Riparian Habitat Dynamics and Wildlife Along the Upper Yellowstone River

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Montana State University

In Cooperation with the Governor's Upper Yellowstone River Task Force

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Contents

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Abstract

The U.S. Army Corps of Engineers, along with the Upper Yellowstone River Task Force, is assessing the cumulative effects of bank stabilization along the upper Yellowstone River. In this study, we collected bird and vegetation data within riparian zones along the river to determine the attributes of avian and shrub communities within eight vegetation successional stages and three geomorphological reach types. Additionally, we used aerial photos from 1948 and 1999 to investigate change in riparian vegetation over time. Finally, we used statistical models to predict bird richness across portions of the study area. A total of 78 bird species and 15 shrub species were recorded overall. We found that the moderately confined and braided reaches supported the highest bird abundance, diversity, and richness. Within the braided reach, the mature cottonwood stages supported the highest bird richness, diversity, and abundance. The best model for predicting richness included successional stage, which explained 51% of the variation. The braided reach exhibited the highest predicted richness because it supported the most mature cottonwood forest. Analysis of the areal distribution of riparian vegetation over time showed different responses within the braided and moderately confined reaches. Braided reaches experienced an increase in both younger and older successional stages, whereas the moderately confined reach experienced a decline in younger stages and an increase in older stages. Land managers interested in maintaining avian diversity should consider the importance of periodic flooding in maintaining the full range of successional stages of riparian vegetation in this river system.

Key words: upper Yellowstone River; successional stage; historical change; bird diversity; bird abundance; river reach types; species richness

Introduction

Periodic floods are vital to the maintenance of biodiversity within many riparian zones. Flood waters differentially impact areas within the floodplain, scouring some areas and initiating successional processes, while leaving other areas of mature vegetation essentially intact. The resulting multiple successional stages create a mosaic of different vegetation types which may support a variety of native wildlife species. Especially in free-flowing rivers, the successional stages generated by flooding may be within a dynamic steady state where the proportions of young, intermediate, and late successional vegetation types stay relatively constant over time (Gregory and others, 1991; Smith and Smith, 2001). Many native wildlife species are associated with a particular successional stage; hence, the presence of the full suite of successional stages maintains habitat for a variety of species.

Within the arid and semiarid portions of the western United States, riparian ecosystems harbor the most species-rich avifauna amongst all habitats (Dobkin and others, 1998). Fifty-nine percent of birds in western Montana use riparian habitats for breeding, and twenty-one percent breed only in riparian habitats (Mosconi and Hutto, 1982). However, riparian habitats have been subjected to numerous human alterations such as agricultural conversion, flood control, and grazing, and have consequently declined by as much as ninety-five percent in the last century in the western U.S. (Ohmart, 1994). Hence, the maintenance of the remaining relatively undeveloped, free-flowing river systems that still sustain ecologically intact riparian communities is an important management issue in the western U.S.

The Yellowstone River of Wyoming and Montana is the longest un-dammed river in the contiguous United States, and sustains large tracts of riparian vegetation across its floodplain. Bank stabilization projects, however, have increasingly been used along the river to deflect flood waters and inhibit channel migration (Decamps, 1993). The U.S. Army Corps of Engineers, in collaboration with the Governor's Upper Yellowstone River Task Force, is currently assessing the cumulative effects of bank stabilization on the riparian ecosystem of the upper Yellowstone River corridor. A goal of this study was to determine the attributes of bird and shrub communities associated with each of the riparian vegetation successional stages within the upper Yellowstone River. This knowledge will allow managers to predict the effects on bird communities of river management strategies that may alter the distribution of successional stages within the floodplain.

A second goal was to determine how bird and shrub communities differ among various river reach types within the study area. Regions of the watershed differ in geomorphology and channel characteristics, varying from a single-thread channel in the upper part of the watershed near Yellowstone National Park to laterally braided channels downstream. These differences in channel morphology influence the characteristics of floods, which in turn influence the distribution of riparian vegetation throughout the floodplain. We hypothesized that areas in the extreme upper part of the watershed, where flooding is confined to the width of the active channel, would support lower habitat diversity and fewer native species (Ward and Tockner, 2001). Conversely, we expected the braided sections to support the highest diversity of riparian vegetation types, the largest area of existing riparian vegetation, and the highest bird diversity, because flooding influences a broader portion of the floodplain. Several studies have shown that as vegetation structure and complexity increases, avifaunal communities become more diverse (Wilson, 1974; MacArthur and MacArthur, 1961; Scott and others, 2003). Knowledge of the relative importance of reach types to the maintenance of biodiversity may be useful for developing land management strategies which are tailored to particular regions of the floodplain.

A third goal was to evaluate possible changes in the occurrence of riparian successional stages over time. Riparian vegetation along many rivers has become decadent and homogenous due to flood control, land use, and other factors which limit the frequency of flooding episodes, and consequently limit opportunities for regeneration (Ohmart, 1994). Therefore, it is important to determine whether the upper Yellowstone River system maintains a dynamic steady-state mosaic of riparian vegetation, with the full suite of successional stages represented throughout the floodplain (Smith and Smith, 2001). Aerial photographs from 1948 allowed us to assess changes in riparian vegetation over the past fifty years.

The objectives of the study were to**:**

1) Quantify the distribution of bird and shrub communities across riparian successional stages and river reach types within the study area.

2) Project bird species richness within portions of the study area as a function of successional stage and reach type.

3) Quantify changes in riparian vegetation community composition within portions of the study area from 1948 to 1999.

Hansen and Rotella (2002) recently studied patterns of bird species richness and abundance throughout the Gallatin, Madison, and Henry's Fork watersheds of the northwest portion of the Greater Yellowstone Ecosystem (GYE). Patterns were consistent across all three watersheds: riparian cottonwood forests were found to support the highest species richness and total bird abundance of all of the six major vegetation types found within the watersheds. Therefore, in this study we focused on examining patterns of bird diversity exclusively within the floodplain of the upper Yellowstone River.

We focused on birds in this study because avian communities have often been used as indicators of biological integrity at a landscape scale (O'Connell and others, 2000; Canterbury and others, 2000), and specifically within riparian zones (Rich, 2002; Bryce and others, 2002; Croonquist and Brooks, 1991). Within a given area, the various bird species fill a wide variety of niches compared with other taxa, allowing for the examination of patterns of distribution across many habitat types. Additionally, birds have relatively small breeding territories which are often completely encompassed within riparian zones, so we would expect riparian habitat associations to be especially strong for birds. Lastly, birds are generally very prolific and easy to survey, so researchers are able to collect a comparatively large amount of data on many species per unit of survey effort. While no group of vertebrates is a perfect indicator of habitat use by other vertebrate groups, our results for bird species richness and diversity are likely to be informative relative to community patterns for mammals, which were not studied. We also analyzed shrub species richness because data on shrubs were collected to characterize habitat attributes for birds.

Study Area

The study area was located along 119 kilometers (74 miles) of the Yellowstone River, between the cities of Gardiner and Springdale in Park County, Montana. Elevation in the study area ranges from 1322 to1592 meters (4337 to 5223 feet), with a mean annual precipitation of approximately 40 centimeters (16 inches; Merrill and Jacobson, 1997). The majority of the study area is located within privately-owned lands, with predominate land-use types being agriculture and livestock production, rural residential development, and urban (around Gardiner and Livingston).

We distinguished three river reach types within the study area (Figure 1) based on the classification of channel patterns by Leopold and Wolman (1957) and Rosgen (1996). The confined reach in the upstream portion of the study area stretches from Gardiner to Tom Miner Basin (Figure 2), and is characterized by a single, relatively straight channel that carries high-velocity flows through steep gradients. Streamside vegetation communities are dominated by plant species adapted to low-moisture conditions (i.e. xeric species) such as juniper (*Juniperus* spp.), Douglas-fir (*Pseudotsuga menziesii*), limber pine (*Pinus flexilus*), and sage (*Artemesia* spp.), with small patches of cottonwood (*Populus* spp.) occasionally interspersed. The moderately confined reach, which extends from Tom Miner Basin to Mallard's Rest in the mid-portion of the study area (Figure 2), is characterized by a single meandering channel, scattered with occasional braids and islands. Vegetation within this reach consists of a mix of plant communities. Xeric species, including grasses, sage, and juniper, dominate the banks of the meandering channel, whereas flood-adapted species, such as cottonwood, willow (*Salix* spp.), snowberry (*Symphoricarpos* spp.), and wild rose (*Rosa woodsii*) dominate the braided sections. Lastly, the braided reach, which stretches from Mallard's Rest to Mission Creek in the downstream portion of the study area (Figure 2), is characterized by the successive division and rejoining of the river, with islands located throughout the active channel. This reach supports a variety of successional stages of riparian plant communities, from mature cottonwood gallery forests, to younger, regenerating cottonwood stands, to wet meadows with willow.

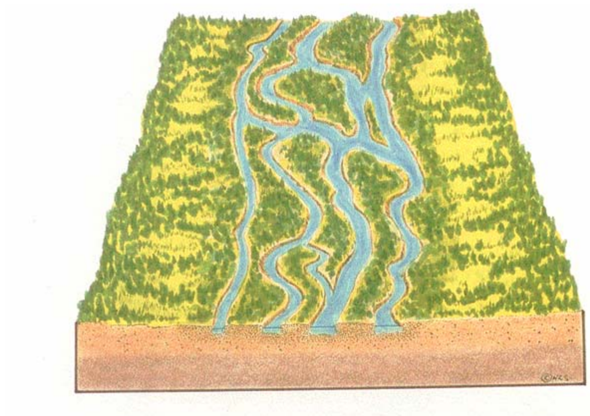
Methods

Site Selection

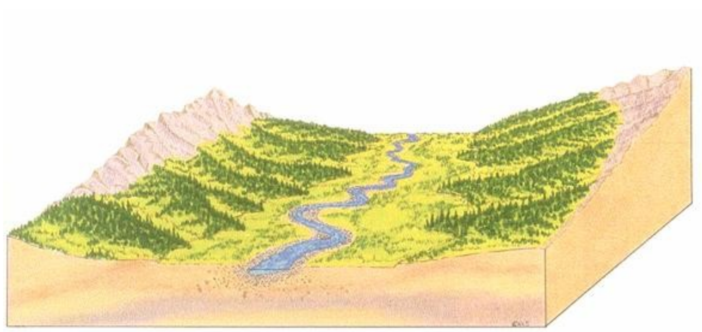
We sampled 130 sites throughout the study area for bird abundance and vegetation characteristics. We initially chose sites with the goal of obtaining at least ten replicates within each successional stage, and established more sites than that where possible. Sites were situated within all three reach types, with 68 sites in the braided reach, 47 in the moderately confined reach, and 15 in the confined reach (Figure 2). We further stratified the points into one of eight successional stages (based on Merigliano and Polzin, 2003), including 1) gravel bar, 2) meadow, 3) meadow with willow, 4) cottonwood-willow shrub, 5) young cottonwood, 6) mature cottonwood with an herbaceous understory, 7) mature cottonwood with a shrub understory, and 8) mixed grassland/sage with scattered trees (Table 1, Figure 3). We included mixed grassland/sage as riparian in order to include a representative sample of birds within the bank-side vegetation throughout all reach types, and mixed grassland/sage was often the only vegetation present within portions of the confined and moderately confined reaches.

We consulted aerial photos from 1999 to determine the locations of suitable vegetation types. Most sites were located on private property, and we obtained permission to conduct field work from landowners through Liz Galli-Noble of the Upper Yellowstone River Task Force. Sites were then located on the ground, and successional stage was verified using ocular assessments of approximate stand age, understory and overstory structural characteristics, and plant species composition. Sites were placed with the center at least 40 meters from any habitat edge so that all birds detected during the bird surveys were actually located within the boundaries of the specified successional stage. To avoid site overlap, we placed the center of each survey site at least 100 meters away from the center of another site. We used a 'Garmin' brand GPS unit to record the spatial location of each survey site.

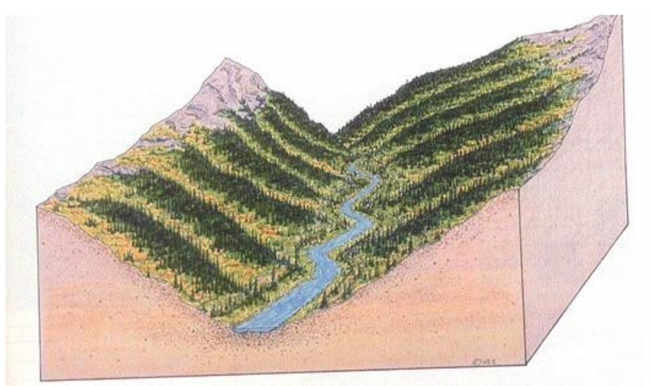
Figure 1. Channel patterns typical of each reach type (adapted from Rosgen, 1996).



