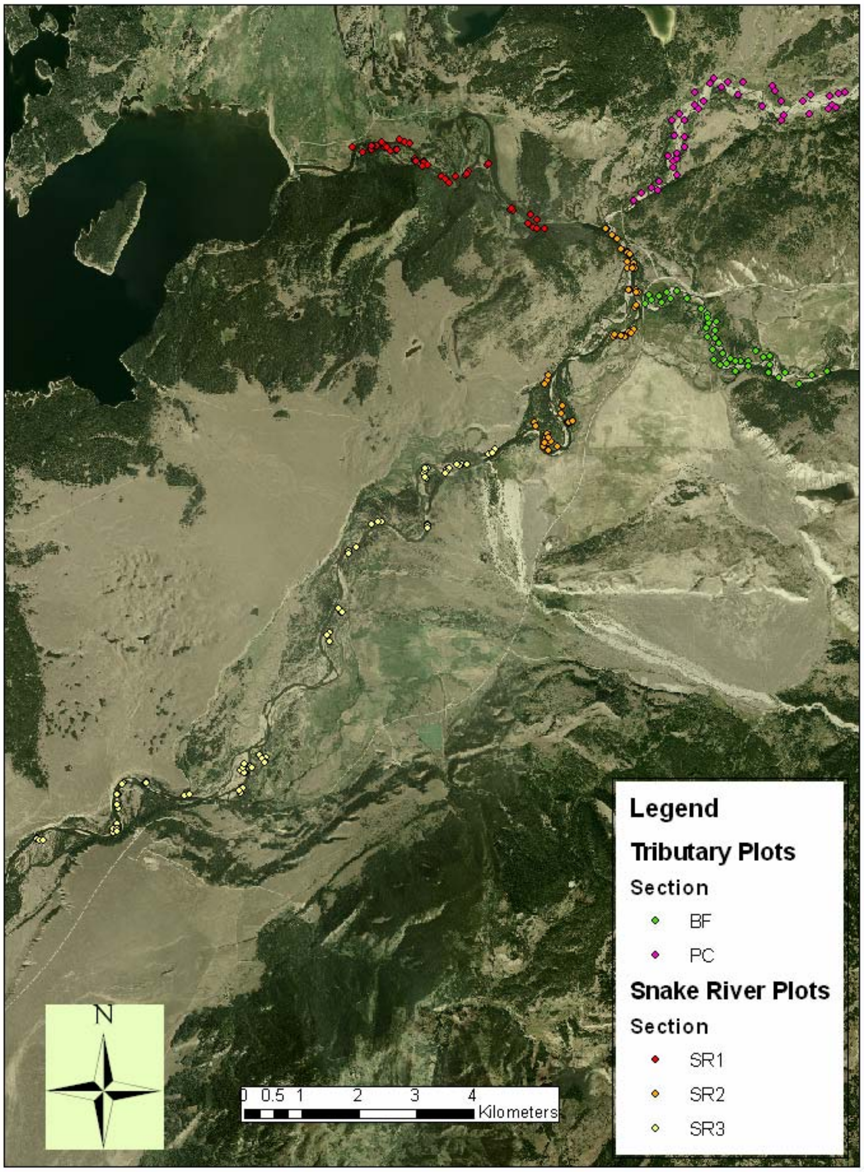

Figure 4.1. The study area, including Jackson Lake, the Snake River from the dam to Deadmans Bar, Pacific Creek and Buffalo Fork. Plots of each river section are displayed in color (BF=Buffalo Fork, PC=Pacific Creek, SR1=Snake River 1, SR2= Snake River 2, SR3= Snake River 3).

The Snake River and its tributaries are, with the exception of the upper SR1 segment and portions of the SR3 segment, predominantly braided rivers. The braid index, defined as the ratio of total bankfull channel length: main bankfull channel length (Schmidt and Nelson, 2007) ranges from 1.0 to 3.14 on the Snake River. Pacific Creek has a mean braid index of 2.43, while Buffalo Fork has an index of 2.12. In comparing Pacific Creek and Buffalo Fork, the former is a more graded river, with elevation changes of 28m over the study area (1.7m /km), and a resulting large area of active alluvium of 0.65km^2 (39,687m^2/km). Buffalo Fork changes only 11m in elevation (0.87m/km), and has an active alluvial area of 0.41 km^2 (32,178m^2/km). The elevation of the entire study area ranges from 2009 to 2082m.

The riparian forests of the Snake River and tributaries in Grand Teton National Park are dominated by the cottonwood species *Populus angustifolia*, and *Populus balsamifera.* All species names are based on Dorn (2001). These cottonwood species are often indistinguishable when young, and seem to occupy similar habitats, but *P. angustifolia* is clearly dominant in the area. As cottonwoods mature, they typically become co-dominant with *Picea pungens* (blue spruce), and eventually spruce becomes dominant (Figure 4.2). The mixed *Picea pungens* and *Populus angustifolia* system is not uncommon (Daubenmire, 1972), and a similar succession has been studied along the Red Deer River, in Alberta Canada (Cordes *et al.*, 1997). Other tree species in the study include lodgepole pine *Pinus contorta* (lodgepole pine), which are abundant in the uplands of Grand Teton National Park, and occur in the riparian corridor. This species will be considered briefly in my analysis. Willow species, including *Salix boothii, S. exigua, S. lasiandra, S. eriocephala*, all shrubby in growth, are common in the area. *Populus tremuloides* occurs very rarely. Analysis of the forest structure will focus on cottonwoods and spruce, as these tree species are overwhelmingly dominant.

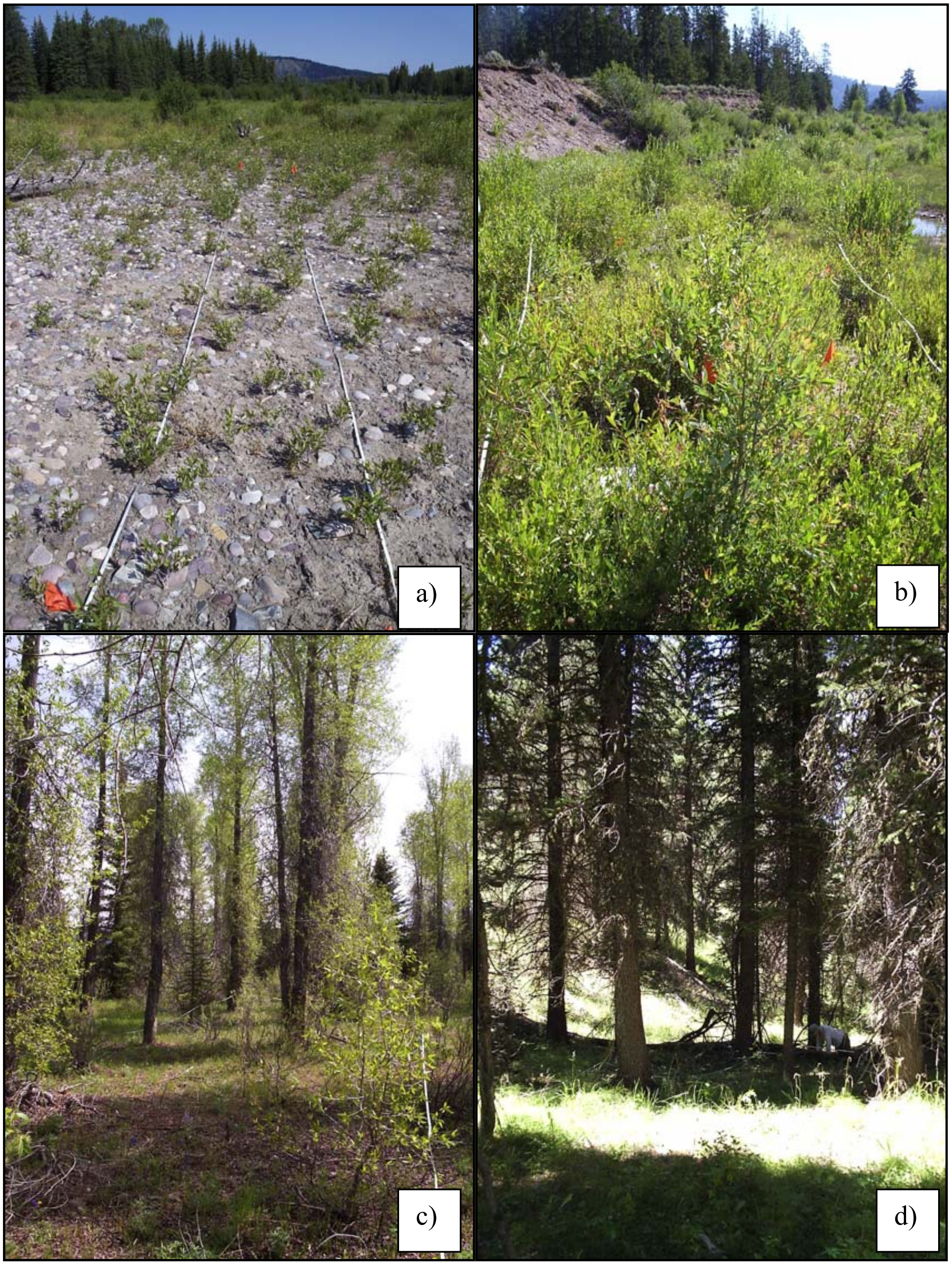

Figure 4.2. a) Young cottonwood trees on a gravel bar. b) Shrubby cottonwood stand. c) Mature cottonwood forest on a terrace. d) Mature spruce forest on a floodplain.

