Relating Geomorphic Change and Grazing to Avian Communities in Riparian Forests

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Abstract: *Avian conservation in riparian or bottomland forests requires an understanding of the physical and biotic factors that sustain the structural complexity of riparian vegetation. Riparian forests of western North America are dependent upon flow-related geomorphic processes necessary for establishment of new cottonwood and willow patches. In June 1995, we examined how fluvial geomorphic processes and long-term grazing influence the structural complexity of riparian vegetation and the abundance and diversity of breeding birds along the upper Missouri River in central Montana, a large, flow-regulated, and geomorphically constrained reach. Use by breeding birds was linked to fluvial geomorphic processes that influence the structure of these patches. Species richness and bird diversity increased with increasing structural complexity of vegetation* ($F_{1,32} = 75.49$, $p < 0.0001$; $F_{1,32} = 79.76$, $p < 0.0001$, *respectively). Bird species composition was significantly correlated with vegetation strata diversity* ($r_{s,33} = 0.98$, $p < 0.0001$). *Bird abundance in canopy and tall-shrub foraging guilds increased significantly with increasing tree cover and tall-shrub cover* ($F_{1,22} = 34.68$, $p < 0.0001$; $F_{1,20} = 22.22$, $p < 0.0001$, *respectively). Seventeen bird species, including five species of concern (e.g., Red-eyed Vireo [*Vireo olivaceus*]), were significantly associated* ($p < 0.10$) *with structurally complex forest patches, whereas only six bird species were significantly associated with structurally simple forest patches. We related the structural complexity of 34 riparian vegetation patches to geomorphic change, woody vegetation establishment, and grazing history over a 35-year post-dam period (1953–1988). The structural complexity of habitat patches was positively related to recent sediment accretion* ($t_{33} = 3.31$, $p = 0.002$) *and vegetation establishment* ($t_{20.7} = -3.63$, $p = 0.002$) *and negatively related to grazing activity* ($t_{19.6} = 3.75$, $p = 0.001$). *Avian conservation along rivers like the upper Missouri requires maintenance of the geomorphic processes responsible for tree establishment and management of land-use activities in riparian forests.*

Relación entre el Cambio Geomórfico y el Pastoreo con las Comunidades de Aves en Bosques Riparios

Resumen: *La conservación de aves en bosques riparios o tierras bajas requiere del conocimiento de los factores físicos y bióticos que sostienen la complejidad estructural de la vegetación riparia. Los bosques riparios del oeste de Norteamérica dependen de procesos geomórficos relacionados con el flujo y que son necesarios para el establecimiento de nuevos parches de álamos y sauces. En junio de 1995 examinamos como los procesos geomórficos fluviales y el pastoreo de largo plazo influyen en la complejidad estructural de la vegetación riparia y la abundancia y diversidad de las aves en reproducción a lo largo de la porción alta del río Missouri en la región central de Montana, un área grande, con flujo regulado y geomorfológicamente limitada. El uso por aves en reproducción estuvo ligado a procesos gemórficos fluviales que influyeron en la estructura de estos parches. La riqueza de especies y la diversidad de aves incrementó al incrementarse la complejidad estructural de la vegetación* ($F_{1,32} = 75.49$, $p < 0.0001$; $F_{1,32} = 79.76$, $p < 0.0001$, *respectivamente). La composición de especies de aves estuvo significativamente correlacionada con la diversidad de los estratos de vegetación* ($r_{s,33} = 0.98$, $p < 0.0001$). *La abundancia de aves en el dosel y las comunidades forrajeras de arbustos altos incrementaron significativamente con un incremento en la cobertura de árboles y la cobertura de arbustos altos* ($F_{1,22} = 34.68$, $p < 0.0001$; $F_{1,20} = 22.22$, $p < 0.0001$, *respectivamente). Diecisiete especies*

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*de aves, incluyendo cinco especies de interés (por ejemplo el vireo ojirojo [*Vireo olivaceus*]), estuvieron significativamente asociados (*$p < 0.10$*) con parches de bosque estructuralmente complejos, mientras que únicamente seis especies de aves estuvieron significativamente asociadas con parches de bosque estructuralmente simples. Relacionamos la complejidad estructural de 34 parches de vegetación riparia con cambios gemórficos, el establecimiento de vegetación leñosa y la historia de pastoreo de 35 años, en el periodo posterior a la construcción de represas (1953–1988). La complejidad estructural de los parches de hábitat estuvo positivamente relacionada con la acumulación reciente de sedimentos.*

Introduction

A subtle but pervasive cause of population declines in terrestrial birds in North America is human alteration of natural disturbance and successional processes (Askins 2000). Throughout the continental United States, large rivers and their bottomlands have been modified by various water-development projects that have altered water delivery patterns and fluvial geomorphic processes. Although these changes produced relatively immediate, tangible benefits in the form of flood control, transportation, power generation, irrigation, and increased agricultural production, they also set in motion detrimental ecological changes, the extent of which are only now being fully appreciated (Hunt 1988; Graf 1999).