Braided



Moderately confined



Confined

Figure 2. Distribution of reach types, bird survey sites, and sample areas.

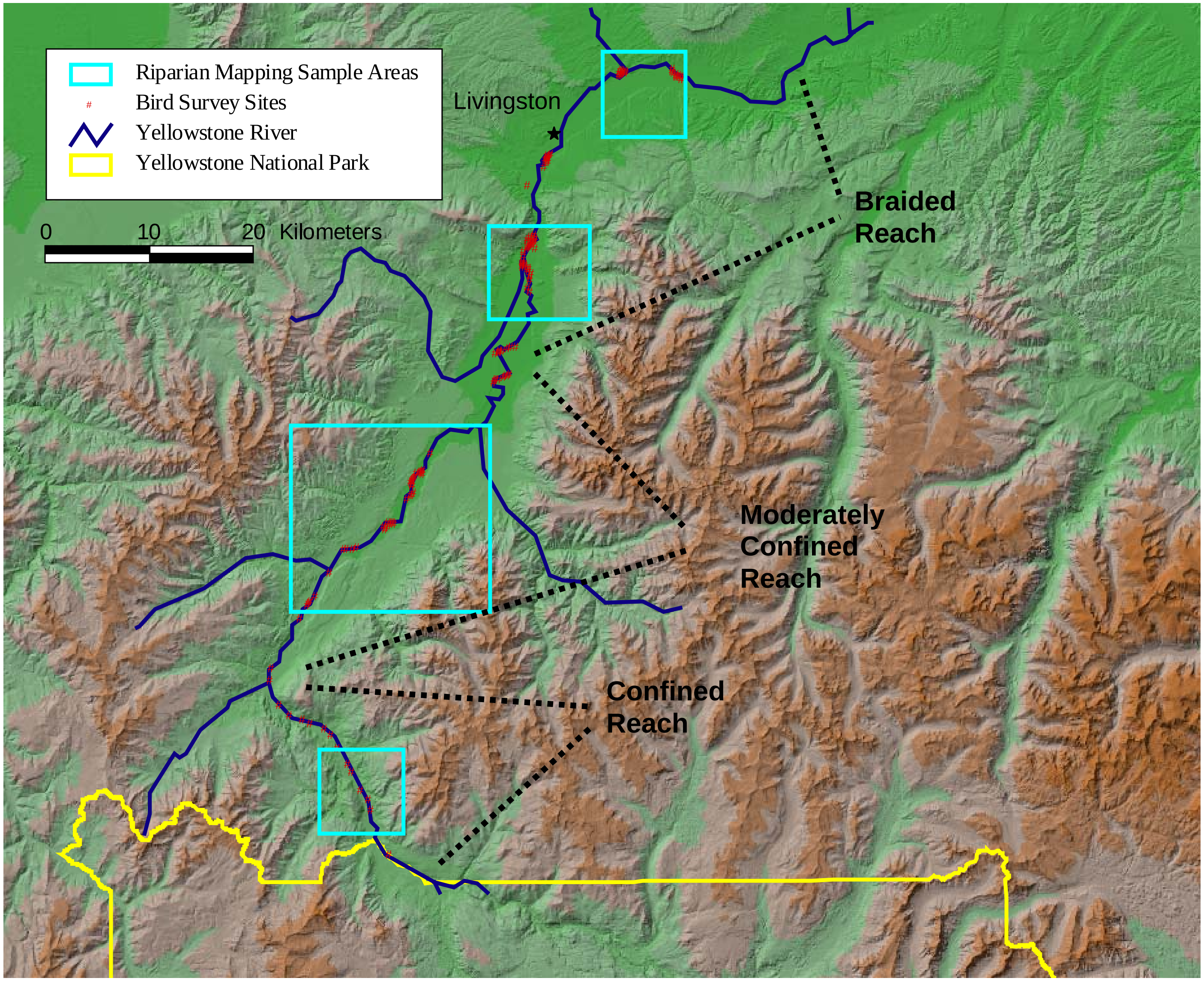


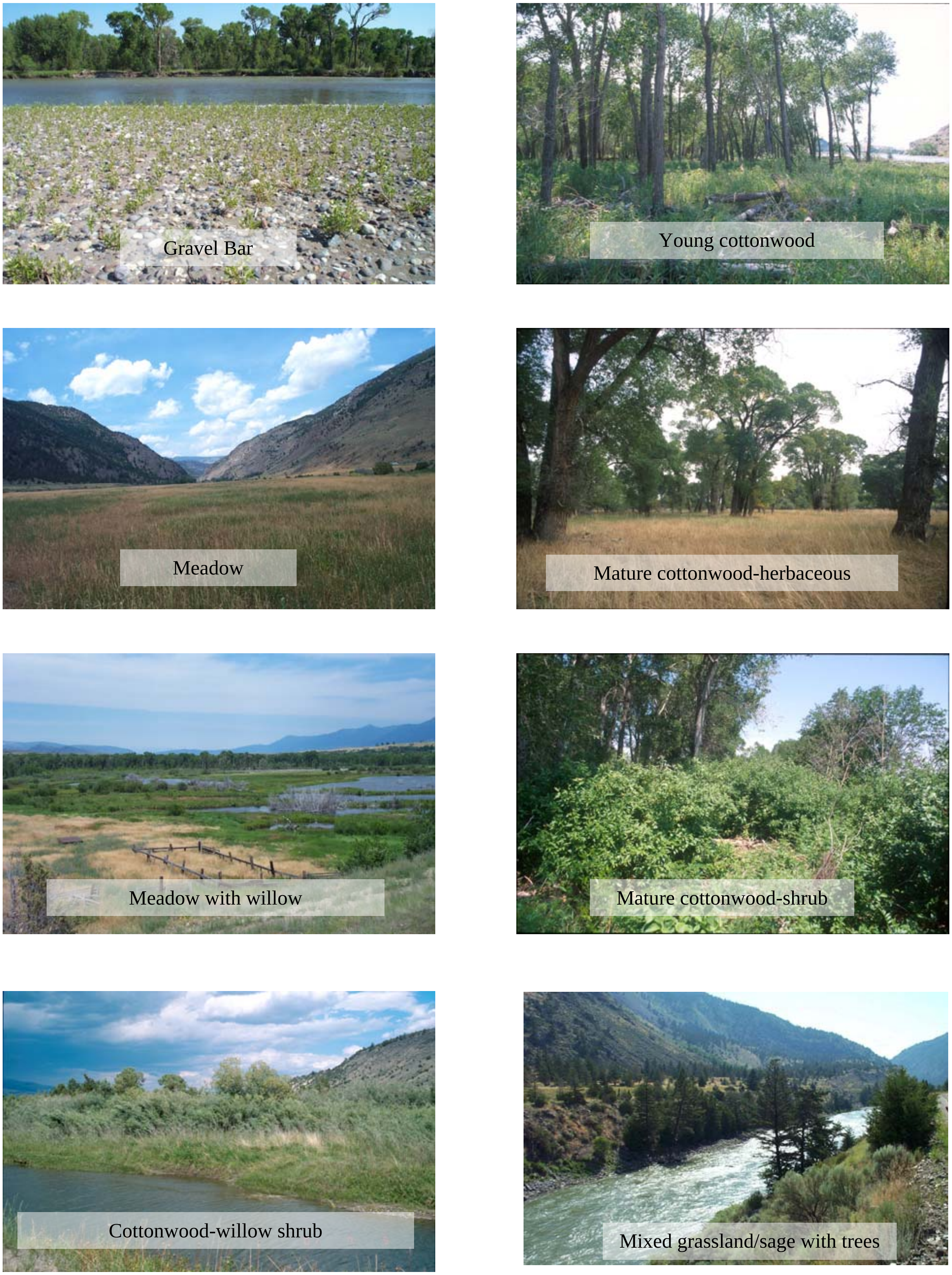
Table 1. Representative vegetation types within the study area.

Successional Stage	Description	Number of Survey Sites			Alpha Code
		Braided	Mod. Conf.	Confined	
Gravel bar	Vegetation <10 years old	10	2	0	GB
Meadow	Herbaceous vegetation	5	8	0	ME
Meadow with willow	All ages	11	4	0	EW
Cottonwood-willow shrub	Cottonwood approximately 10-20 years old; willow all ages	7	8	0	SH
Young cottonwood	Cottonwood approximately 20-100 years old	12	3	0	YC
Mature cottonwood with herbaceous understory	Cottonwood approximately 100+ years old, shrub cover <25%	13	2	0	CH
Mature cottonwood with shrub understory	Cottonwood approximately 100+ years old; Shrub cover >25%	10	5	0	CS
Mixed grassland/sage with scattered trees	Juniper, Douglas-fir, limber pine all ages; grass; sage	0	15	15	MIX

Bird Sampling

From June 1 through July 15 of 2001 and 2002, we surveyed breeding birds using a standard point count method (Ralph and others, 1993). Before the field season began, all members of the field crew participated in an intensive two-week training period to become familiar with the identification of local bird species by sight, song, and call (Reynolds and others, 1980). In order to survey sites during times of peak bird activity, all point counts were conducted between the times of local sunrise and 10:00 a.m., and were not conducted during conditions of high wind or heavy rain. We visited each of the 130 sites for ten minutes, three times per summer (for a total of six visits over the two-year period), recording all birds detected by sight and sound within a 40 meter radius of the site center (or 'point'). To minimize observer bias, three researchers were employed to conduct surveys each summer, with each researcher visiting each site once. To ensure that surveys were conducted across the entire breeding season, we spaced the three visits to a single site at least seven days apart. Furthermore, we conducted the three surveys for each site at a different time of the morning to eliminate any bias created by daily bird activity patterns.

Figure 3. Representative successional stages of the upper Yellowstone River.



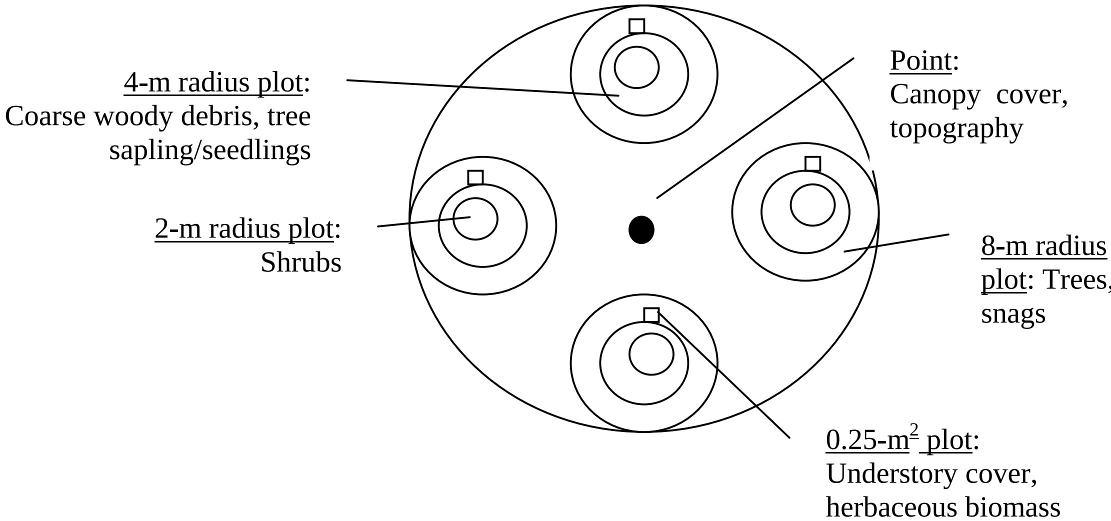
Vegetation Sampling

Several attributes of vegetation structure and composition were measured at each survey site according to the protocol outlined by Hansen and others (2000). To capture characteristics of the entire survey site, we quantified attributes of the vegetation within four plots located 20 meters in each cardinal direction from the point. Within those plots, attributes were measured within either a .25 square meter sub-plot located two meters north of the center of each plot, or within a two, four, or eight meter radius sub-plot (Figure 4). See Table 2 for details on the metrics and data collection methods for each vegetation attribute. We used this vegetation data to quantify and describe the vegetation community and structural characteristics of the different successional stages, as well as for calculating shrub species richness.

Table 2. Vegetation data collected at each survey site.