Methods

During the summers of 2005 and 2006, 175 plots were established on the Snake River. In 2007, 82 plots were established on Pacific Creek and Buffalo Fork. Plots were stratified across all vegetation types and geomorphological landforms. Plots size differed depending on growth form: tree plots were $100m^2$, shrub plots $25m^2$, and herbaceous plots $10m^2$. To accommodate the linear nature of riparian plant communities, plots were rectangular. Plant community data, environmental data and tree measurements were recorded for each plot.

All vascular plant species were identified to species based on Dorn (2001), and percent cover was estimated visually using a modified Braun-Blanquet scale (Braun-Blanquet, 1932). Cover classes between one and five were assigned, and a trace category of 0.5 was included for species with less than 1% cover (0.5: *<1%*, 1: *1-5%*, 2: *5-25%*, 3: *25-50%*, 4: *50-75%*, 5: *75-100%*). Cover was recorded separately for each vegetation layer, so that members of a species growing in the herb layer were considered independently from those of the same species growing in the shrub and tree layers. Herb (H), shrub (S), and tree (T) layers were defined by height (H: *<=0.5m*, S2: *>0.5m-1.5m*, S1: *>1.5-3m*, T2: *>3-10m*, T1: *>10m*).

Several descriptive environmental variables were derived using ARC-GIS (version 9.2, ESRI Inc.), including active alluvial area and braid index (ratio of total bankfull channel length: main bankfull channel length), as defined by Schmidt and Nelson (2007).

Height, diameter, growth form (single, few stems: <5, or many stems:>5) browsing impact (single, few: <5, or many:>5 stems browsed), and type of browsing (beaver or ungulate) were recorded for all trees in each plot. Beaver browsed trees are removed near the base and show distinct teeth marks, compared to the higher, cleanly severed branches of ungulate browsed trees. Trees that were less than 3 years old were counted, but were not measured or included in the current analysis. Many young cottonwood stands are entirely destroyed during the first year (Johnson, 2000), since seeds often germinate in low areas which are prone to scouring, or in areas with high drought stress in the late summer. I have focused analysis on established cottonwood trees, and excluded young spruce for consistency. In plots with a high density of trees, subsamples were used. Tree data were expressed as densities (trees/100m^2) for analysis. A total of 7477 cottonwoods and 933 spruces was measured.

Base diameter measurements were taken as a surrogate for age. In cases where basal measurements were not possible due to excessive flaring, diameter at breast height (DBH) was used. A linear regression of base diameter as a function of DBH was calculated, using measurements from trees in the study area, supplemented by additional *Populus angustifolia* trees from the Yellowstone River near Livingston MT. This regression was used to standardize diameter, converting all measurements to a base diameter value. Unless stated otherwise, the two cottonwood species, *Populus angustifolia* and *Populus balsamifera* will be considered together for cottonwood analysis. The program R (R Development Core Team, 2007) was used for all statistical analyses.

Tree cores or cross sections from the largest tree of each species per plot were collected and aged. A regression of spruce and cottonwood age as a function of base diameter was calculated. Similar methods were used by Scott *et al.* (1997) and Merigliano (1996) to infer cottonwood age from diameter. Additional cross sections were collected for smaller trees from the study area to supplement the data, so that age could be estimated for each cottonwood and spruce tree measured. The age distribution of cottonwoods and spruce were analyzed using barcharts of density (trees/100m^2) for each river segment and for each major geomorphological landform. Barcharts of the total density of all age classes cottonwood, lodgepole, and spruce trees were also made for each river section.

To determine how understory vegetation varies with overstory tree sizes, the understory vegetation data were ordinated with NMDS (Non-metric multidimensional scaling), using the NMDS function in R (labdsv package; Roberts, 2007, MASS package; Venables and Ripley, 2002). NMDS is an ordination algorithm that is "non-metric" in that functions are calculated on rankings, with values simply ranked from minimum to maximum, rather than on a ratio scale (Kruskal and Wish, 1978). The rank distances of samples in the ordination should reflect the rank distances in the underlying matrix, which was calculated using a Bray-Curtis dissimilarity index (Bray and Curtis, 1957). NMDS is considered to be one of the more robust ordination techniques, especially if based on a Bray-Curtis dissimilarity matrix (Minchin, 1987, Faith *et al.*, 1987). This analysis was for the unregulated tributary plots that had cottonwood trees present, giving a sample size of 54 plots. To focus analysis on the understory composition, cottonwood species were excluded from the matrix. The variables 'mean tree diameter' and 'mean tree age' were evaluated for explanatory value, by fitting a generalized additive model (GAM; Wood, 2008) to the ordination. GAMs are similar to generalized linear models, except that they fit a smoothed surface, and do not require a linear function. My NMDS techniques are similar to those used by Fierke and Kauffman (2005) to evaluate importance of mean tree size in determining understory composition. The single cohort nature of cottonwoods forests (Merigliano, 1996, Dykaar and Wigington, 2000, Baker, 1990) makes this method applicable, since the mean diameter is representative of the entire stand.

Browsing affects on tree growth form were calculated using a Chi-square test of proportions, to determine whether browsed or unbrowsed trees were more likely to display multi, few, or single-stemmed growth. Size preferences for browsed trees were also identified, using a Welsh two-sample t-test to compare mean diameter of ungulate and beaver browsed trees to the mean diameter of unbrowsed trees. The dataset used for this analysis was from the unregulated tributaries, collected in 2007, since these data were inconsistent across field seasons.

Results

Regression Models for Diameter and Age

The R^2 values of the regressions used to standardize tree diameter measurements were 0.97 for spruce and 0.99 for cottonwoods. Base diameter was estimated as a function of DBH. For cottonwoods, the relationship is $base=1.01dbh + 4.33$; for spruce $base=1.12dbh + 2.02$.

To estimate age from diameter, separate regressions were necessary for cottonwoods less than 3cm in diameter (Figure 4.3), and cottonwoods over 3cm in diameter (Figure 4.4). For spruce, a 5cm diameter was a more suitable break point (Figures 4.5, 4.6). Higher accuracy levels were possible for smaller trees, which were aged via cross sections rather than cores. Growth patterns seemed to be different for smaller trees, particularly in the case of spruce, further justifying the use of separate regressions. Y-intercepts occur at approximately 3 years old, for regressions of small trees. For trees under 3 years old, age was estimated in the field. Only established trees over 3 years old were included in the current analysis. This makes the inability to estimate the age of very young trees with these regressions less problematic. The regression for spruce over 5cm in diameter has a y-intercept of 29.4; this means that a 5cm tree is 34 years old, which is reasonable.

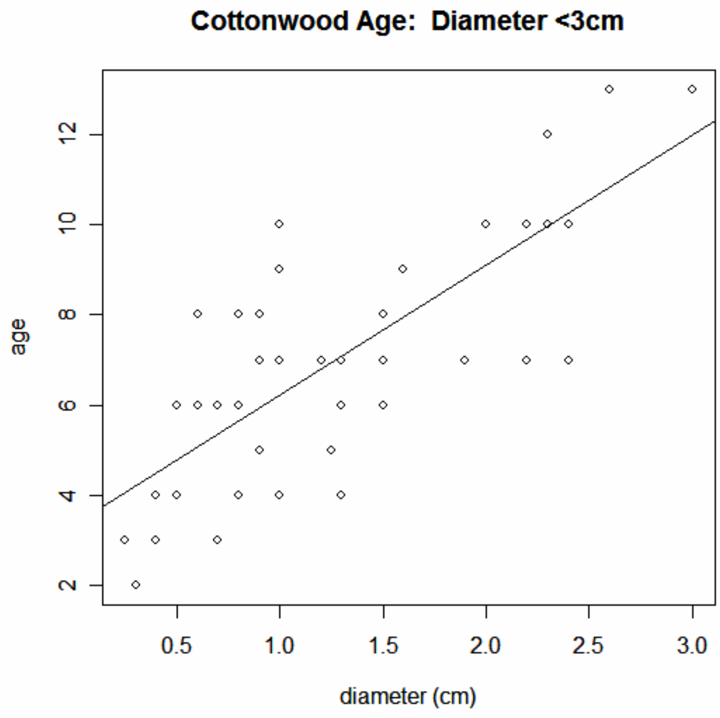

Figure 4.3. Cottonwood age as a function of diameter for trees </=3 cm diameter R^2=0.57, N=42. *Age=3.34+2.89(diam)*