We provide examples from three regions to illustrate these points. Stream flow along major rivers of the American southwest has been modified by large storage dams in response to intense human demands for water. Because water storage is large relative to runoff, the disruption of riverine ecosystems is correspondingly greater in this region (Graf 1999). Indeed, throughout the southwestern United States and especially the lower Colorado River system, only relict patches of native riparian forest remain (Briggs & Cornelius 1998), and many of these are heavily modified by flow regulation and livestock grazing. Without large-scale restoration efforts, many riparian-dependent bird species are expected to disappear from the region (Askins 2000).

On the lower Mississippi River, extensive engineering of the channel and bottomland to control flooding has contributed to the conversion of bottomland hardwood forests to agriculture (Gosselink et al. 1990). Destruction of large, unbroken tracts of old-growth bottomland forests in the Mississippi Valley has led to the extirpation of area-sensitive species such as the Ivory-billed Woodpecker (*Campephilus principalis*; Tanner 1942) and to declines in species richness and population density of some forest-interior species (Burdick et al. 1989). In contrast, the upper Mississippi River still retains some degree of natural flow variability and approximately 50% of its original bottomland forests (Sparks et al. 1998). These forests support higher bird densities and provide a unique habitat structure for species of concern that are rare in adjacent upland habitats (Knutson et al. 1996). However, modified hydrologic regimes and geomorphic processes resulting from lock and dam construction appear to have altered forest successional processes. Progressive forest simplification, involving a net loss of early successional species and a trend toward monospecific stands of silver maple (*Acer saccharinum*), presents emerging problems for wildlife dependent on the unique diversity of habitat typically found in bottomland forests (Knutson & Klaas 1998).

Across the western Great Plains of North America, stands of plains cottonwood (*Populus deltoides* subsp. *monilifera*) represent the principal natural forest in a largely treeless landscape. Riparian deciduous forest is one of five habitats in Montana of highest conservation priority (Montana Partners in Flight 2000). Although limited in aereal extent (Knopf et al. 1988), these bottomland or riparian forests provide important habitat for native vertebrates, including birds (Brinson et al. 1981; Finch & Ruggiero 1993). Bird distribution and abundance in riparian forests may be influenced by the ecological attributes of these habitats at different spatial scales, such as the structural diversity of vegetation (Stauffer & Best 1980; Brinson et al. 1981), the size, shape, and connectivity of forest patches (Stauffer & Best 1980; Decamps et al. 1987; Saab 1999), and the pattern and composition of the surrounding landscape (Saab 1999).

More than 233 bird species reside within the upper Missouri River corridor in Montana (U.S. Department of the Interior 1993). Several species of concern (Montana Partners in Flight 2000) occur in our study area, including the Red-eyed Vireo (*Vireo olivaceus*), Downy Woodpecker (*Picoides pubescens*), Least Flycatcher (*Empidonax minimus*), American Redstart (*Setophaga ruticilla*), Song Sparrow (*Melospiza melodia*), Gray Catbird (*Dumatella carolinensis*), and Warbling Vireo (*Vireo gilvus*). Because of its scenic qualities, historical significance, and wildlife resources, portions of a 240-km reach of the upper Missouri River have been designated "wild and scenic." Recently, the river and adjoining public lands, administered by the U.S. Bureau of Land Management (BLM), have received increased recreational use, resulting in conflicts between traditional grazing uses and recreation. The wild and scenic Missouri River has become the nexus of a debate over how future land and water management can best protect this resource. Of concern is how management of flow from upstream dams and livestock grazing influence the distribution and abundance of riparian cottonwoods and associated wildlife species. To address these concerns, we initiated a study of the influences of post-dam fluvial geomorphic processes and long-term grazing on the structural complexity of riparian vegetation and the abundance and diversity of breeding birds.