Attribute	Description and Collection Method	Scale of Data Collection
Canopy cover	Record percent canopy cover for all vegetation above 2 m height, using a densiometer	Measured at point and at centers of four plots
Topography	Record slope and aspect of plot	Measured at point
Understory cover	Make ocular estimate of percent cover for each of woody conifer, woody deciduous, and herbaceous vegetation at both 0-1 m height class and >1-2 m height class	0.25-m^2 sub-plots
Herbaceous biomass	Clip and keep all non-woody live vegetation; allow to dry, then weigh	0.25-m^2 sub-plots
Trees	Count all trees that are >=2 cm Diameter at Breast Height (i.e. diameter of the trunk at breast height = DBH); record tree species and DBH	8-m radius sub-plots
Tree seedlings/ saplings	Count all tree seedlings and saplings >=10 cm tall; record tree species and basal diameter (diameter of stem at the base)	4-m radius sub-plots
Shrubs	Count all shrubs with >=0.5 cm basal diameter; record shrub species and basal diameter	2-m radius sub-plots
Snags	Count all snags >=10 cm DBH; record DBH, state of decay, and height	8-m radius sub-plots
Coarse woody debris	Count all pieces of downed wood >=7.5 cm in diameter; record diameter at both ends of the piece of wood, as well as length, for calculating total volume; record state of decay	4-m radius sub-plots

Figure 4. Sampling scheme for vegetation around each bird point-count location.



Riparian Vegetation Mapping

Riparian vegetation was mapped within the study area to 1) create maps of current riparian vegetation for use in extrapolating bird species richness from the survey sites to other parts of the study area (see ‘Statistical Analysis’ for description of methods), and 2) compare current and historical vegetation maps to determine if the floodplain has, over the past fifty years, maintained a dynamic steady-state mosaic across the riparian landscape. Due to limited resources, we were not able to map the entire region; instead, we chose four sample areas in the braided (21 river kilometers /13 river miles), moderately confined (29 river kilometers/18 river miles), and confined (10 river kilometers/6 river miles) reaches of the river (Figure 2). These sample areas encompassed approximately 50% of the entire study area. In order to facilitate data sharing across research teams, sample areas were chosen that overlapped with those of the geomorphology (Dalby and Robinson, 2003), riparian trend (Merigliano and Polzin, 2003), and land use/land change (Brelsford and others, 2003) studies.

We obtained recent black and white digital aerial photo mosaics spanning the years 1997 to 1999 (hereafter this time period will be referred to as ‘1999’), as well as historical digital photos from 1948. Portions of the sample areas were mapped previously by Merigliano and Polzin (2003) using compatible methods; we obtained those digital maps and used these data where available. A computer mapping software program (Arcview 3.2; ESRI, 1999) was used to trace around distinct vegetation patches on the aerial photos and create digital riparian coverages representing seven successional stages, including cottonwood-willow shrub, young cottonwood, middle-aged cottonwood, mature cottonwood, mixed conifer, meadow, and gravel bar (Table 3, Figure 5). All vegetation was classified within the riparian zones of the four sample areas for both time periods (see Appendix 2 for completed coverages of each sample area). The boundaries of the riparian zones were based on an approximation of the 100-year floodplain, delineated by Merigliano and Polzin (2003).

Before beginning our mapping efforts, we referred to Merigliano and Polzin’s (2003) riparian vegetation maps (which were created from field-sampled data), to train ourselves as to what the different successional stages looked like on the aerial photos. After creating our maps, we visited the sample areas and ground-truthed approximately 10% of the vegetation patches (79 of 707) from the 1999 data. Accuracy was relatively high; seventy-seven percent (61 of 79) of the patches were classified as the correct successional stage.

Table 3. Riparian vegetation mapping classification system.

Successional stage	Age/Description
Cottonwood-willow shrub	Willow of all ages; cottonwood approximately 10-20 years old
Young cottonwood	Cottonwood patches approximately 20-40 years old
Middle-aged cottonwood	Cottonwood patches approximately 40-100 years old
Mature cottonwood	Cottonwood patches approximately 100+ years old
Meadow	Herbaceous vegetation
Mixed grassland/sage with scattered trees	Juniper, Douglas-fir, and limber pine of all ages; grass; sage
Gravel bar	Bare gravel bars; gravel bars with cottonwood seedlings less than 10 years old

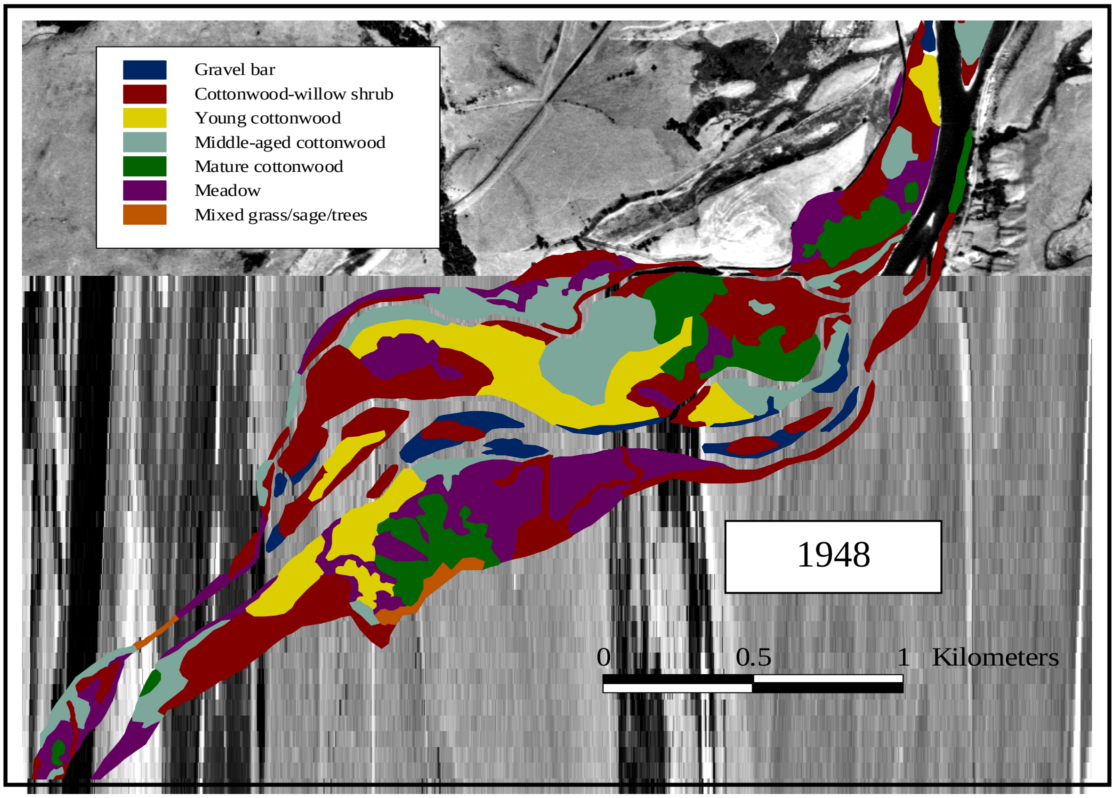
Statistical Analysis

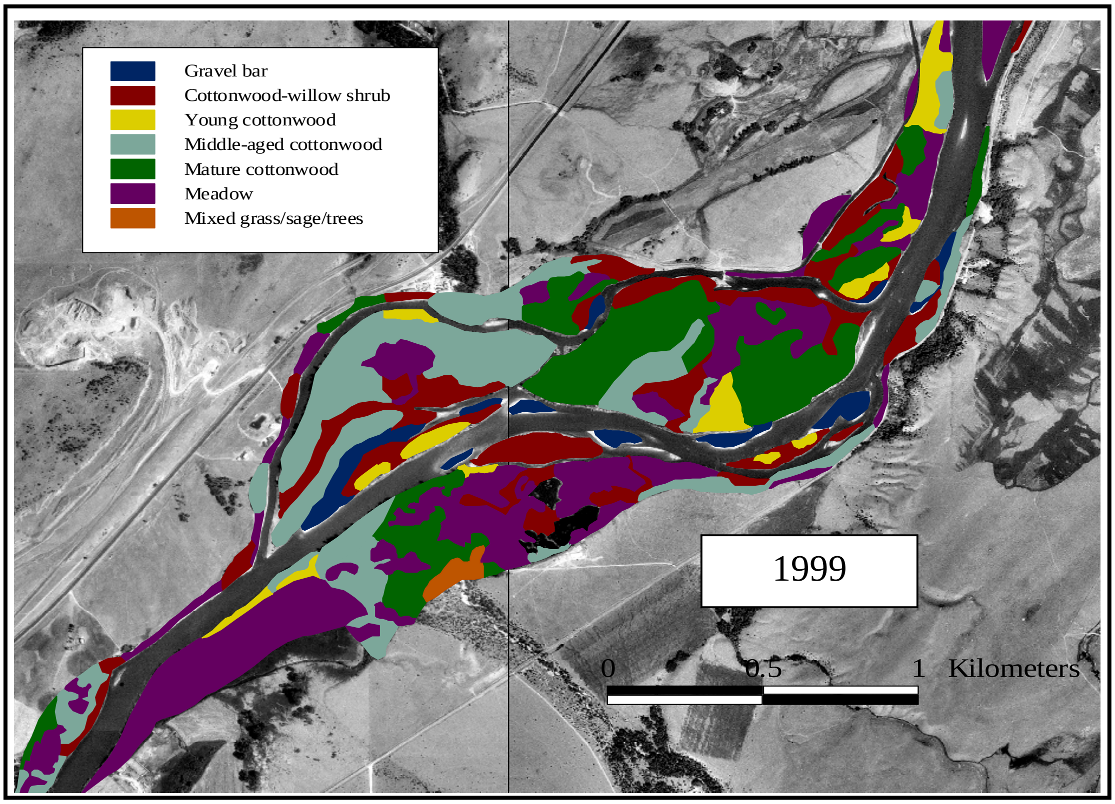
Bird and Vegetation Characteristics

Bird survey data was averaged across the three visits and two years to control for temporal correlation. Bird abundance was expressed as the mean number of observations per hectare per visit. We confirmed the assumption of spatial independence of bird surveys using semivariograms to asses the degree of spatial autocorrelation of the data. Finally, we log transformed the data on abundances of individual bird species to bring them closer to a normal distribution. For the vegetation data collected at each survey site, the abundance of each attribute was averaged across the four sample plots in order to get a mean value per hectare for each survey site.

Analysis of variance with multiple range tests was used to assess differences between key biodiversity response variables among successional stages (for birds, shrubs, and vegetation attributes) and reach types (for birds and shrubs). We examined differences between successional stages only within the braided reach because all stages were well-represented and replication was sufficient (Table 1). The response variables were: bird species richness (number of bird species), Shannon's Diversity Index for birds (combination of number and relative abundance of bird species), total bird abundance (abundance of all birds detected), abundance of individual bird species, shrub species richness (number of shrub species), and abundance of individual vegetation attributes (e.g. trees, coarse woody debris, etc.).

Figure 5. Example of riparian vegetation classification using aerial photos from 1948 and 1999.





Extrapolation of Bird Species Richness

Bird species richness was extrapolated across the four sample areas used for riparian vegetation mapping (Figure 2), which constituted approximately 50% of the study area. We did not extrapolate across the entire study area because vegetation classification was not available outside those sample areas. A map of predicted bird species richness was created by assigning values of richness to data layers (or 'predictor variables') which exist continuously across the sample areas. To assign values of richness, we evaluated models which quantified relationships between predictor variables and bird species richness (calculated from the bird survey data), determining which variable or combination of variables best predicted richness. Our models included successional stage (from riparian vegetation maps), reach type, and elevation (derived from digital elevation models) as possible predictor variables. The primary criterion for determining best models for the extrapolation was Akaike's Information Criterion (AIC) (Anderson and others, 1998). AIC estimates the distance between the specified model and some full truth or reality. "Best" models are those that best approximate the true model in a parsimonious manner. Thus AIC is useful for selecting from among several competing models. However, AIC only provides a measure of model strength relative to other models being examined, and does not inform on the overall accuracy of the model. Hence, we used the coefficient of determination (R^2) as a measure of how much variation in the response variables was explained by the best model. The resulting best statistical model was used to extrapolate bird species richness across the four sample areas.

Results

We sampled a total of 78 species of birds within the entire study area over the two-year period (Appendix 1), and included all of these species in calculations of bird species richness, diversity, and total abundance across reach types, as well as for predicting bird species richness across portions of the study area. For all analyses across successional stages within the braided reach, only species with greater than a total of 20 observations were included to ensure large enough sample sizes for quantifying differences in individual species abundance. Forty-eight species met this criterion (Appendix 1). Additionally, fifteen shrub species were recorded and used for calculating differences in species richness across successional stages and reach types (Appendix 1).