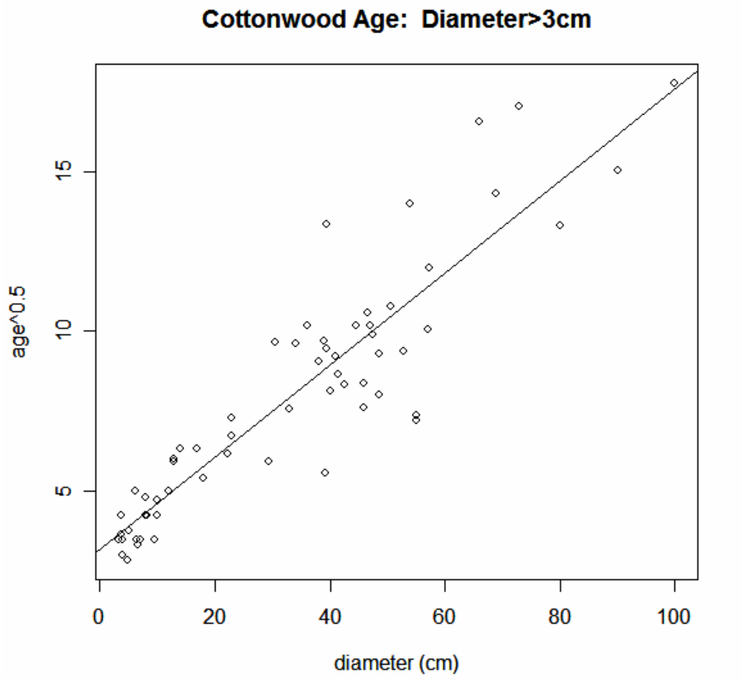

Figure 4.4. Cottonwood age as a function of diameter, for trees >3cm diameter. R^2=0.83, N=61. *Age = (3.14 + 0.144 (diam))* ^{2}

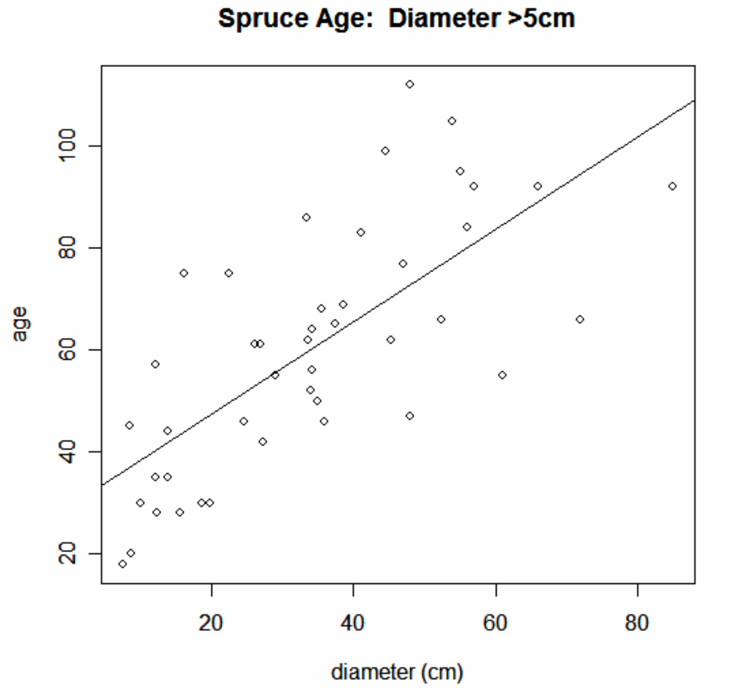

Figure 4.5. Spruce age as a function of diameter, for trees > 5cm diameter. R^2= 0.51, N=44. *Age=29.4 + 0.91 (diam)*

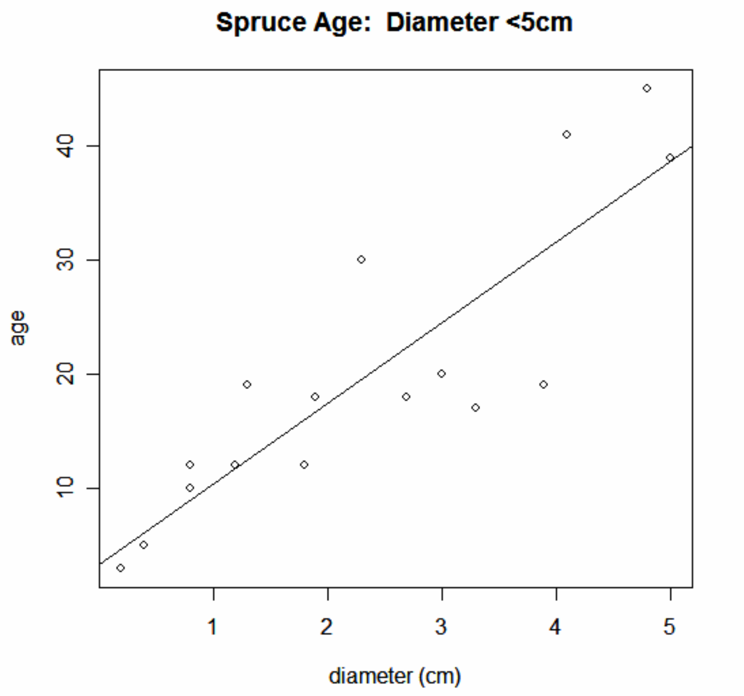

Figure 4.6. Spruce age as a function of diameter, for trees </= 5cm diameter. R^2=0.76, N=16. *Age= 3.29 + 7.08(diam)*

A transformation was applied to the large cottonwood tree regression, increasing the R^2 value (Figure 4.4). The log-likelihoods of power values to use for transformation were calculated, and the optimal transformation was found to be 0.5, applying a square root to the dependent variable, age.

Age Class and Species Distributions

The age class distribution of cottonwoods in the study area can be described as a reverse J curve (Daniel *et al.*, 1979), with younger age classes being most abundant. Reverse J curves are common in many forests (Johnson and Bell, 1975, Daniel *et al.*, 1979), but in single cohort cottonwood stands the distribution tends to be truncated

(Baker, 1990). The reverse J curve in my data represents the combined age distribution of many single cohort sites within the study area (Figure 4.7). This curve is particularly pronounced, with the frequencies of young ages being several orders of magnitude greater than older age classes. Due to the extremely high densities of young cottonwoods (up to 206 trees/100m^2 on the SR2 section in the <4 age class), density was plotted on a log scale. Additionally, age classes are on a natural log scale.