Study Area

The 240-km study reach extends from Fort Benton, Montana (river km 0), downstream to the U.S. Geological Survey gage at Landusky, Montana. Here the Missouri River traverses the highly dissected topography of the Missouri Breaks and occupies a relatively narrow, post-glacial valley incised from 150 to 560 m below the surrounding landscape (Alden 1932). The principal tree species along the Missouri River is plains cottonwood. Box elder (*Acer negundo*), green ash (*Fraxinus pennsylvanica*), and peach-leaf willow (*Salix amygdaloides*) occur as less common associates, particularly on islands and in former back channels that have been filled by alluvial sediments. Understory shrubs on alluvial surfaces include yellow willow (*Salix lutea*), sandbar willow (*Salix exigua*), western snowberry (*Symphoricarpos occidentalis*), Wood's rose (*Rosa woodsii*), silver sagebrush (*Artemisia cana*), and common chokecherry (*Prunus virginiana*) (Ross & Hunter 1976).

The landscape surrounding the river consists of undisturbed prairie vegetation dominated by black greasewood (*Sarcobatus vermiculatus*), big sagebrush (*Artemisia tridentata*), and mixed grasses, including western wheat grass (*Agropyron smithii*), blue grama (*Bouteloua gracilis*), and downy brome (*Bromus tectorum* L.). North-facing slopes contain isolated stands of Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), and juniper (*Juniperus scopulorum*), and south-facing slopes contain scattered grasses, ponderosa pine, or bare exposures of shale.

This reach of the Missouri River has a snow-melt hydrograph with annual peak flows typically occurring in May or June. The natural flow regime has been influenced by irrigation withdrawals and upstream dams on the mainstem and major tributaries. Two large upstream dams, Canyon Ferry on the Missouri River and Tiber on the Marias River, were constructed in 1953 and 1956, respectively. Whereas the seasonal timing and frequency of large peak flows (>1850 m^3/second) have not changed in the post-dam period, their magnitude has been reduced 40–50% as a result of flow regulation (Bovee & Scott 2002).

Because of geologic constraints on channel movement throughout much of the study reach, the majority of cottonwood forest patches are small and scattered, matching pre-settlement descriptions (Coues 1893). These stands originate after infrequent floods exceeding 1850 m^3/second (Bovee & Scott 2002) establish cottonwood seedlings on high, narrow alluvial deposits. Trees established on these flood deposits are most likely to survive the physical effects of ice drives, common along large rivers of the northern Great Plains (Smith 1980; Auble & Scott 1998). In less constrained channel reaches, cottonwood and willow forest patches are more spatially extensive and become established more frequently on actively accreting, lower-elevation alluvial surfaces such as point bars and channel islands (Scott & Auble 2002). Alluvial surfaces without trees are typically dominated by grasses and silver sagebrush.

Modern agricultural development within the river corridor is limited and confined primarily to Missouri River terraces. Both the river corridor and surrounding uplands have been subject to livestock grazing since settlement. Grazing occurs on all or parts of 55 grazing allotments totaling 91,769 ha of public land along the wild and scenic reach (U.S. Department of the Interior 1993). But because of a shortage of upland water sources and steep, rugged terrain between the uplands and the bottomland, livestock within the Upper Missouri wild and scenic river corridor concentrate preferentially along the river, where water and shade are available. Monitoring data (BLM) indicate heavy to severe livestock use of the bottomland in most grazing allotments (J. Frazier, personal communication), but not all sites are accessible to cattle.

Methods

Site Selection

In September 1994, structurally complex riparian cottonwood stands with well-developed, woody shrub layers (herein referred to as cottonwood-shrub), and stands of cottonwoods with comparatively little woody understory (cottonwoods) were identified on the ground in the study reach by M.L.S. A subsample of these forest patches on public land was selected at random and located on 1:15840 aerial color photographs from 1988. Treeless areas on adjacent alluvial surfaces dominated by grasses and shrubs (shrub-steppe) were identified from the aerial photographs as a third patch type. Thirty-four riparian patches were selected along a 96-km reach for sampling of vegetation structure and bird species diversity.

Vegetation Sampling

In June 1995, we placed one to four 10-m-wide belt transects (mean 3.2), with the number depending on patch size, systematically across each patch orthogonal to the channel, beginning at the water's edge and extending landward 100 m. Most (30 of 34) sites had a minimum of three transects, and four sites had fewer than three transects. Transects were 100 m apart in forested patches and 150 m apart in nonforested patches. Total plant canopy cover for each woody species, all herbs, and vegetation canopy strata were visually estimated for each transect. Four vegetation strata were examined: (1) tree (>4 m in height), (2) tall shrub (1–4 m), (3) low shrub (<1 m), and (4) herbs. The tall-shrub stratum included the lower canopy of trees within this height range. Canopy-cover estimates for all strata were based on the methods of Daubenmire (1959). We weighted canopy cover for each stratum by its proportional coverage along the transect. Weighted cover values by stratum were summed by transect and averaged across transects to give a single value for a patch. For descriptive purposes, mean cover and standard deviation of the four vegetation structural variables were used to characterize differences in microhabitat or within-patch structure for each patch type.