Objective 1: Bird and Shrub Communities Across Successional Stages and Reach Type

Vegetation species composition and structure differed substantially across the seven successional stages within the braided reach (Table 4). Gravel bars supported sparse vegetation overall, with regenerating shrubs dominating the vegetation that was present. Meadows were characterized mostly by herbaceous vegetation, with no trees and few shrubs. Both of these stages had relatively low levels of herbaceous biomass. The cottonwood-willow shrub stage and the meadow-willow stage had few large trees, but shrubs of all sizes classes were denser than in other stages. All three cottonwood stages were dominated by trees, with the mature cottonwood stages having the most large diameter trees, the greatest densities of large shrubs, higher volumes of coarse woody debris, and higher biomass of understory vegetation.

Birds were distributed disproportionately across the different successional stages in the braided reach. Total bird abundance, species richness, and Shannon's Diversity Index were highest in the mature cottonwood-shrub and mature cottonwood-herbaceous stages compared with other stages, while the gravel bar and meadow stages were lowest. Additionally, shrub species richness was highest in the mature cottonwood-shrub and cottonwood-willow shrub stages, and lowest in the gravel bar, young cottonwood, and mature cottonwood-herbaceous stages (Figure 6, Table 5).

Individual bird species were significantly associated with particular successional stages within the braided reach. Veery (*Catharus fuscescens*), House Finch (*Carpodacus mexicanus*), European Starling (*Sturnus vulgaris*), and Black-headed Grosbeak (*Pheucticus melanocephalus*) all occurred at higher abundances in the two mature cottonwood stages than other stages. Mourning Dove (*Zenaida macroura*), Warbling Vireo (*Vireo gilvus*), Western Wood-Pewee (*Contopus sordidulus*), Yellow Warbler (*Dendroica petechia*), Black-capped Chickadee (*Poecile atricapillus)*, Brown-headed Cowbird (*Molothrus ater*), Cedar Waxwing (*Bombycilla cedrorum*), Bullock's Oriole (*Icterus bullockii*), Downy Woodpecker (*Picoides pubescens*), House Wren (*Troglodytes aedon)*, and Least Flycatcher (*Empidonax minimus*) were all associated equally with the two mature cottonwood, young cottonwood, and shrub stages. The shrub and willow stages supported higher abundances of Red-winged Blackbird (*Agelaius phoeniceus*), Savannah Sparrow (*Passerculus sandwichensis*), Song Sparrow (*Melospiza melodia)*, Willow Flycatcher (*Empidonax traillii*), and Common Yellowthroat (*Geothlypis trichas*). Finally, abundances of Killdeer (*Charadrius vociferus*) and Spotted Sandpiper (*Actitus macularia*) were significantly higher within gravel bars than other stages.

Among reach types, the braided and moderately confined reaches had significantly higher bird species richness, Shannon's Diversity Index, and total bird abundance than the confined reach, but were not significantly different from each other. Shrub richness did not differ among reach types (Figure 7, Table 6).

Objective 2: Projected Bird Species Richness Across Sample Area

Candidate models for the extrapolation included successional stage, reach type, and elevation. The best model included only successional stage, which explained 51% of the variation in bird species richness. Consequently, the resulting map was an extrapolation of species richness across the sample areas, based on successional stage (Figure 8). For this extrapolation, we pooled the mature cottonwood-shrub and cottonwood-herbaceous successional stages, as well as the meadow and meadow-willow stages to correspond with the vegetation classification system used for riparian vegetation classification. Additionally, we pooled the young cottonwood and the middle-age cottonwood classes used in vegetation mapping to correspond with the young cottonwood successional stage described for bird surveys (Table 7).

The floodplain was much wider in the braided reaches, and consequently, the areal extent of each of the successional stages was greater overall in that reach type (Figure 9). Most notably, there was much more mature cottonwood forest, which supports the highest bird species richness of all successional stages (Figure 6), and this was reflected in the map of predicted richness (Figure 8). The extent of riparian vegetation was very limited in the confined reach, and the vegetation that did exist supported relatively low predicted species richness.

Table 4. Average abundance (per hectare) of vegetation attributes within each successional stage.

Vegetation attribute	Successional Stage						
	Gravel bar	Meadow	Meadow with willow	Cottonwood – willow shrub	Young cottonwood	Mature cottonwood - herbaceous	Mature cottonwood-shrub
Tree dbh 2-10cm	0.00^{b}	0.00^{b}	8.29^{b}	721.23^{a}	23.21^{b}	10.77^{b}	114.40^{b}
Tree dbh 10-20cm	0.00^{c}	0.00^{c}	0.83^{c}	91.19^{b}	149.22^{a}	17.41^{c}	52.23^{b}
Tree dbh 20-30cm	0.00^{c}	0.00^{c}	2.49^{c}	7.46^{c}	153.37^{a}	42.28^{b}	41.45^{b}
Tree dbh 30-40cm	0.00^{a}	0.00^{a}	0.00^{a}	0.83^{a}	56.37^{a}	44.77^{a}	38.13^{a}
Tree dbh 40-60cm	0.00^{c}	0.00^{c}	0.00^{c}	0.83^{c}	9.95^{bc}	57.20^{a}	24.04^{b}
Tree dbh 60-90cm	0.00^{d}	0.00^{d}	0.00^{d}	0.00^{d}	3.32^{c}	8.29^{a}	9.95^{a}
Tree dbh 90-120	0.00^{a}	0.00^{a}	0.00^{a}	0.00^{a}	0.00^{a}	0.83^{a}	0.83^{a}
Tree dbh >120cm	0.00^{c}	0.00^{c}	0.00^{c}	0.00^{c}	0.00^{a}	0.00^{a}	0.83^{ab}
Shrub 0.5-1cm	2586.27^{bc}	1775.19^{bc}	26260.57^{ab}	30716.90^{a}	1962.91^{bc}	23714.09^{abc}	20212.68^{abc}
Shrub 1-2cm	729.46^{c}	0.00^{c}	14111.74^{ab}	21910.33^{a}	848.83^{c}	3023.94^{c}	7904.70^{bc}
Shrub 2-3cm	0.00^{b}	0.00^{b}	8912.68^{a}	9018.78^{a}	477.46^{b}	0.00^{b}	2281.22^{b}
Shrub 4-6cm	0.00^{b}	0.00^{b}	2970.89^{a}	2334.27^{ab}	0.00^{b}	0.00^{b}	318.31^{b}
Shrub 6-10cm	530.52^{ab}	0.00^{b}	901.88^{a}	530.52^{ab}	106.10^{ab}	159.16^{ab}	371.36^{ab}
Shrub >10cm	0.00^{a}	0.00^{a}	0.00^{a}	265.26^{a}	159.15^{a}	0.00^{a}	265.26^{a}
Snag density	0.00^{b}	11.48^{b}	0.00^{b}	0.00^{b}	59.96^{a}	55.82^{a}	53.06^{a}
Coarse woody debris volume	104.26^{abc}	0.87^{c}	9.53^{bc}	59.22^{bc}	91.21^{bc}	134.29^{ab}	221.84^{a}
Canopy cover	0.20^{d}	0.55^{d}	15.77^{bc}	33.28^{a}	28.51^{a}	24.37^{ab}	29.40^{a}
Herbaceous biomass	12.71^{c}	17.68^{bc}	81.09^{a}	35.97^{bc}	34.60^{bc}	59.45^{ab}	59.89^{ab}

$^{a\ b\ c}$ t test groupings across successional stages: means with the same letter are not significantly different.

Figure 6. Response variables across successional stages (error bars represent ±SE).

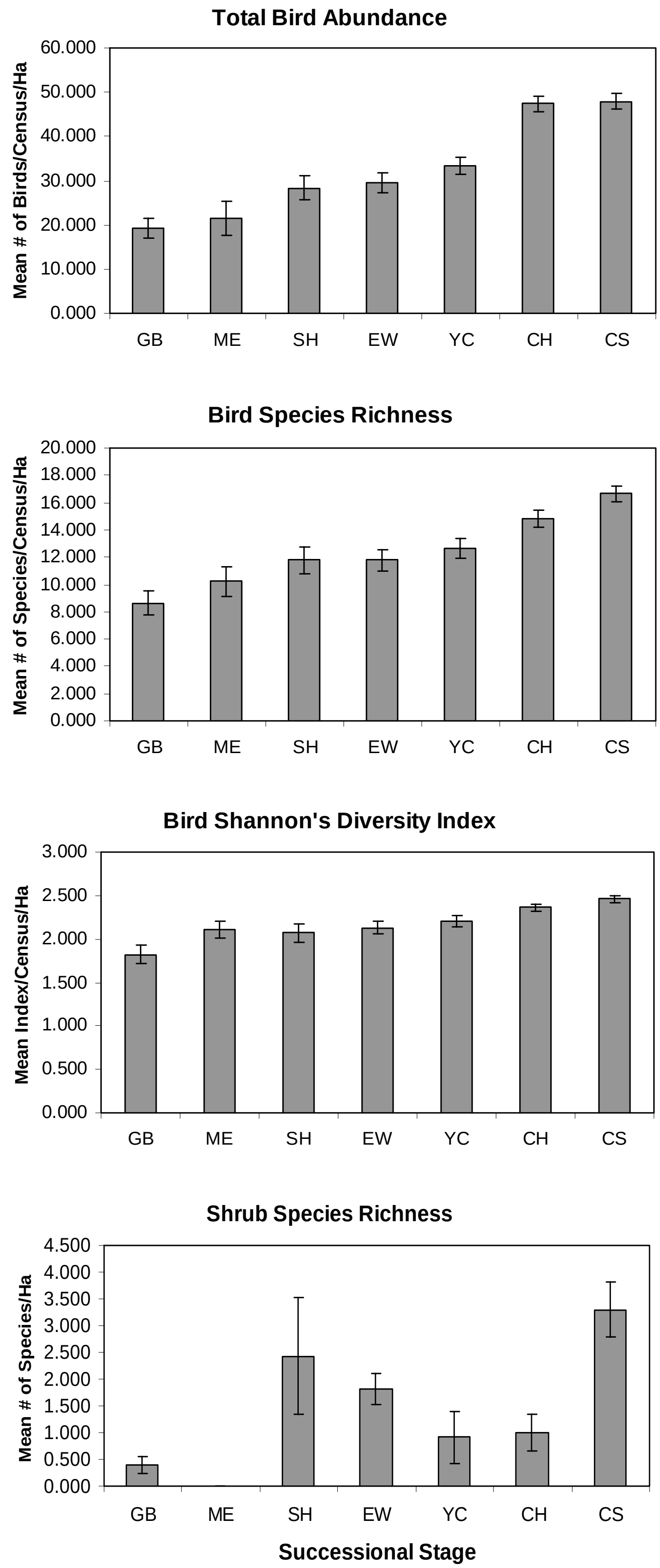


Figure 7. Response variables across reach types (error bars represent ±SE).