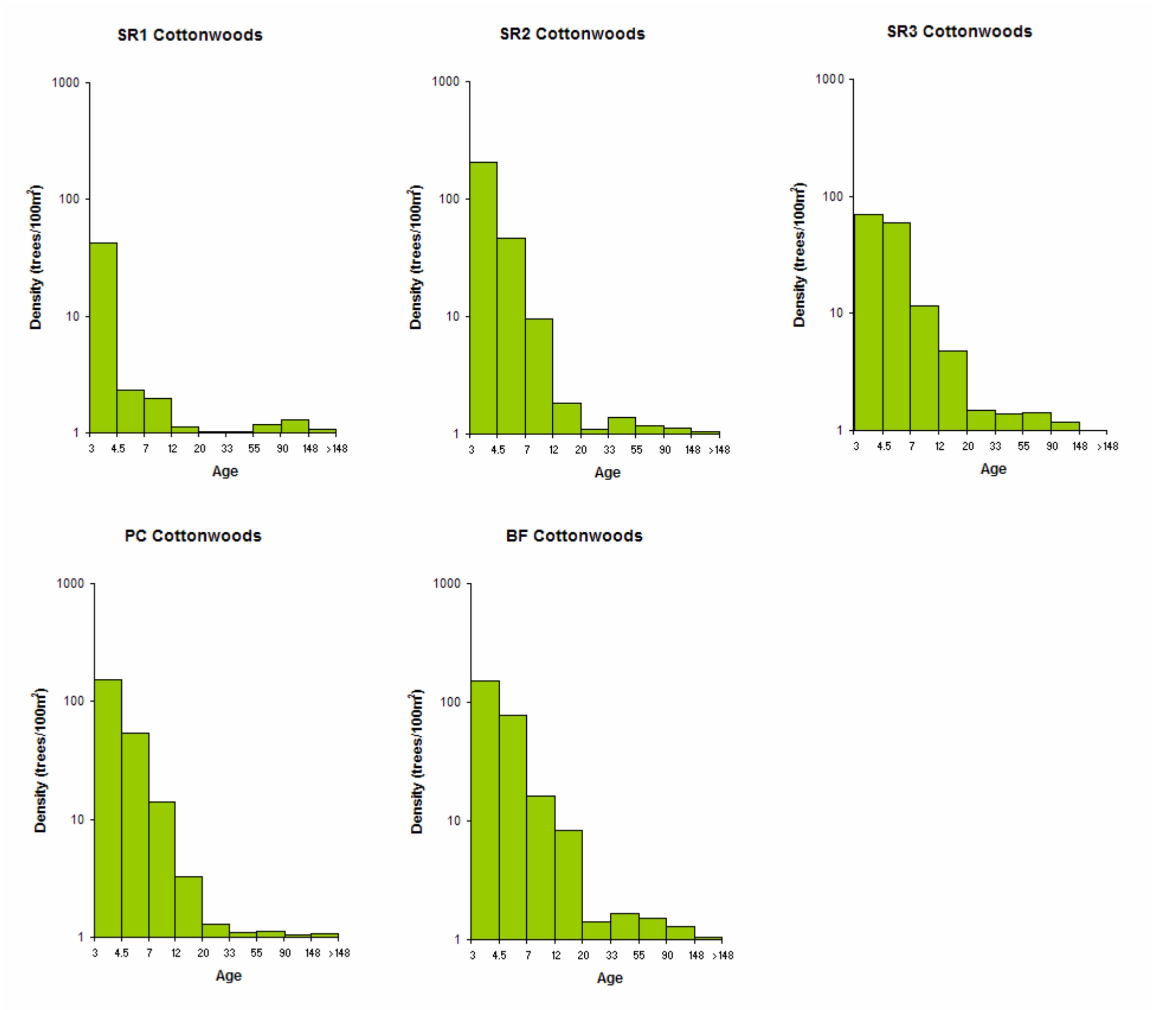

Figure 4.7. Log-density of cottonwood age classes (on a natural log scale), across river sections (SR1-Upper Snake River, SR2-Middle Snake River, SR3-Lower Snake River, PC-Pacific Creek, BF-Buffalo Fork).

Histograms of cottonwood age class distribution reveal an overall lower density of trees on SR1 (Figure 4.7). However, there is no obvious trend towards older stands. Additionally, the Snake River does not have a clear age gap corresponding to the pre-1958 years when dam regulation of flood timing was most severe. There is an apparent age gap in trees corresponding to the years 1953-1988 on SR1. However, there are also low densities of 20-33 year old trees on PC and SR2.

Histograms of cottonwood age class distribution were also examined with respect to landform (Figure 4.8). There is a clear trend, with older cottonwood age classes having higher densities on floodplains and terraces, and younger age classes having higher densities on gravelbars.

Age class distributions of spruce are very different from cottonwoods, with more normally distributed patterns (Figure 4.9). Overall densities are much lower than for cottonwoods, with a maximum density of approximately 2.3 trees/100m^2, for 30-40 year old spruce in SR2. Most sections have an additional peak in the 0-10 year range. The density of older spruce gradually declines, with the maximum age around 100 years. The growth pattern of this species seems to be quite slow in the early years. This is a possible cause of error for trees estimated to be less than 10 years old. The variation in growth for older trees of this species is also extremely high, with an R^2 value of only 0.51 for the age/diameter regression. Additionally, sample size is much smaller than for cottonwoods. Despite these sources of error, there is a definite peak in approximately 30

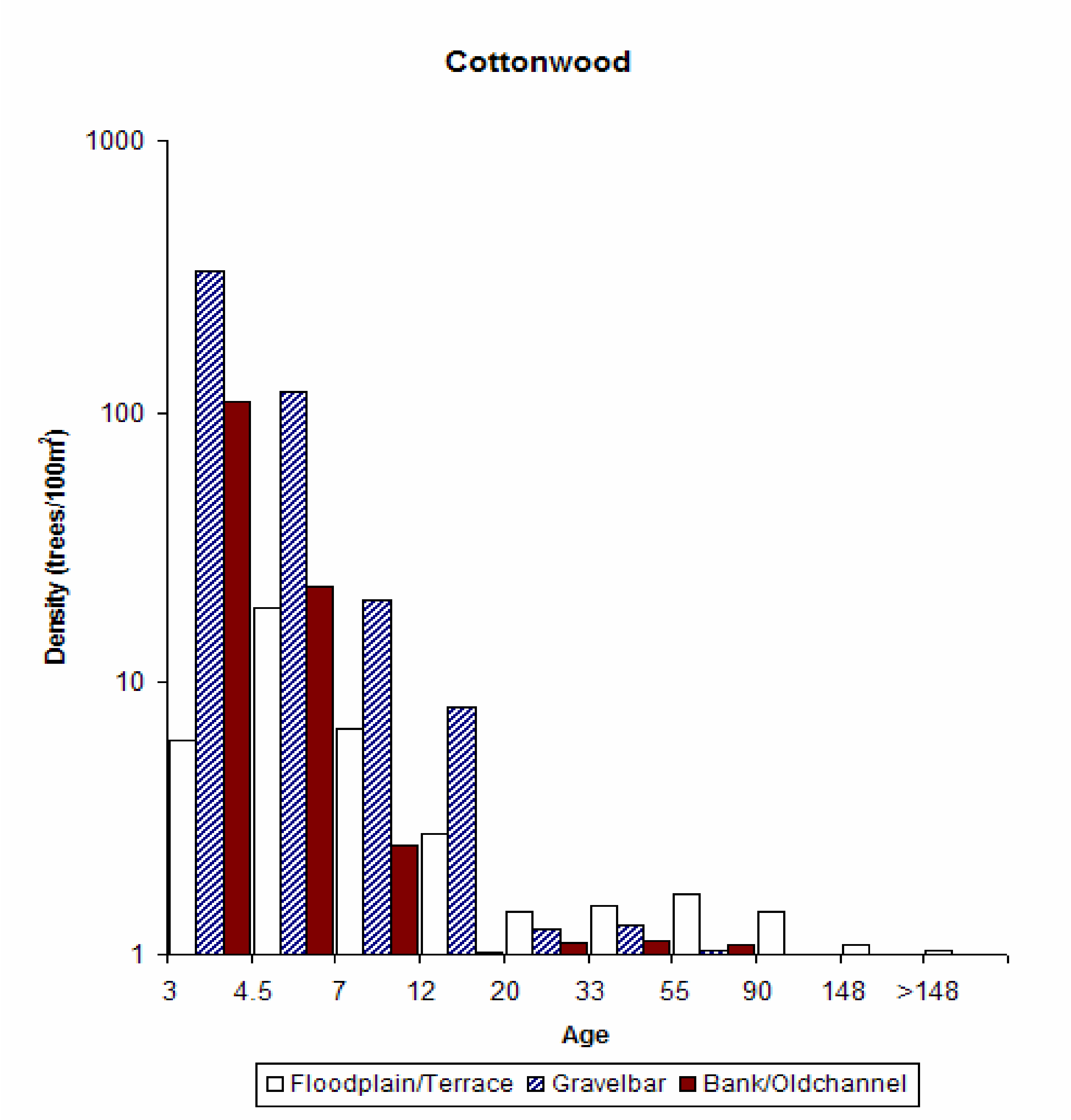

Figure 4.8. Log-density of cottonwood age classes (on a natural log scale), across geomorphological landforms.

year old spruce trees. The general pattern of spruce age distributions is similar from one section to the next, except for a relative lack of young spruce in SR2, compared to the high density in the 30-40 age class. This section has a higher overall density of spruce, while SR1 and SR3 have low densities. Spruce density is associated with floodplains for older age classes, and gravelbars and edges for younger age classes (Figure 4.10).