Site Classification

Our initial classification of habitat type was made according to ground-based visual inspection. We used a simple hierarchical sorting technique to refine patch classifications based on vegetation structure measured along transects. Patches were first sorted according to the presence or absence of tree cover to discriminate shrub-steppe from cottonwood and cottonwood-shrub types. Cottonwood and cottonwood-shrub patches were then hierarchically sorted by the variables of tall shrub, low shrub, and herbs. A break in these ordered sites allowed the grouping into cottonwood-shrub and cottonwood types.

Bird Sampling

The day after establishing transects, we surveyed birds in each patch between sunrise and 0930 hours. We recorded all birds seen and heard within 100 m of transects and recorded distances in 10-m intervals. In distance sampling, counting of birds previously recorded in another transect does not bias estimates when observations are independent. Forest birds, grassland birds, and Wood Ducks (*Aix sponsa*) were used in the statistical analyses. We omitted sightings of raptors, gulls, shorebirds, and waterfowl. We used the program DISTANCE, Version 3.5 (Buckland et al. 1993), to calculate densities for species with sample sizes adequate to calculate detection functions ($n > 40$).

Bird species were assigned to several foraging microhabitat guilds similar to those of Skagen et al. (1998). The guilds included (1) terrestrial generalist; (2) aerial insectivore, sweeper; (3) aerial insectivore, sallying and hawking; (4) tree-canopy foragers, foliage gleaner; (5) tall-shrub foragers, foliage gleaner; (6) low-shrub forager, foliage gleaner; (7) ground and forb forager, foliage gleaner; (8) trunk insectivore, trunk and branch gleaner; and (9) forest generalist.

Patch Size and Landscape Measurements

Measurements of patch dimensions and surrounding landscape variables were made from 1988 color aerial photographs at a scale of 1:15,840. We limited these measurements to forested patches because shrub-steppe patches consisted of treeless alluvial surfaces that were not structurally distinct from the landscape matrix. On the aerial photographs, cottonwood-shrub and cottonwood patches commonly appeared as discrete, linear patches of woody vegetation on channel islands or banks, separated by water or grassland from adjacent patches. Distances were measured from the photos to the nearest 0.01 mm with calipers and then converted to meters. Average patch length was based on two measurements along the long axis of the patch, and average patch width was based on three measurements along the short axis. Patch area was estimated as average length multiplied by average width.

Landscape variables consisted of (1) average distance from a patch to the nearest adjacent cottonwood patch and (2) the nature of the landscape surrounding a patch. Average distance to the nearest cottonwood patch was based on two measurements from the center of the patch to the center of the two nearest cottonwood patches. The surrounding landscape was measured within a 1-km radius of each patch and expressed as the percentage of land area in the following land-cover types: wetted channel, nonforested alluvial surface, upland grass, upland forest, cottonwood forest, agriculture, and other. A grid of points on 8-mm centers was used to estimate the relative land area in each of the cover types. Patch dimensions and landscape metrics were compared by means of pair-wise t tests and a Bonferroni-adjusted significance level of 0.05 where appropriate.

Geomorphic Change, Vegetation Establishment, and Grazing History

Using aerial photographs and field notes, we classified all habitat patches by the geomorphic surface or surfaces upon which they occurred, including flood deposits, channel islands, overflow channels, and tributary fans. For each patch, we evaluated evidence of geomorphic change and quantified establishment of woody riparian vegetation within the last 35 years. We evaluated these changes by comparing field information from the transects and the most recently available aerial photographs (1988) with 1953 aerial photographs (1:19,878 scale). Observed changes in the shape or elevation of alluvial surfaces along the transects, reflecting geomorphic activity, were assessed categorically as "sediment accretion" (lateral and vertical) and "no accretion." We quantified vegetation change by assessing the proportion of transects that included surfaces with woody vegetation established since 1953. Repeated annual grazing was assessed for each patch based on aerial photos, BLM grazing records, and on-site indicators. If grazing history was not clearly documented in BLM grazing records, we assumed that a vegetation patch was not being grazed if the patch had no on-site indicators (e.g., manure) and was (1) on an island inaccessible to livestock or (2) adjacent to cropland but not fenced separately from the cropland.