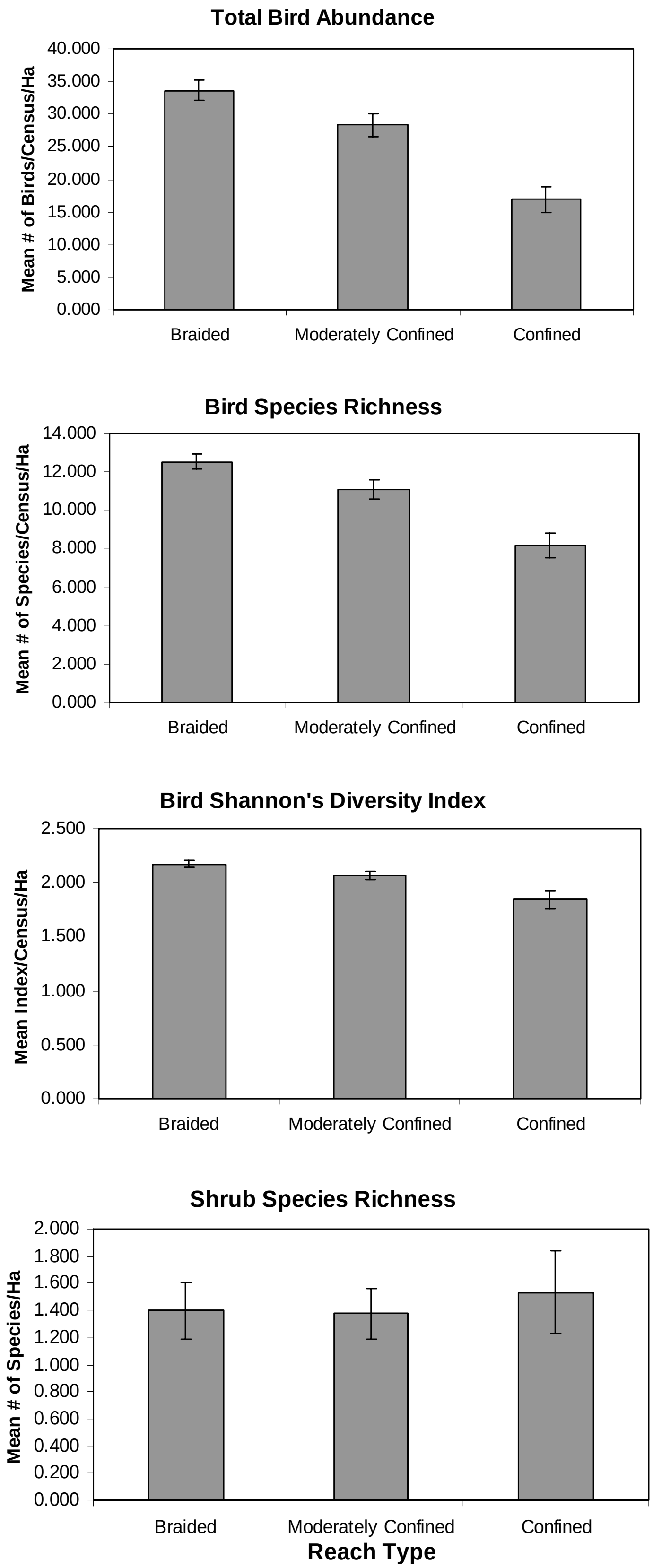


Table 5. Mean values of biodiversity response variables within the braided river reach.

Response variables	Successional stage						
	Gravel bar	Meadow	Meadow with willow	Cottonwood-willow shrub	Young cottonwood	Cottonwood herbaceous	Cottonwood shrub
Bird abundance	19.27[c]	21.52[c]	29.58[b]	28.36[b]	33.45[b]	47.41[a]	47.97[a]
Bird richness	8.65[e]	10.22[de]	11.77[cd]	11.79[cd]	12.67[bc]	14.81[ab]	16.65[a]
Bird Shannon Index	1.82[d]	2.10[c]	2.13[c]	2.07[c]	2.21[bc]	2.36[ab]	2.46[a]
Shrub richness	0.40[d]	0.00[d]	1.82[bc]	2.43[ab]	0.92[cd]	1.00[cd]	3.30[a]

[a b c d e] t test groupings across successional stage: means with the same letter are not significantly different.

Table 6. Mean values of biodiversity response variables across reach types.

Response variables	Reach types		
	Braided	Moderately confined	Confined
Bird abundance	33.65[a]	28.37[a]	16.92[b]
Bird richness	12.54[a]	11.09[a]	8.17[b]
Bird Shannon index	2.17[a]	2.07[a]	1.85[b]
Shrub richness	1.40[a]	1.38[a]	1.53[a]

[a b] t test groupings across reach types: means with the same letter are not significantly different

Table 7. Pooling of successional stages and vegetation classes for species richness extrapolation.

Modified Successional Stage	Modified Vegetation Class
Meadow + Meadow-willow	Meadow
Cottonwood-willow shrub	Cottonwood-willow shrub
Young cottonwood	Young + Middle-aged cottonwood
Mature cottonwood-herbaceous + Mature cottonwood-shrub	Mature cottonwood
Mixed grassland/sage with scattered trees	Mixed grassland/sage with scattered trees

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Figure 8. Extrapolation of bird species richness across the four sample areas.

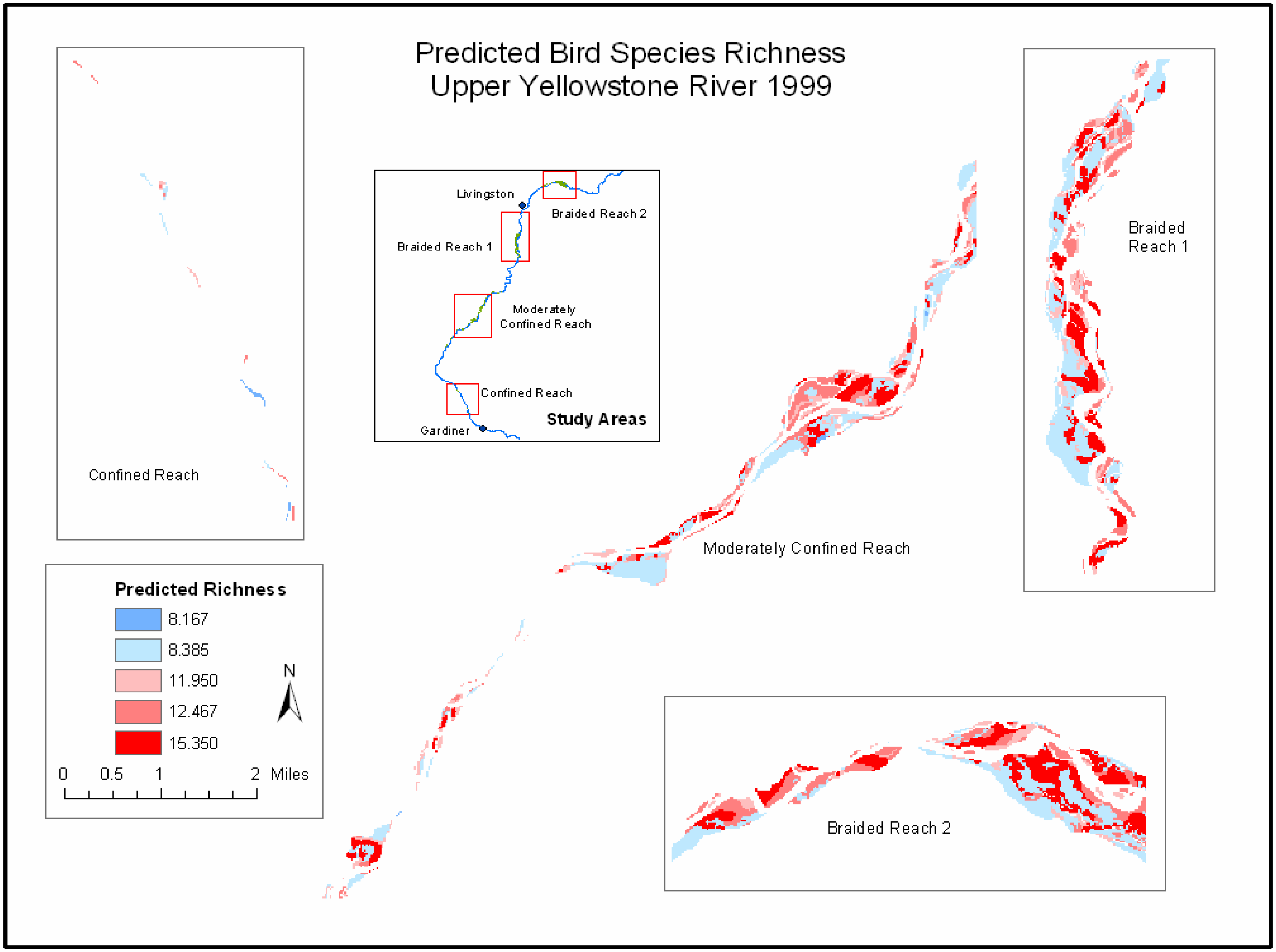
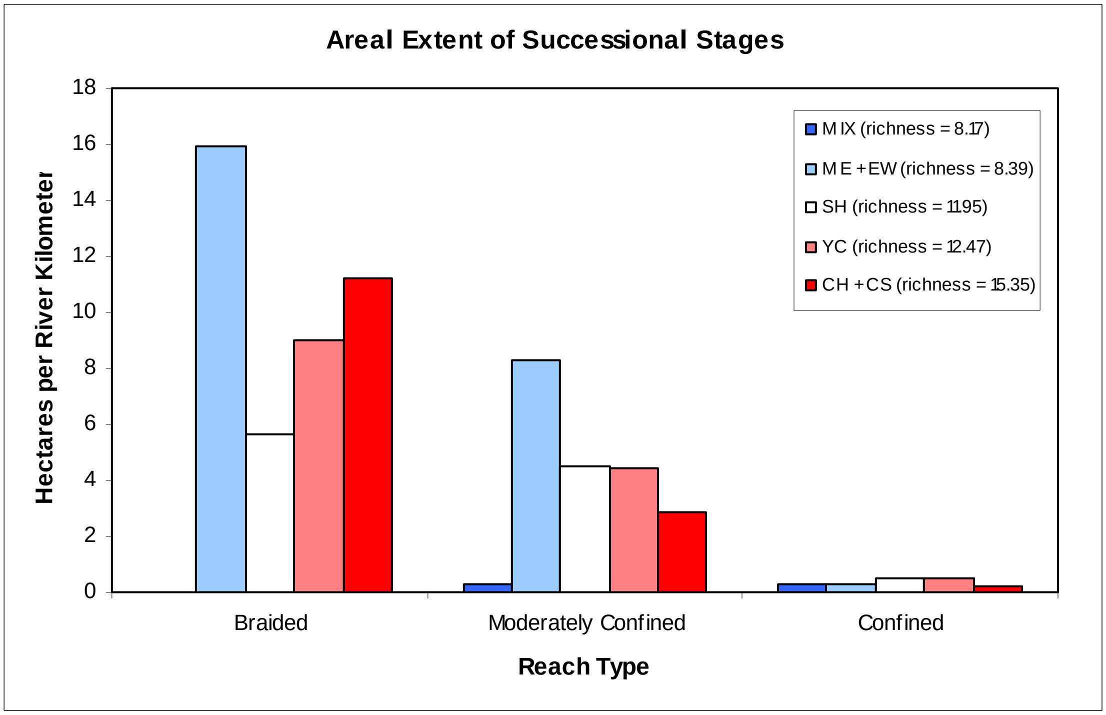


Figure 9. Representation and extent of successional stages across reach type.

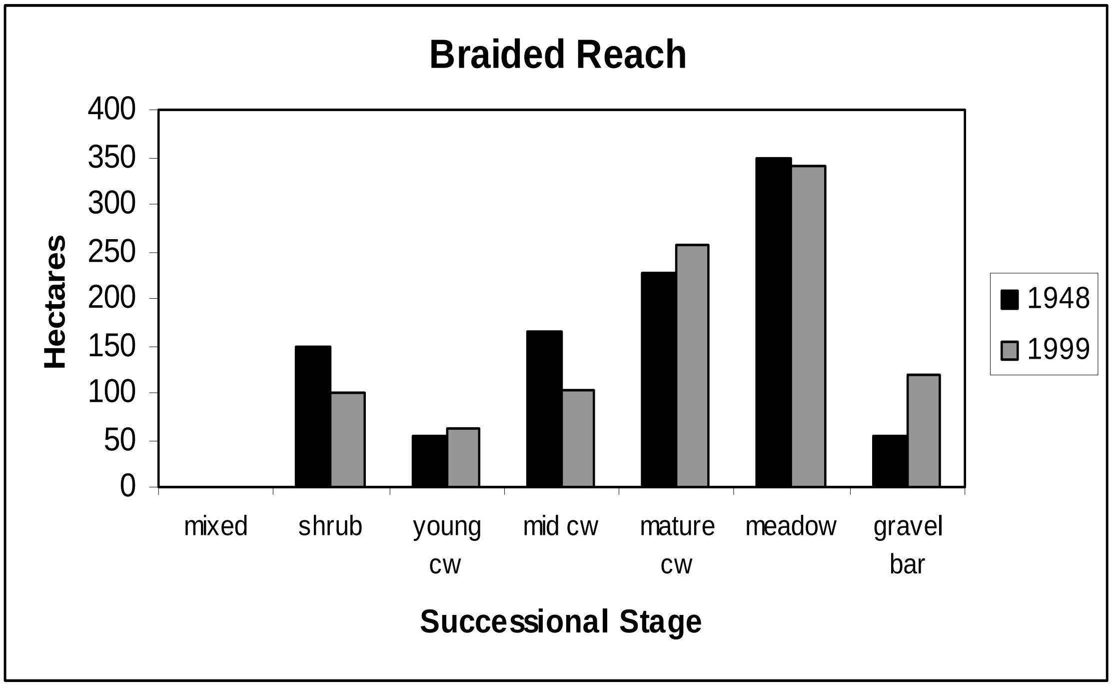


Objective 3: Change in the Representation of Successional Stages from 1948 to 1999

To identify changes in riparian vegetation community composition over time, we quantified for both 1948 and 1999 the total hectares and relative abundance (i.e. percent of total riparian vegetation) of each of the seven successional stages (Table 3) within the four sample areas. Percent changes in total area and abundance over time were then calculated using the formula [(new – old)/old]. For this historical change analysis, we did not consider the confined reach of the river because the riparian vegetation is very sparse, so we would not expect the maintenance of a steady-state mosaic to be an important phenomenon in this reach. Separate change comparisons were made for the braided and moderately confined reaches in order to detect different patterns of change for the different reach types.