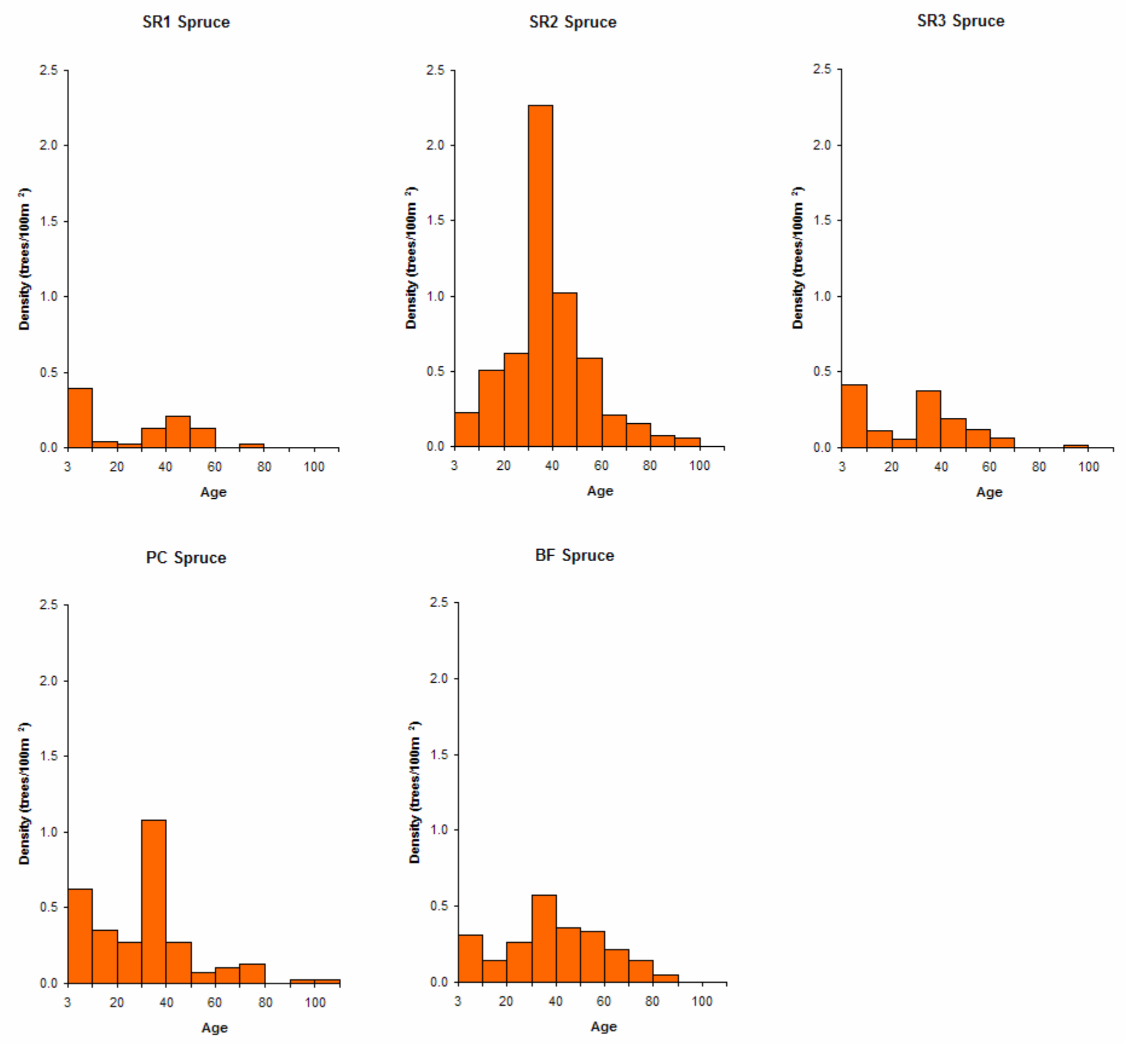

Figure 4.9. Density of spruce age classes across river sections (SR1-Upper Snake River, SR2-Middle Snake River, SR3-Lower Snake River, PC-Pacific Creek, BF-Buffalo Fork).

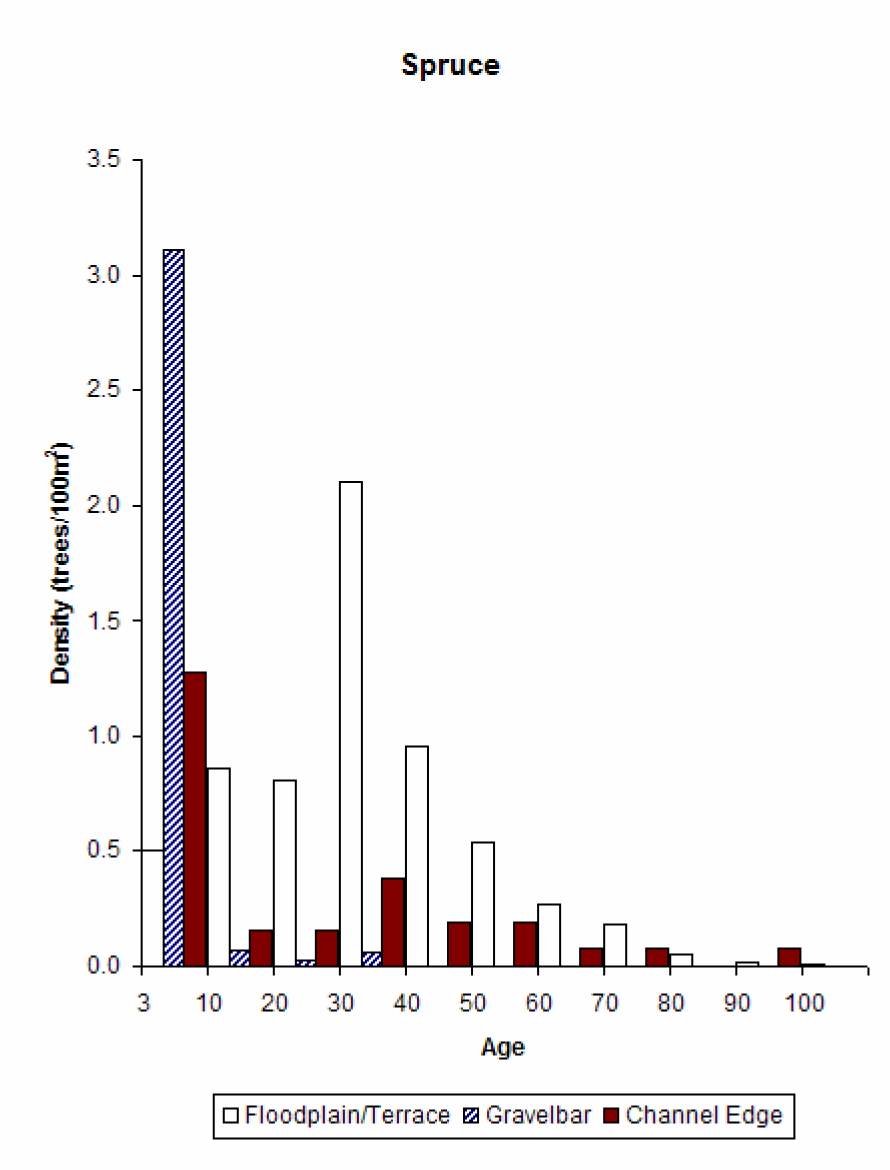

Figure 4.10. Density of spruce age classes across geomorphological landforms.

Barcharts of total tree density of all age classes (trees/100m^2) have been considered for each tree species across river sections (Figure 4.11). In addition to spruce and cottonwood, I also included lodgepole pine in this section of the analysis. Relative to other sections, SR1 plots have a greater density of lodgepole trees. This section also has lower densities of spruce and cottonwood than any other section. The tributaries have the greatest densities of cottonwoods, followed by SR3, then SR2 and SR1. SR2 has the highest density of spruce.

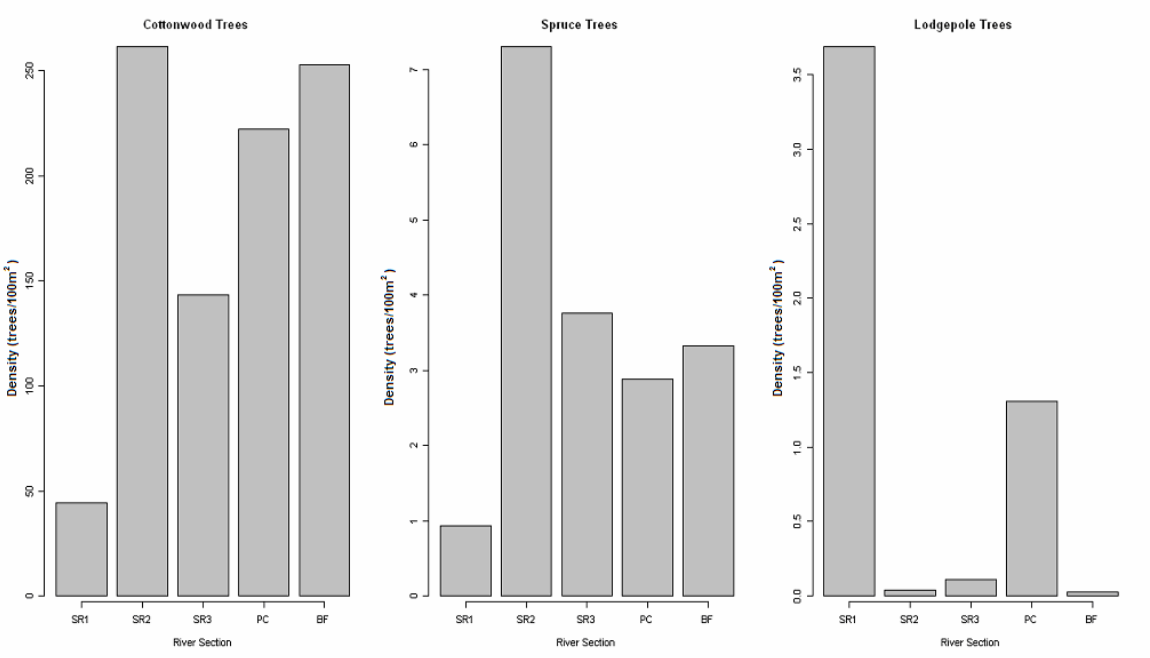

Figure 4.11. Density of all age classes of cottonwood, spruce, and lodgepole trees, across river sections (SR1-Upper Snake River, SR2-Middle Snake River, SR3-Lower Snake River, PC-Pacific Creek, BF-Buffalo Fork). Y-axes for the 3 species are on different scales.