Statistical Analyses

We calculated two measures of bird diversity, species richness (S = number of species) and the Shannon index of diversity (H' birds; $H' = -\Sigma p_i \ln p_i$, where p_i is the proportion of individuals found in the ith species; see Greig-Smith 1983). Similarly, we used the Shannon index to calculate diversity of vegetation strata (H' veg, where p_i is the proportion of vegetation cover found in the ith stratum). To extract a gradient in bird species composition across sample sites, we used detrended correspondence analysis (DCA; Hill & Gauch 1980) in PC-ORD 3.17 (McCune & Mefford 1997). Detrended correspondence analysis has been effectively used to characterize bird assemblages (Rotenberry & Chandler 1999). The first DCA axis of site scores (Gauch 1982) served as a continuous variable to represent the gradient in bird species composition; site scores were based on the abundance of species found on sampled sites. The site score was related to beta diversity or species turnover and was derived in the context of all species occurring on all sites. In contrast, species richness for a given site accounted only for the number of species at that site, not the particular species or shifts in species composition across sites. We used Spearman Rank correlation (r_s) to examine the relation between bird species composition (DCA-derived site scores) and vegetation structure (H' veg). Independent variables used in regression analyses were transformed to fit a lognormal distribution.

We calculated an effort-adjusted mean abundance (individuals/400 m), frequency (proportion of sites at which a species occurs within a habitat type), and importance value (IV) for each bird species. The IV was calculated as (relative abundance × frequency) × 100, where relative abundance was defined as the mean abundance for a given species in a habitat type divided by the sum of that species' mean abundances in all habitat types. Using indicator-species analysis (ISA) and associated Monte Carlo tests (Dufrêne & Legendre 1997), we tested the null hypothesis that the observed maximum IV for a species, across habitat types, is no larger than would be expected by chance alone. For a given species, the Monte Carlo test compares observed maximum IV across habitat types to the IVs obtained from 1000 randomly shuffled trials using a matrix of abundances and frequencies from the habitat patches being tested. We tested across all habitat patches and across forested habitat patches only. Each test was considered independent, so we did not use Bonferroni corrections (Scheiner 1993; Cabin & Mitchell 2000). Species with p values of ≤ 0.10 were considered significantly associated with one of the three habitat patch types.

We used Welch's t tests to examine differences in vegetation strata diversity (H' veg) between sites categorized by (1) sediment accretion or no accretion, (2) woody vegetation establishment or no establishment, and (3) grazing or no grazing. Statistical analyses were performed with SYSTAT 9.0 (SPSS 1999).

Results

Characterization of Habitat Patches

The hierarchical sorting of forested patches resulted in a classification that closely mirrored field classifications, with the exception of patches 154.8, 196.9, and 210.9, which were reclassified from cottonwood to cottonwood-shrub. Tree cover distinguished the three patch types, with cover in cottonwood-shrub greater than that in cottonwood, and, in turn, cover in cottonwood greater than that in shrub-steppe (Table 1). Tall-shrub cover was also significantly greater in cottonwood-shrub than in either cottonwood or shrub-steppe. The predominant species in the tall-shrub layer of cottonwood-shrub patches were cottonwood (59% of total tall-shrub cover), three willow species (peach-leaf, yellow, and sandbar; 30.4% of tall-shrub cover), and green ash (5.6% of tall-shrub layer). Herbaceous cover was significantly greater in shrub-steppe than in cottonwood-shrub. Cottonwood-shrub patches were significantly greater in width, length, and area than cottonwood patches (Table 1).

The landscape matrix surrounding the forested patch type was relatively uniform (Table 1), with upland grass, nonforested alluvial surfaces, and wetted-channel cover types comprising approximately 75% of all surface area within 1 km of the sampled patches. There were no differences in landscape metrics between cottonwood and cottonwood-shrub patches (Table 1).

Bird Species Composition Relative to Habitat Variables

We recorded 58 species of forest and grassland birds. Yellow Warblers (*Dendroica petechia*), American Goldfinches (*Carduelis tristis*), and House Wrens (*Troglodytes aedon*) were the most abundant species with maximum densities of 7.4, 4.1, and 4.5 birds/ha, respectively.