The total area of the various successional stages differed from 1948 to 1999 within both the braided and moderately confined reaches (Tables 8 and 9; Figure 10). In the braided reach, a loss of cottonwood-willow shrub (-33%) was offset by a gain in gravel bar (+115%), with the total area in early successional stages (i.e. gravel bar, cottonwood-willow shrub, and young cottonwood) increasing by 8%. The middle-aged cottonwood successional stage decreased by 36%, while the mature cottonwood stage increased by 13%. This suggests that some of the middle-aged cottonwood stands succeeded to mature cottonwood, while other stands were scoured by flood waters, and converted to younger successional stages. However, within the moderately confined reach, there was a 29% decline in the occurrence of younger successional stages, and subsequent increase in later successional stages; mature cottonwood gained 38%, while mixed grassland/sage increased 33%. This suggests a decline in the initiation of succession, and subsequent cottonwood regeneration, in the moderately confined reach.

Figure 10. Total area of each successional stage in 1948 and 1999.



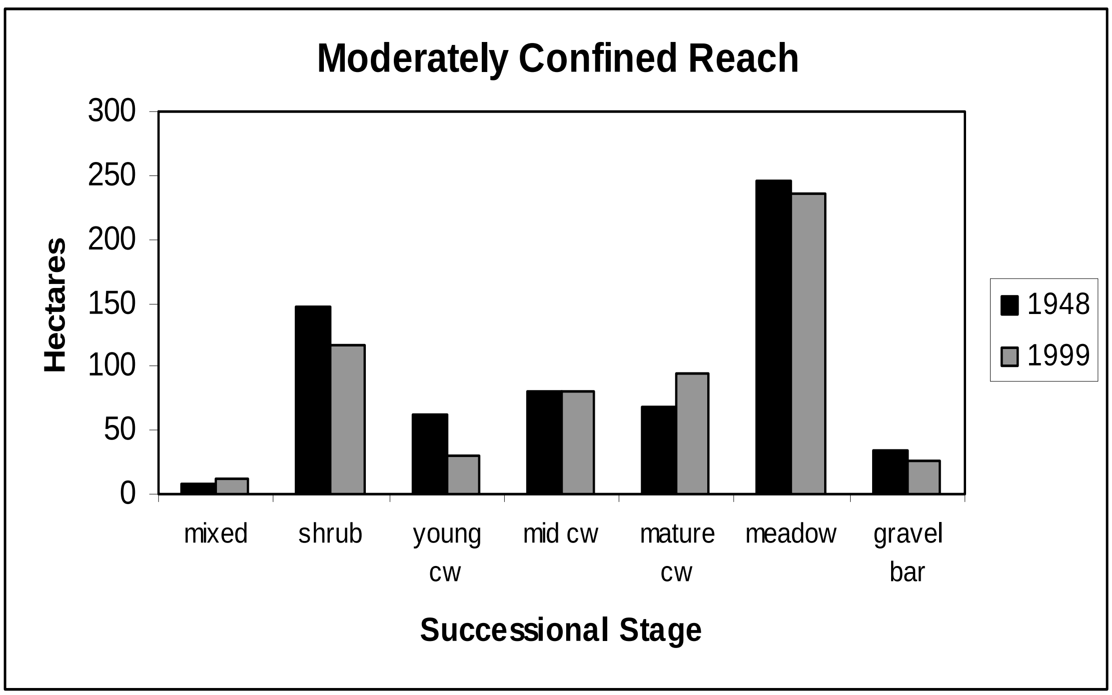


Table 8. Changes in riparian vegetation over the past fifty years within the braided reach. (Total early successional = gravel bar + cottonwood-willow shrub + young cottonwood.)

Successional Stage	Total Area (Hectares)		% Change in Total Area	Relative Abundance (%)		% Change in Relative Abundance
	1948	1999		1948	1999	
Gravel Bar	55	118	+115.0	5.5	12.0	+118.2
Cottonwood-willow shrub	149	99	-33.2	15.8	11.5	-27.0
Young cottonwood	55	63	+15.8	5.8	7.3	+26.5
Total early successional	259	280	+8.1			
Middle-aged cottonwood	164	104	-36.5	17.4	12.0	-30.7
Mature cottonwood	227	256	+13.1	24.0	29.7	+23.5
Meadow	349	341	-2.3	37.0	39.4	+6.7
Mixed grassland/sage/trees	0	0	0	0	0	0
Total riparian	998	981	-1.7	--	--	--

Table 9. Changes in riparian vegetation over the past fifty years within the moderately confined reach. (Total early successional = gravel bar + cottonwood-willow shrub + young cottonwood.)

Successional Stage	Total Area (Hectares)		% Change in Total Area	Relative Abundance (%)		% Change in Relative Abundance
	1948	1999		1948	1999	
Gravel bar	34	26	-23.5	5.3	4.4	-17.0
Cottonwood-willow shrub	146	117	-20.3	23.9	20.5	-14.4
Young cottonwood	63	30	-51.6	10.3	5.3	-48.0
Total early successional	243	173	-28.8	37.6	29.0	-22.9
Middle-aged cottonwood	81	81	0.0	13.2	14.2	+7.4
Mature cottonwood	69	94	+37.5	11.2	16.5	+47.7
Meadow	245	236	-3.6	40.0	41.4	+3.6
Mixed grassland/sage/trees	9	12	+33.4	1.4	2.0	+43.3
Total riparian	647	596	-7.9	--	--	--

Discussion

Our results from the upper Yellowstone River are consistent with the findings of other studies which concluded that floodplains support a mosaic of successional stages of riparian vegetation (Arscott and others, 2002; Shankman, 1993; Salo and others, 1986; Hupp and Osterkamp, 1985; Merigliano and Polzin, 2003). Our results showed that successional stages vary in structural complexity and shrub species richness, with the oldest successional stages providing the greatest habitat diversity overall. Mature cottonwood forests had the largest trees, greatest variety of tree sizes, highest volume of coarse woody debris, and a higher biomass of understory vegetation when compared with all other successional stages (Table 4).

Some individual bird species specialized on the resources provided by a particular successional stage. For instance, gravel bars supported high abundances of Spotted Sandpipers and Killdeer, which feed on aquatic insects and nest on the open sand and gravel substrates. The Red-winged Blackbird and Savannah Sparrow predominated in wet meadows, a vegetation type which provides dense herbaceous cover and rich food sources for these ground-nesting and ground-foraging birds. The Black-headed Grosbeak and Veery were most abundant in the mature cottonwood forests, which provide a complex understory layer for these shrub-nesting species. Downy Woodpeckers were also significantly associated with mature forest, which provide snags for nesting and large trees for insect foraging. Overall, these mature forests support vast numbers of birds using many different niches. Some of the species associated with mature cottonwood were identified by Hansen and others (1999) as most sensitive to land use change. Many bird species within the western U. S. are dependent on riparian habitats, which are very small in size and localized in the Northern Rockies. Several of these species are open-cup nesters (as opposed to cavity- and ground-nesters), so may experience lower reproductive rates due higher susceptibility to brood parasitism by brown-headed cowbirds, and higher nest predation by birds and mammals. Furthermore, predators and brood parasites are more abundant in agricultural and rural residential areas; these land use types are increasing in area within the region, and have been disproportionately located near riparian habitats (Hansen and Rotella, 2002; Saab, 1999).

The greatest number of bird species and highest total bird abundance were found in the mature cottonwood stage with a well-developed shrub understory. This is likely due to the high level of structural complexity, high snag and coarse woody debris abundance, and overall diversity of shrub species. Hansen and Rotella (2002) also concluded that mature cottonwood forests were the richest of all vegetation types in the northwest portion of the GYE, even though riparian forests covered only 1% of that landscape. This pattern has additionally been reported throughout the Northern Rockies (Dobkin and others, 1998). Furthermore, cottonwood forests are important not only for the biodiversity they maintain within riparian zones, but also because they may act as population source areas for bird sub-populations at high elevations in surrounding areas, including Yellowstone National Park (Hansen and Rotella, 2002). Therefore, floodplain management not only influences local bird populations, but also likely has implications for bird species viability many miles away. However, mature cottonwood-dominated floodplains are often intensively used by humans for farming, grazing, rural homes, and urban development, which can all have strong negative effects on wildlife (Hansen and others, in review). Hence, mature cottonwood forests may be one of the most threatened habitats in the region (Scott and others, 2003; Saab, 1999).

The distribution of riparian successional stages is a function of river geomorphology and the flooding regime (Scott and others, 1996, 1997; Stromberg and others 1991; Merigliano and Polzin 2003). It is in the braided, and to a lesser extent the moderately confined, reach types where the river is able to move laterally, cutting new channels, scouring older riparian vegetation, and initiating succession. Hence, the greatest abundance of each of the riparian successional stages is in the braided reach type (Figure 9). The total area of mature cottonwood forest was 2.8 times greater in the braided reach type than the moderately constrained reach type, and 31.2 times greater than in the confined reach type. Given that species richness is highest in these mature cottonwood forests, and given that the braided reach type occurs along only 36% of the length of the study area (Figure 2), we conclude that these braided areas are especially important to bird communities and should be a high conservation priority.

Our findings demonstrate the clear link between geomorphology, riparian succession, and bird diversity. The variety of successional stages and number of bird species observed in the riparian zone is a consequence of river dynamics and flood regimes which sustain heterogeneous riparian vegetation communities in the braided reaches. If bank stabilization projects reduce channel migration, and levee projects reduce over-bank flooding, then incidences of flooding disturbance and the initiation of riparian succession will decrease. This may initially lead to a decline in the abundance of early successional stages of riparian vegetation. Eventually, the aging cottonwood stands will become decadent and, without subsequent regeneration, will likely be replaced by grasslands, leading to a collapse of the natural riparian ecosystem. Evidence of this outcome is found in the Gallatin Valley (Montana), where streams were dewatered in the early 1900s at the outset of irrigation development. The last of the decadent cottonwood stands can now be seen along the former stream channels (A.J. Hansen, personal observation).

Our historic analysis of riparian vegetation along the upper Yellowstone River suggests that successional dynamics differed among the braided and moderately confined reach types. In the braided reach, both younger and older cottonwood stands increased in area, while the mid-successional cottonwood stage decreased in area (Table 8, Figure 10). These results are consistent with the expected consequences of back-to-back 100-year floods; many middle-aged cottonwood stands were likely scoured by flood waters and converted to early successional stages (mostly gravel bar) after the floods of 1996/1997, while the remaining middle-aged stands succeeded to mature cottonwood. This is also consistent with that expected under a dynamic steady-state equilibrium, with floods initiating succession and creating opportunities for the regeneration of riparian vegetation, while leaving other areas of the floodplain intact.

Within the moderately confined reach, early successional vegetation decreased in area, while the area of older successional vegetation increased (Table 9, Figure 10). These results may suggest that the composition of riparian vegetation within this reach is changing directionally over time, with riparian vegetation growing older, but not regenerating. This may be due to bank stabilization structures or levees within this reach which restrict channel migration and overbank flooding, and subsequently restrict the initiation of successional processes. However, the difference in successional dynamics between the braided and moderately confined reaches may also be explained by the differential influence of flood waters within these two reach types. It is possible that smaller floods can maintain a dynamic steady state mosaic within the braided reach type, but that larger floods are required to modify riparian vegetation along the steeper banks in the moderately confined reach type. Studies along the Missouri River have shown that strategies for cottonwood regeneration vary among reach types, with cottonwood seedlings establishing at higher elevations (away from the active channel) within more confined reaches in order to avoid frequent scouring by the high velocity flows characteristic of constrained channels (Scott and others, 1996, 1997). It may be that regeneration within the moderately confined reach is not yet evident since the 1996/1997 floods, because regeneration occurs on deposition bars at higher elevations, so cannot be indirectly measured by the presence of gravel bars (which are easy to detect on aerial photos).