Community Understory Composition

To explore how understory communities of various cottonwood forests differ, I used NMDS, based on a Bray-Curtis dissimilarity matrix, for unregulated plots with cottonwood trees present (n=54). The NMDS model is an unconstrained, 2 dimensional model, with an R value of 0.88 (Figure 4.12). By fitting a gaussian GAM surface for the variable ‘mean tree diameter’, I examined the association with vegetation patterns, as modeled by the ordination (Figure 4.13). The variable ‘mean tree diameter’ is quite relevant (D^2= 0.77). Additionally, I fit the variable ‘mean tree age’, using the same techniques (Figure 4.14). This variable also explains a very high proportion of the variation in the ordination (D^2= 0.85).

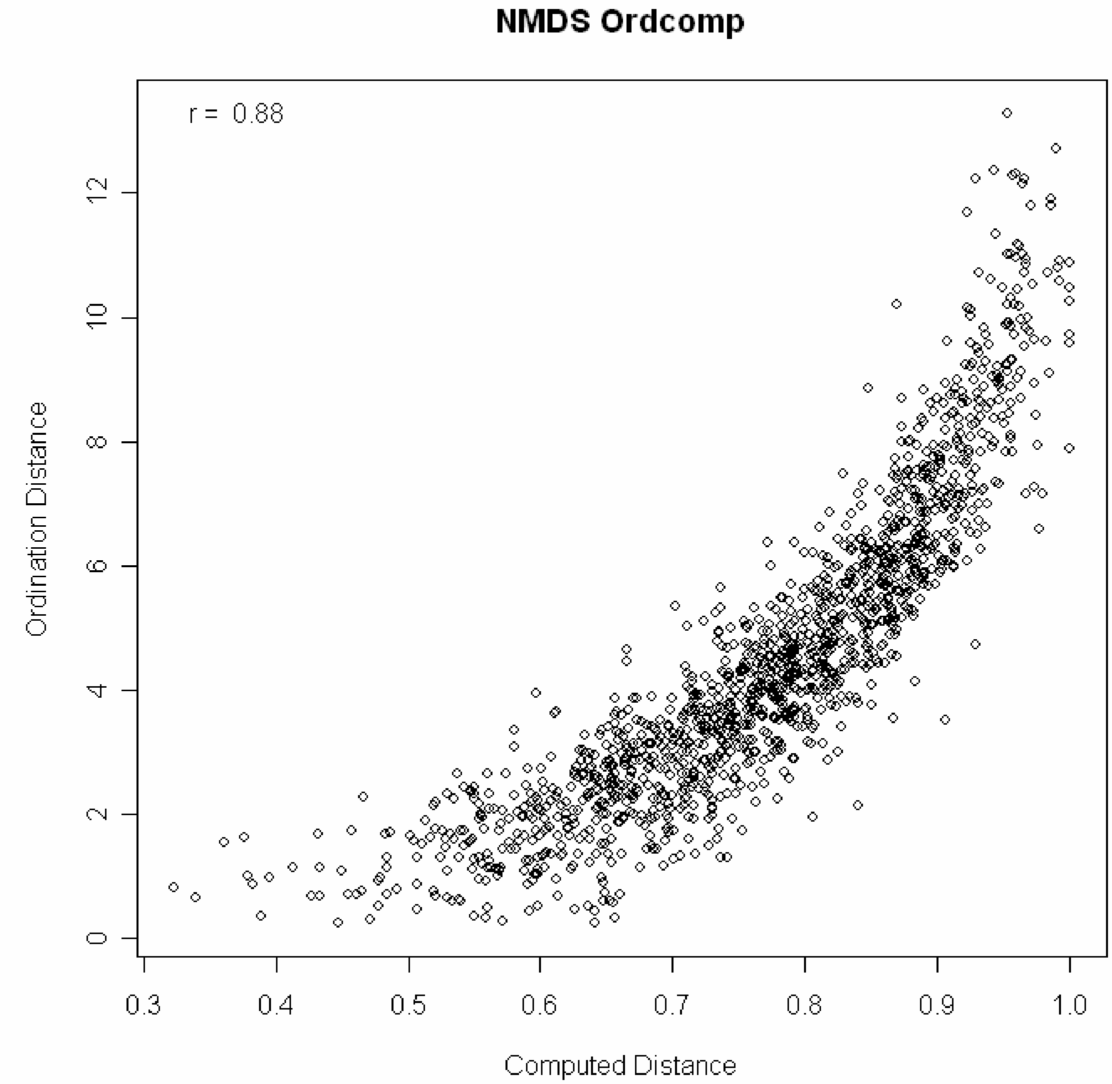

Figure 4.12. Correlation of ordination and computed distances of sample plots, giving an indication of the ordination quality (r=0.88).

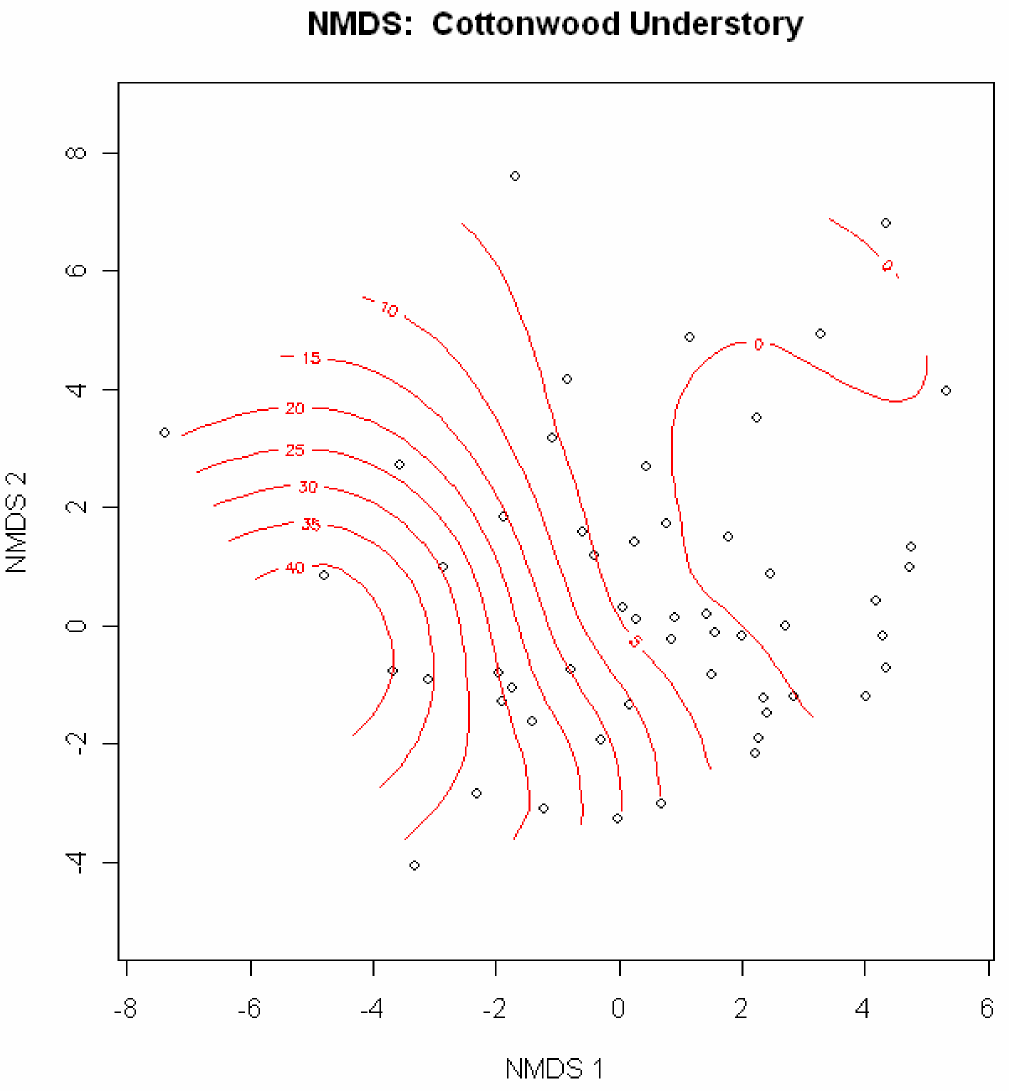

Figure 4.13. Gaussian GAM surface of mean tree diameter (R^2=0.77), fit to a 2-dimensional NMDS ordination of understory vegetation.