Our results are consistent with the overall trends reported within the same study area by Merigliano and Polzin (2003) over that same time period. In the braided reach types they found an increase in the occurrence of older cottonwood stand types, as well as an increase in the occurrence of gravel bars. In the moderately confined reaches they found, as we did, an aging of cottonwood forests and a small decrease in the abundance of gravel bar. Additionally, they considered river dynamics over a time period greater than 100 years based on the distribution of tree ages, and concluded that the river is less dynamic in more recent decades, with cottonwood stands succeeding to older age classes without subsequent regeneration. The causes of the stabilization of river dynamics remains unknown. They suggest that human activities, including agriculture and bank stabilization, may have contributed, as well as phenomenon such as climate change and changes in sediment loading.

In sum, the results from change analysis suggest that the braided reach type has experienced adequate flooding to maintain a dynamic steady-state of successional stages over this fifty-year time period. Conversely, the moderately confined reach has apparently transitioned to older successional stages. We urge caution in using these results to make inferences about long-term changes within the floodplain, because these data are from only two time periods within these fifty years. Given that the flooding regime varies over tens to hundreds of years, and riparian succession occurs over similar time scales, the observed changes in riparian vegetation composition may be influenced by the recent flood histories of these 'snapshots' in time. However, it is possible that changes in riparian vegetation composition may be due to the cumulative effects of past human activities along the river, whose consequences may be more complex and difficult to determine. Future studies should directly investigate the causes of these observed changes, so that managers can further understand their possible ecological consequences.

Management Implications

The maintenance of flood dynamics within the Yellowstone River may be the most important management activity for sustaining avian diversity within the floodplain. The current riparian bird community reflects the natural flooding regime, river dynamics, and riparian succession that characterize the Yellowstone River system. Birds inhabit the full suite of successional stages, and depend on the regeneration of vegetation to maintain this heterogeneous floodplain. Human activities, such as bank stabilization, that alter channel migration and overbank flooding are likely to inhibit riparian succession, leading to a homogenization of riparian vegetation, and a loss of structural and species complexity; this could be detrimental to local riparian bird communities. Furthermore, given that bird populations within the study area are likely linked to sub-populations in Yellowstone National Park (Hansen and Rotella 2002), decisions made on the private lands in the upper Yellowstone River system will likely have consequences considerable distances away on public lands.

Need for Further Study

Additional studies would be very beneficial for providing understanding about the consequences of river management on wildlife communities. Because the maintenance of the full suite of successional stages is crucial to maintaining biodiversity, investigations which better quantify the past and possible future effects of bank stabilization on flood dynamics and riparian succession would be helpful in developing possible management scenarios for the river. Furthermore, studies which evaluate the combined effects of different types of bank stabilization and rural residential development on the demography of bird populations and other wildlife species may provide insight into some of the possible causes and consequences of different human activities along the river. With this information, managers could then use simulation models to project the likely future effects of alternative management scenarios on wildlife populations. Additionally, evaluation of the biodiversity value of the upper Yellowstone River relative to the other major river systems of the GYE may provide information on the importance of this river system for maintaining regional biodiversity. Finally, this study focused on breeding riparian birds. More study is needed to understand patterns of abundance and diversity for mammals, amphibians, and reptiles, as well as for migrating and wintering birds.

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Appendix 1:

Bird and Shrub Species Lists

Birds

Common name	Scientific name
American Crow	*Corvus brachyrhynchos*
American Goldfinch**	*Carduelis tristis*
American Kestrel	*Falco sparverius*
American Redstart	*Setophaga ruticilla*
American Robin**	*Turdus migratorius*
American White Pelican	*Pelecanus erythrorhynchos*
Audubon's Warbler**	*Dendroica coronata*
Bald Eagle	*Haliaeetus leucocephalus*
Bank Swallow**	*Riparia riparia*
Belted Kingfisher	*Ceryle alcyon*
Black-billed Magpie**	*Pica pica*
Black-capped Chickadee**	*Poecile atricapillus*
Black-headed Grosbeak**	*Pheucticus melanocephalus*
Brewer’s Blackbird**	*Euphagus cyanocephalus*
Brown-headed Cowbird**	*Molothrus ater*
Bullock's Oriole**	*Icterus bullockii*
Calliope Hummingbird	*Stellula calliope*
Canada Goose	*Branta canadensis*
Cassin's Finch	*Carpodacus cassinii*
Cedar Waxwing**	*Bombycilla cedrorum*
Chipping Sparrow**	*Spizella passerina*
Cinnamon Teal	*Anas cyanoptera*
Cliff Swallow**	*Petrochelidon pyrrhonota*
Common Grackle**	*Quiscalus quiscula*
Common Merganser	*Mergus merganser*
Common Nighthawk**	*Chordeiles minor*
Common Raven	*Corvus corax*
Common Snipe**	*Gallinago gallinago*
Common Yellowthroat**	*Geothlypis trichas*
Cooper's Hawk	*Accipiter cooperii*
Downy Woodpecker**	*Picoides pubescens*
Dusky Flycatcher**	*Empidonax oberholseri*
Eastern Kingbird**	*Tyrannus tyrannus*
European Starling**	*Sturnus vulgaris*
Gray Catbird**	*Dumetella carolinensis*
Great Blue Heron	*Ardea herodias*
Great Horned Owl**	*Bubo virginianus*
Green-tailed Towhee**	*Pipilo chlorurus*
Hairy Woodpecker	*Picoides villosus*
Hammond's Flycatcher	*Empidonax hammondii*
House Finch**	*Carpodacus mexicanus*
House Wren**	*Troglodytes aedon*
Killdeer**	*Charadrius vociferus*
Least Flycatcher**	*Empidonax minimus*
MacGillivray's Warbler	*Oporornis tolmiei*
Mallard	*Anas platyrhynchos*
Mountain Bluebird	*Sialia currucoides*
Mountain Chickadee	*Poecile gambeli*
Mourning Dove**	*Zenaida macroura*
Northern Rough-winged Swallow**	*Stelgidopteryx serripennis*

** Denotes species included in comparisons between successional stages.

Birds cont'd

Common name	Scientific name
Northern Waterthrush	*Seiurus noveboracensis*
Pine Siskin**	*Carduelis pinus*
Red-naped Sapsucker**	*Sphyrapicus nuchalis*
Red-shafted Flicker**	*Colaptes auratus*
Red-tailed Hawk**	*Buteo jamaicensis*
Red-winged Blackbird**	*Agelaius phoeniceus*
Rose-breasted Grosbeak	*Pheucticus ludovicianus*
Ruby-crowned Kinglet	*Regulus calendula*
Sandhill Crane	*Grus canadensis*
Savannah Sparrow**	*Passerculus sandwichensis*
Song Sparrow**	*Melospiza melodia*
Sora	*Porzana carolina*
Spotted Sandpiper**	*Actitus macularia*
Tree Swallow**	*Tachycineta bicolor*
Veery**	*Catharus fuscescens*
Vesper Sparrow**	*Pooecetes gramineus*
Violet-green Swallow**	*Tachycineta thalassina*
Warbling Vireo**	*Vireo gilvus*
Western Meadowlark**	*Sturnella neglecta*
Western Tananger	*Piranga ludoviciana*
Western Wood-pewee**	*Contopus sordidulus*
White-breated Nuthatch	*Sitta carolinensis*
White-throated Swift	*Aeronautes saxatalis*
Willow Flycatcher**	*Empidonax traillii*
Wilson's Warbler	*Wilsonia pusilla*
Yellow Warbler**	*Dendroica petechia*
Yellow-headed Blackbird**	*Xanthocephalus xanthocephalus*

** Denotes species included in comparisons between successional stages.

Shrubs

Common Name	Scientific Name
American Silverberry	*Elaeagnus commutata*
Big Sagebrush	*Artemisisa tridentata*
Black Greasewood	*Sarcobatus vermiculatus*
Buffaloberry	*Shepherdia argentea*
Ninebark	*Physocarpus malvaceus*
Oregon Grape	*Berberis vulgaris*
Willow	*Salix spp.*
Red-osier Dogwood	*Cornus stolonifera*
Russian Olive	*Elaeagnus angustifolia*
Serviceberry	*Amelanchier alnifolia*
Silver Sagebrush	*Artemisia cana*
Skunkbrush	*Rhus trilobata*
Snowberry	*Symphoricarpos spp.*
Sticky Currant	*Ribes viscosissimum*
Wild Rose	*Rosa woodsii*

Appendix 2:

Vegetation Classification Maps for 1948 and 1999

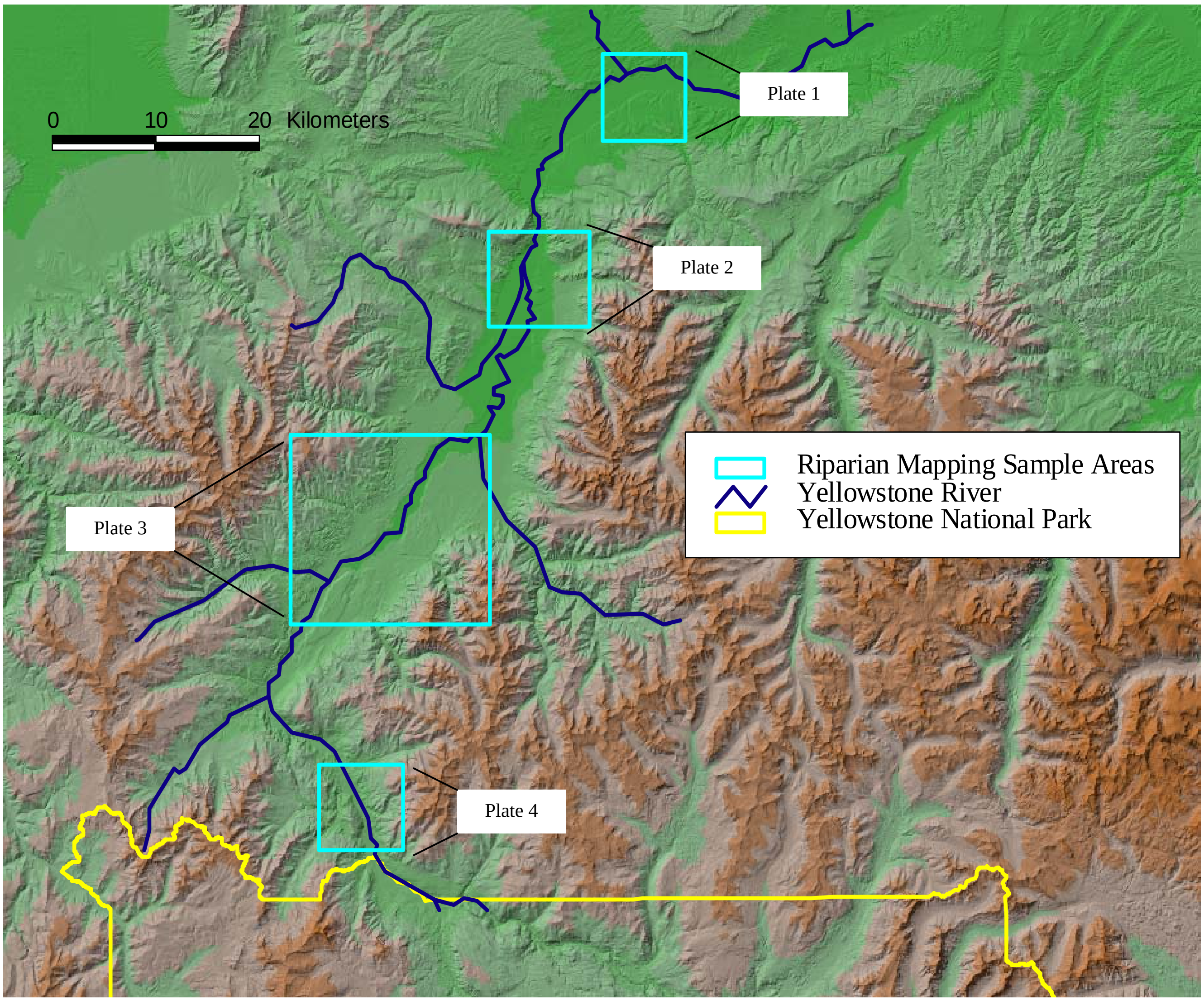

0
10
20 Kilometers
Plate 1
Plate 2
Plate 3
Plate 4
Riparian Mapping Sample Areas
Yellowstone River
Yellowstone National Park

Plate 1. First sample area in braided reach (east of Livingston).