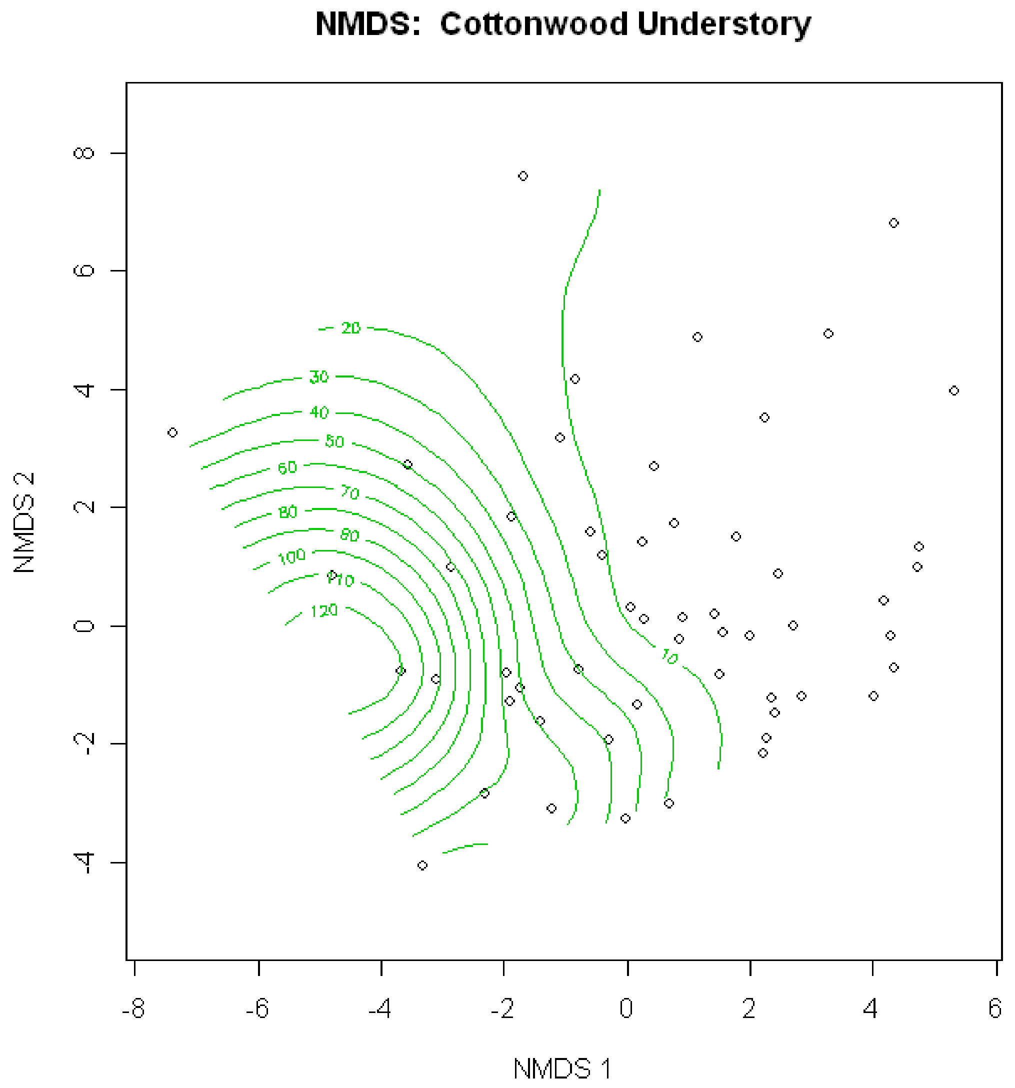

Figure 4.14. Gaussian GAM surface of mean tree age (R^2=0.85) fit to a 2-dimensional NMDS plot ordination of understory vegetation.

The distributions of these two GAM surfaces are nearly identical, which is inevitable given age is estimated as a function of diameter. Plots on the right side of the ordination plot (Figures 4.13, 4.14) contain younger cottonwood trees, with smaller diameters. Plots dominated by young trees (<10 years old; diameter <5cm) are most prevalent.

Browsing Impacts on Riparian Forests

Beaver browsing of *Populus angustifolia* is most concentrated on trees 3-4 cm in basal diameter (Table 4.2). Ungulates do not show a strong preference for a particular size of tree. The very large proportion of small cottonwoods in the study area influences Table 4.2, since median tree diameter of all unbrowsed trees is only 0.6cm. Median diameter of beaver browsed trees is 3cm (mean=4.6cm), and for ungulate browsed trees it is 2.0cm (mean=2.2cm). Median values better reflect the size most frequently browsed, while mean values incorporate the minority of browsed trees which are very large. On average, beaver browsed trees are significantly larger than unbrowsed trees (p<.001, Welsh two-sample t-test). The mean size of ungulate browsed trees does not differ significantly from unbrowsed trees.

Table 4.2. Mean and median diameter of beaver and ungulated browsed versus unbrowsed cottonwood trees. Asterisk indicates where mean diameter of browsed is significantly different from unbrowsed.

	Base Diameter	**Browsed**	**Unbrowsed**
Beaver	mean	4.6*	1.8
	median	3.0	0.6
Ungulate	mean	2.2	1.9
	median	2.0	0.6

There is a strong significant relationship (p<.001, chi-square test of proportions) between browsing by ungulates and beaver, and the growth form of *Populus* (Table 4.3). The trend seems to be particularly important for beaver browsing. Of the 243 multi-stemmed trees, 107 were browsed (29 by ungulates, 78 by beaver). By comparison, 77 of 581 few stemmed trees were browsed, and only 111 of the 2100 single stemmed were browsed.

Table 4.3. Percentage of single-stemmed, few-stemmed, and many stemmed trees browsed by beavers and ungulates.

	Ungulates		**Beaver**		**Total Browsing**		
	Un-browsed	Browsed	Un-browsed	Browsed	Un-browsed	Browsed	**n=**
Single-stemmed	95.9	4.1	98.8	1.2	94.7	5.3	2100
Few-stemmed	90.2	9.8	96.6	3.4	86.7	13.3	581
Many-stemmed	88.1	11.9	67.9	32.1	56.0	44.0	243

Discussion

Age Class and Species Distributions

One of my primary purposes was to understand how hydro-geomorphology and tree forest structure are related. Figure 4.8 shows a clear relationship between dominant age class of cottonwoods, and geomorphological landform. Young cottonwoods have highest densities on gravelbars and old channels, while older cottonwoods have higher densities on floodplains and terraces. Mature spruce trees are also most dense on floodplains and terraces. Young spruce are common on gravelbars, but also along channel edges. Spruce seedlings seem to be well suited to this edge habitat, possibly due to high levels of sunlight. *Picea engelmanii* regeneration occurs primarily in canopy gaps (Kneeshaw and Burton, 1997), and *Picea pugens*, being closely related (Daubenmire, 1972), may also require canopy openings or edge habitat. The strong relationship between cottonwood and spruce age distribution and geomorphological landform (Figures 4.7, 4.9), is consistent with previous research emphasizing the importance of this factor (Bendix and Hupp 2000, Hupp and Osterkamp, 1996, Hupp and Osterkamp, 1985).

This supports the notion that a variety of geomorphological landforms, maintained by natural river processes, lead to diversity in forest structure.

With respect to my hypotheses on river section, no evidence was found to suggest that an age gap in cottonwoods corresponding to the years prior to 1958 exists on the Snake River (Figure 4.7). Such a gap would have indicated that years of intense river management, affecting the timing of peak floods, resulted in reduced cottonwood recruitment. However, a gap is apparent for trees in the 20-55 age class, corresponding to the years 1953-1988. This gap exists to a lesser degree on other sections. It is possible that trees in this age class were underestimated by sampling, due to multi-stemmed growth form. Of the 7477 cottonwood trees measured in the field, 248 (3.3%) did not have a dominant main stem, and the diameter of the largest branch may have been smaller than for a single-stemmed tree of the same age. Thirty of these individuals were in the 12-20 age class, and may actually be older than 20. Additionally, despite the relatively high R^2 of 0.83, there is error associated with the age estimate. However, even considering these sources of error, there is no indication of a pre-1958 age gap.

The continuous pattern of cottonwood recruitment may reflect the lack of geomorphological changes in the river due to dam regulation (Nelson and Schmidt, 2008, in review). Current levels of regeneration are high on all river sections, with densities of 42-206 trees/100m^2 in the <4 age class year range (compared to spruce, which have a maximum density of 2.3 trees/100m^2, occurring for the 30-40 age class) (Figures 4.7, 4.9). This reinforces the importance of mass seed production, followed by seedling thinning, in the life history strategy of cottonwoods.

The SR3 section of the Snake River has an overall high density of cottonwoods, although slightly below the tributaries, and the SR2 section has an overall cottonwood density similar to the tributaries (Figure 4.11). This suggests that the tributaries may have a mitigating effect on both the geomorphology (Nelson and Schmidt, 2008, in review), and the cottonwood forests of the Snake River.

In general, modeling spruce age was not very successful, due in part to high levels of variation in the age/diameter relationship (R^2=0.76 and 0.51) (Figures 4.5, 4.6). I observed multiple periods of apparent suppression, followed by periods of rapid growth in many spruce cores. *Picea rubens* have been found to exhibit similar cycles of suppression and release prior to canopy recruitment (Wu *et al.*, 1999). Such growth makes estimating age from diameter difficult, and is likely the primary reason behind the poor regression for this species. In general, there seems to be a pattern of spruce recruitment appearing early in succession, followed by slow growth, and eventual rapid growth. The rapid growth may be associated with canopy gaps due to cottonwood thinning in mature forests.

I did not find direct evidence for a shift toward late succession forests (*i.e.* mature cottonwood and spruce) in the upper section of the Snake River (Figures 4.7, 4.9, 4.11). These findings are inconsistent with those of Marston *et al.* (2005). However, the overall density of cottonwoods is substantially lower on SR1, which provides some indication that the spatial extent of cottonwood forests may be limited in this section. Smaller stand sizes of cottonwoods have been described along the Snake River in Idaho, below Palisades dam (Merigliano, 1996). The lower densities on SR1 are likely related to the lack of gravelbars on the upper Snake River, since Jackson Lake acts as a sediment trap

(Nelson and Schmidt, 2008, in review). High densities of cottonwoods are associated with gravelbars, and without sediment to form extensive gravelbars, dense cottonwood stands do not occur. These trends cannot be attributed to the dam, since Jackson Lake existed historically, effectively eliminating sediment supply to this section (Nelson and Schmidt, 2008, in review).

Given the relatively low density of cottonwoods, I would have expected spruce numbers to be higher on the SR1 section of the Snake River, indicating a shift toward later successional forests. Marston *et al.* (2005) predicted such an expansion of spruce forests. However, spruce density on this section is quite low, compared to the high densities on SR2 (Figure 4.11). On all river sections, particularly SR2, there is a peak in approximately 30-50-year old spruce trees (Figure 4.9). This peak corresponds with the gap found in cottonwood age distribution (Figure 4.7). It is possible that several decades of limited cottonwood regeneration occurred, and that spruce expanded during these years. This may explain previous observations of spruce expansion (Marston *et al.*, 2005), however, the lack of younger age classes suggests that this trend has subsided.

The SR1 section seems to lack typical cottonwood/spruce riparian forests, and instead lodgepole density is relatively high (Figure 4.11). Given the abundance of this species in the uplands, it is not surprising to find it in the riparian corridor. However, the high proportion of this species in the upper section suggests the conditions may be more similar to the uplands. The river in this segment is single channel, and relatively incised, so that plots are at greater elevations above water (although only marginally significant, p=.07; Welsh two-sample t-test). The typical riparian forests, dominated by cottonwoods and spruce, seem to be spatially limited in this segment, while upland forests occur in close proximity to the river. Whether this phenomenon is the result of dam regulation, or the single strand nature of the river is debatable. Dam regulation can certainly cause rivers to incise (Leopold *et al.*, 1964), but the geomorphological changes to the Snake River since the dam was built have been minimal (Nelson and Schmidt, 2008, in review), and may not fully explain these forest differences.

Community Understory Composition

The maintenance of cottonwood forests, including young stands, promotes overall biodiversity (Fierke and Kauffman, 2005). This is evident in my NMDS analysis, which shows that mean tree age and diameter in the overstory are associated with variation in understory vegetation (Figures 4.13, 4.14). Similar conclusions, also based on NMDS using mean tree diameter, have been made in the Willamete Valley in Oregon (Fierke and Kauffman, 2005). The fact that understory composition varies with tree diameter and age reinforces the importance of maintaining a mosaic-like forest through natural hydro-geomorphological processes.

Management, with the goal of maximizing biodiversity, should aim to maintain a variety of forest age/size classes. The value of riparian ecosystems, for their richness of flora and fauna, as well as economic importance, has been previously emphasized (Nilsson and Berggren, 2000). Forest age classes correspond to certain geomorphological landforms, which are the result of natural hydro-geomorphological processes. Healthy riparian ecosystems, along the Snake River and other systems, are dependent on flow regimes remaining as natural as possible. It appears that the current management regime, combined with naturally flowing tributaries, is sufficient to maintain these processes.

Browsing Impacts on Riparian Forests

Biological processes, in particular animal impacts in the form of browsing, play a role in the forest structure of the study area. The important role of beaver in riparian ecosystems has been documented in the context of tree destruction and the implications for remaining vegetation, as well as for wetland formation and hydrological alterations through damming (Naiman *et al.*, 1988). The extent to which beavers can cause multi-stemmed growth through root coppicing of browsed stems has received little attention. There are several implications to my findings that beaver browsing induces multi-stemmed tree growth. Primarily, cottonwood shrublands may be maintained, in part, by browsing. Beavers typically target the main stem of cottonwoods in the 3-4cm diameter range, and the subsequent root coppicing results in shrubby growth with no dominant stem (Table 4.2, 4.3). The size preference of 3cm diameter for beaver browsed trees has been previously recorded (Baker, 1990). The large proportion of young cottonwoods in the study area is a function of the life history of this species. However, the strongly left-skewed distribution of age classes may be further exaggerated by beavers promoting multi-stemmed growth of trees, whose ages are likely underestimated by branch diameter. Further research in this area is necessary to determine the extent to which tree maturity is inhibited by browsing and root coppicing.

Conclusions

The complexity of riparian zones makes them enticing objects of study, but accounting for all interacting processes is difficult. I have described forest dynamics of two dominant species, based on hydro-geomorphological processes and the resulting landforms. I compared the forests of regulated versus unregulated river segments. In general, the age class distribution of the Snake River is similar to the unregulated tributaries, suggesting that forests in this area are not heavily impacted by the dam, nor have they been historically. The limited presence of cottonwood forests in the upper segment of the river is not necessarily attributable to the dam, and may be the result of natural river incising, low sediment supply, and few gravelbars in this constrained segment. Landform is an important geomorphological variable, and clearly influences age class of cottonwoods. Cottonwood age explains a large proportion of variation in ordinations of understory vegetation, and therefore a variety of age classes should promote overall biodiversity. It follows that natural hydro-geomorphological processes, which maintain various landforms, lead to structural diversity of age and size classes of cottonwoods, and ultimately to increased biodiversity. The current flood regime on the managed Snake River seems to maintain these processes. The biological process of browsing, particularly by beavers, also plays a role in the growth form of cottonwoods and may influence the long-term forest structure. In general, cottonwood forests along most of the Snake River do not differ substantially from those of the unregulated tributaries, suggesting that this system does not suffer from many of the dam related problems imposed on similar rivers. These findings are consistent with the geomorphologically intact state of this river (Nelson and Schmidt, 2008, in review), and, given the decline of many riparian forests, are encouraging for managers and conservationists.

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CHAPTER 5

CONCLUSIONS

I did not find direct evidence for dam-related vegetation trends on the Snake River. This suggests that the current management regime is adequate to support cottonwood regeneration, and natural riparian plant communities. By classifying community types, evaluating environmental variables, and examining forest structure, I identified hydro-geomorphological processes essential for riparian vegetation.

In the second chapter, I evaluated a wide range of environmental variables to determine how they structure vegetation, and community type. Depth to gravel, soil texture, pH, distance to bankfull channel, elevation above water and geomorphologic landform were the most important variables. While vegetation and environmental factors are interrelated in riparian zones, the overall trends are clear. Understanding how vegetation relates to specific gradients on these tributaries may help prioritize management on the Snake River, and other regulated rivers. Seven plant communities were identified, and related to environmental variables. These variables are linked to large-scale hydro-geomorphological processes. Maintaining these processes through a natural, dynamic flow regime will support the persistence of biodiverse riparian ecosystems.

In the third chapter, I explored riparian plant community trends of the dam-regulated Snake River, using the unregulated tributaries as a control. Additionally, I identified several important variables that are related to vegetation, including elevation above water, depth to gravel, and geomorphological landform. Plots on the tributaries have a greater α-diversity than the Snake River, despite the higher β-diversity of the main river. This may be related to dam regulation, but is more likely due to differences in community patch sizes. The upper section of the Snake River is distinct from the tributaries, consisting of more lodgepole pine communities, more wetland sedge communities, and fewer young cottonwood communities. This may be due to dam-related changes in the flood regime, or it may be due to the incised, single channel nature of this section. I have no direct evidence to suggest that the dam influences plant communities below the tributaries. In general, riparian vegetation along the Snake River in Grand Teton National Park seems to be exempt from many of the dam-induced problems facing other regulated rivers.

In chapter 4, I described trends in the age distributions of cottonwood and spruce across river sections, and geomorphological landforms. Browsing, particularly by beavers, also plays a role in the growth form of cottonwoods and may influence the long-term forest structure. In general, the age class distribution of the Snake River is similar to the unregulated tributaries, suggesting that forests in this area are not heavily impacted by the dam, nor have they been historically. The limited presence of cottonwood forests in the upper segment of the river is not necessarily attributable to the dam, and may be the result of natural river incising, low sediment supply, and few gravelbars in this constrained segment. Cottonwood age explains a large proportion of variation in ordinations of understory vegetation, and therefore a variety of age classes should promote overall biodiversity. It follows that natural hydro-geomorphological processes, which maintain various landforms, lead to structural diversity of age and size classes of cottonwoods, and ultimately to increased biodiversity. The current flood regime on the managed Snake River seems to maintain these processes.