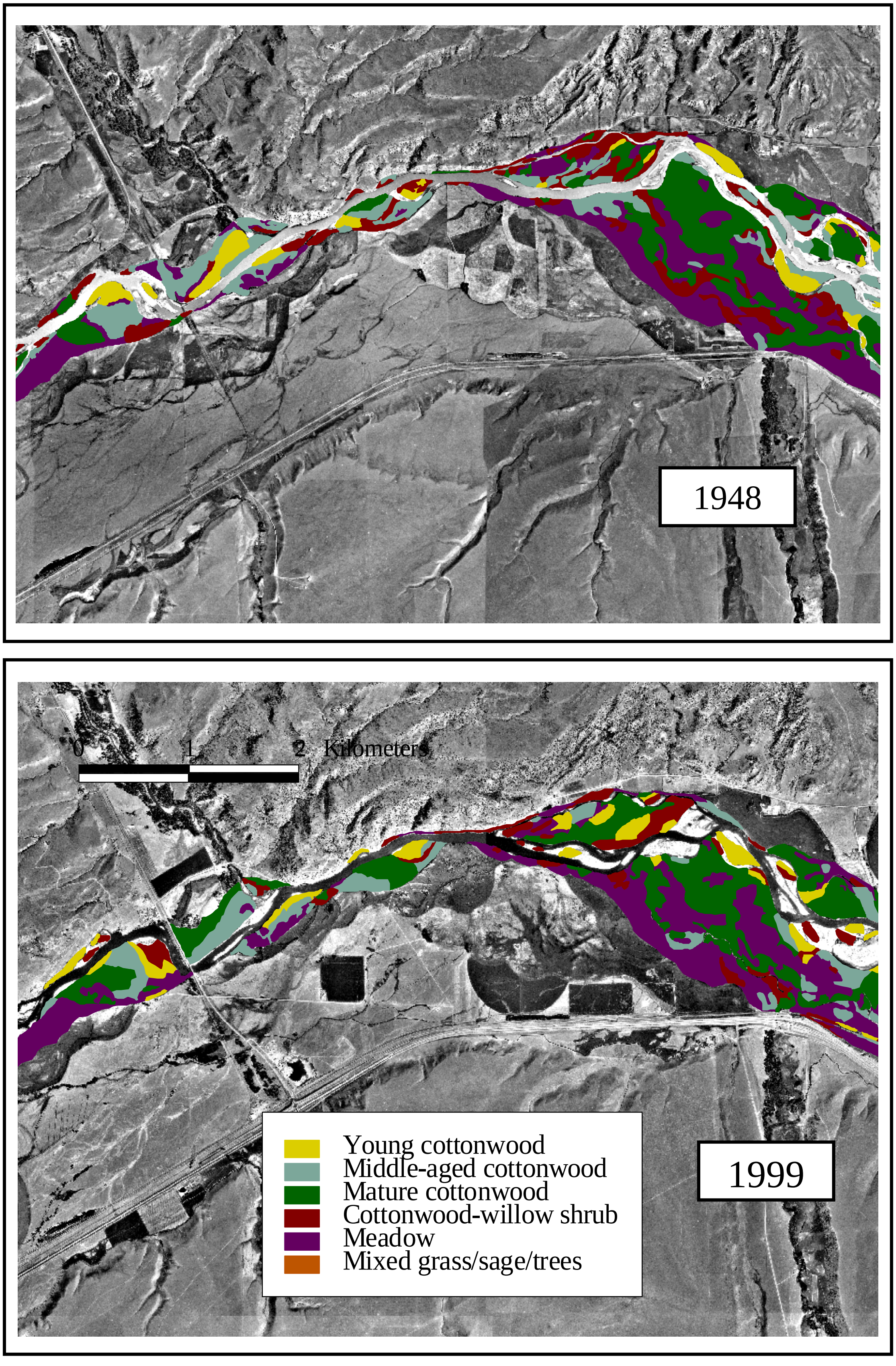


Plate 2. Second sample area in braided reach (south of Livingston).

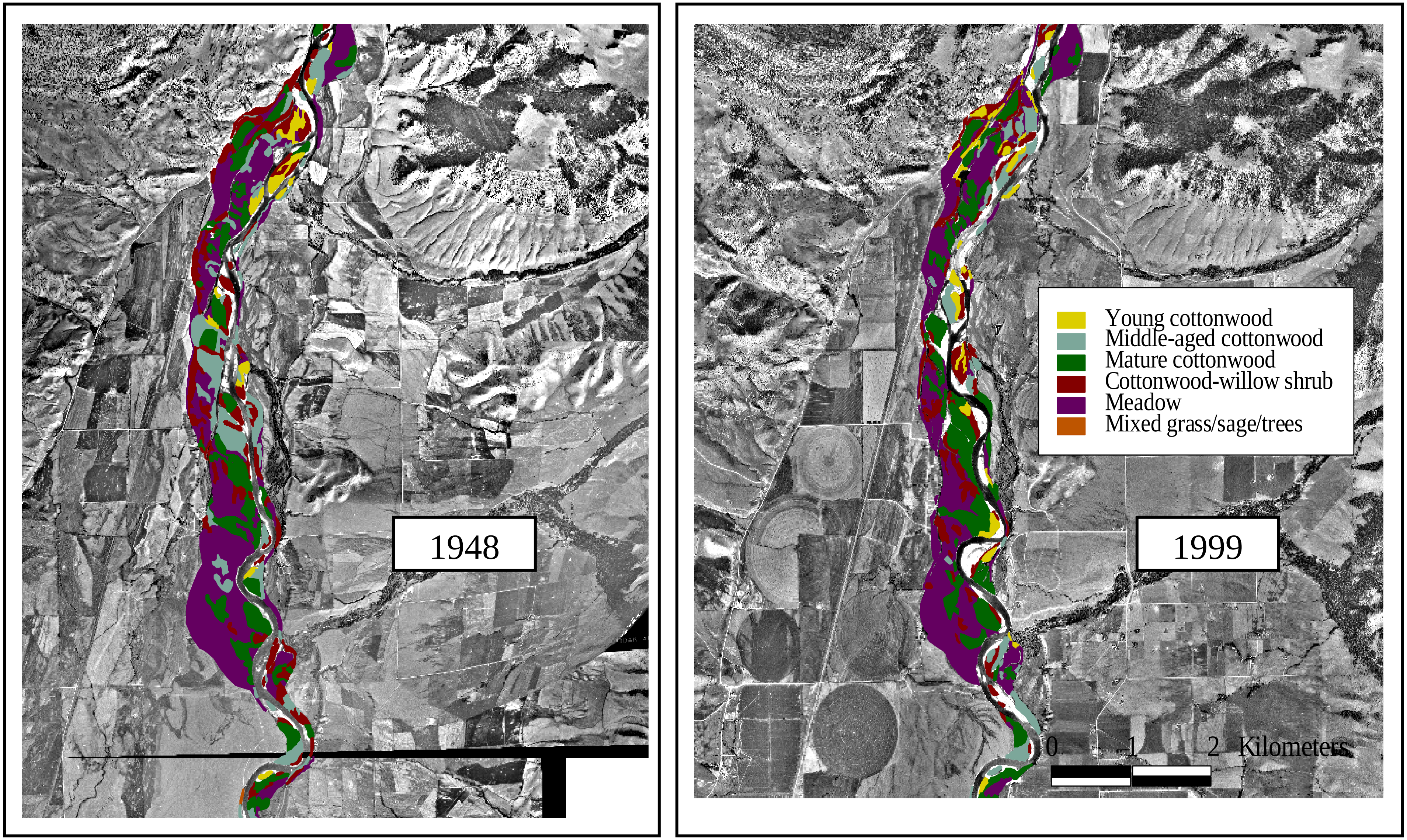
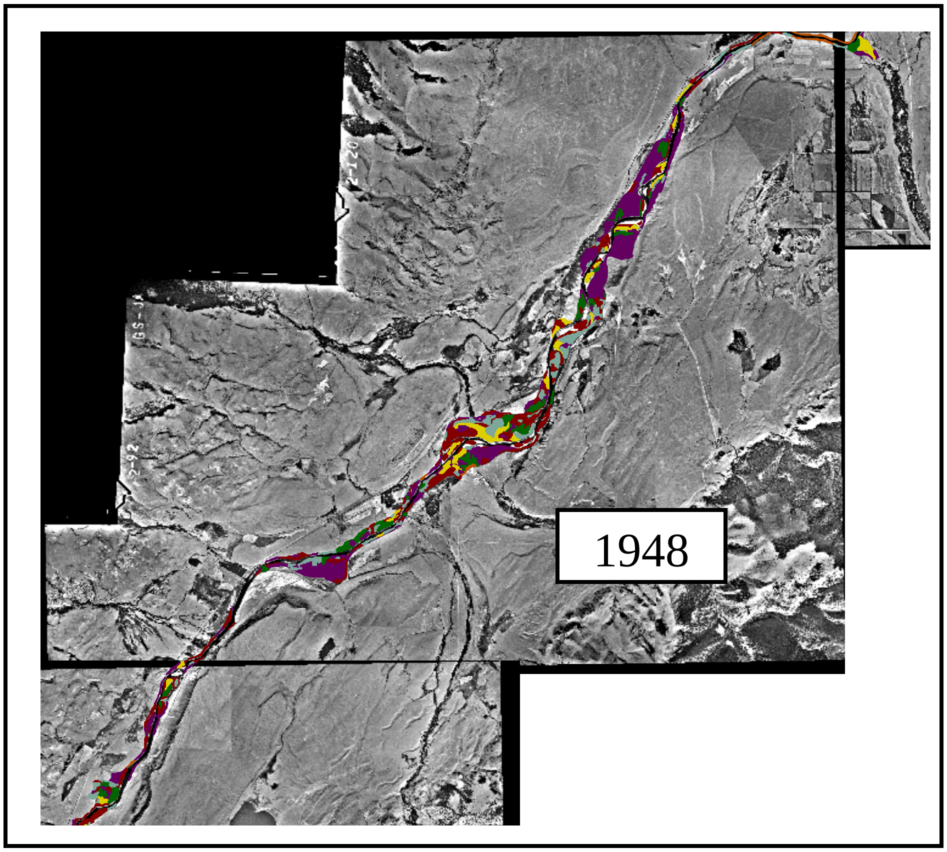


Plate 3. Sample area in moderately confined reach.



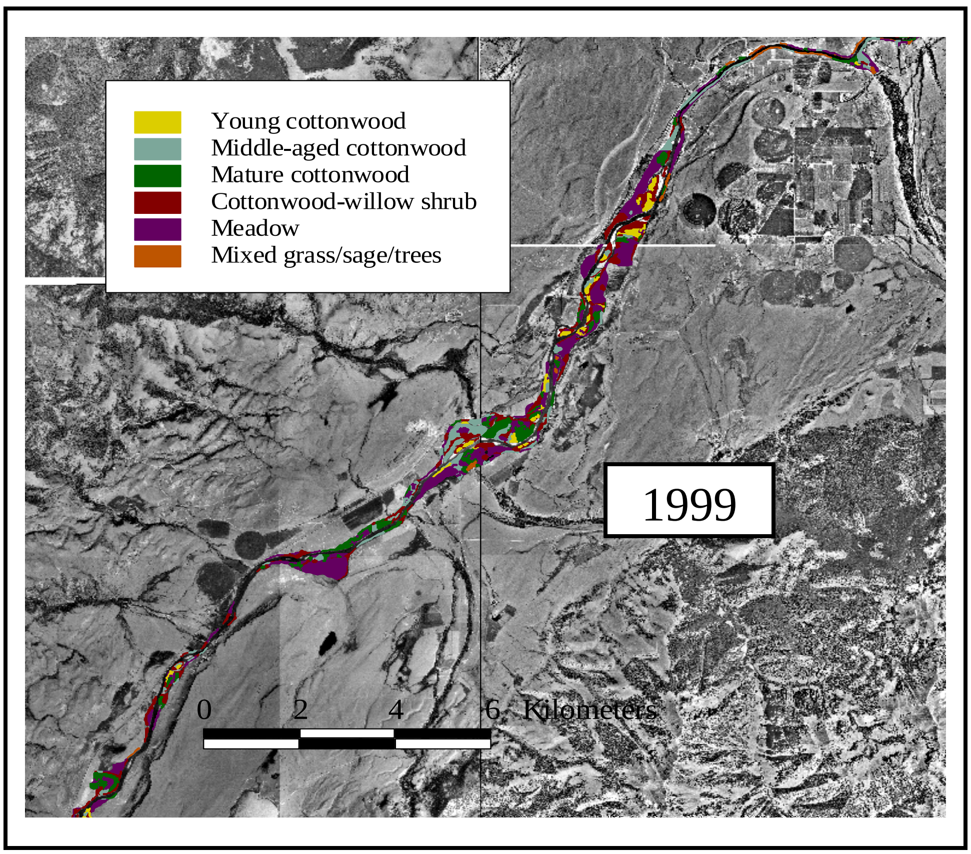


Plate 4. Sample area in confined reach.