Table 1. Comparison of measured habitat and landscape variables among three riparian vegetation patch types (n) within the study area along the Missouri River, Montana (U.S.A.).*

	Vegetation type		
Vegetation structure, patch dimension, and landscape variables	*cottonwood-shrub (12)*	*cottonwood (10)*	*shrub-steppe (12)*
Tree cover (%)	23.6 (1.7) a	13.2 (2.7) b	0.0 (0.0) c
Tall-shrub cover (%)	26.6 (3.2) a	3.4 (1.0) b	0.4 (0.2) b
Low-shrub cover (%)	22.6 (5.6)	22.8 (3.7)	21.7 (3.0)
Herb cover (%)	68.3 (3.2) a	77.5 (3.8) ab	83.0 (2.4) b
Patch width (m)	92.4 (19.4) a	47.3 (8.0) b	
Patch length (m)	627.4 (105.7) a	408.5 (48.2) b	
Patch area (ha)	5.8 (1.2) a	1.9 (0.4) b	
Distance to adjacent cottonwoods (m)	20.3 (3.8)	29.9 (6.6)	
Nonforested alluvial surface (%)	17.7 (2.7)	22.7 (2.7)	
Upland grass (%)	45.3 (2.9)	44.4 (5.0)	
Upland forest (%)	8.9 (1.7)	8.5 (1.9)	
Wetted channel (%)	13.6 (0.9)	12.5 (0.5)	
Agriculture (%)	3.1 (2.8)	1.5 (1.4)	
Cottonwood forest (%)	4.8 (1.1)	3.1 (2.8)	
Other (%)	6.7 (0.9)	6.6 (1.2)	

* *Values are means (SE) for each variable. Different lowercase letters for variables within row denote statistically significant differences ($p = 0.05$, Bonferroni adjustment).*

Species richness increased nonlinearly with increasing vegetation strata diversity (H' veg) across all sites and also across the subset of forested patches (Table 2 and Fig. 1a). Bird diversity (H′ birds) also was significantly positively correlated with vegetation strata diversity (H' veg), again for all patches and for forested patches only (Table 2). To test whether greater species richness was due to more intensive sampling in larger patches, we reran the analysis with one randomly selected transect from each site. There were no differences in results from this subset and the more inclusive model with all data (one transect: $r^2 = 0.72$, $F = 33.92$, $p < 0.0001$; all inclusive model: $r^2 = 0.70$, $F = 75.49$, $p < 0.001$), so we present the more inclusive model in Table 2.

Bird species composition as characterized by DCA axis 1 was significantly correlated with vegetation strata diversity (Fig. 1b). As vegetation structure increased in complexity across the 34 sites, bird community structure changed from the few bird species associated primarily with grassland habitats to more diverse bird communities of shrub- and canopy-foraging birds, as illustrated by the following analyses. Based on the indicator-species analysis across all habitat types, 26 of the 58 bird species used in the ordination were significantly ($p \leq 0.10$) associated with one of the three habitat patch types (Table 3; species are listed in descending order of their association with the cottonwood-shrub patch type). Seventeen species were significantly associ-

Table 2. Relationships between bird species diversity and vegetation strata diversity (H' veg) of all sites and forested sites only, and relationship of guild abundance with cover of vegetation strata most likely to influence abundance.

Dependent variable (sites)	*Independent variable*	N	*Slope*	r^2 (r_s)*	*SE*	F	p
Species richness (all sites)	lnH′ veg	34	14.64	0.70	4.04	75.49	<0.0001
Species richness (forest sites)	lnH′ veg	22	11.06	0.22	1.51	5.76	0.026
Bird diversity (all sites)	H′ veg	34		(0.98)			<0.0001
Bird diversity (forest sites)	H′ veg	22		(0.92)			<0.0001
Abundance of guild							
Aerial insectivores, sweeper	lnTree	22	− 0.56	0.01	3.97	0.29	0.60
Aerial insectivores, hawking	lnTree	22	1.29	0.04	5.70	0.78	0.39
Canopy-foraging guild	ln(Tree + TallShrub)	24	6.36	0.61	5.74	34.68	<0.0001
Tall-shrub foraging guild	lnTallShrub	22	5.31	0.53	6.49	22.22	<0.0001
Low-shrub foraging guild	lnLowShrub	34	1.01	0.02	5.00	0.78	0.38
Ground-foraging guild	lnHerb	34	− 7.76	0.02	9.13	0.68	0.42
Trunk insectivores	lnTree	22	0.07	0.001	1.88	0.03	0.88
Forest-generalist guild	lnTree	22	− 2.43	0.28	3.46	7.60	0.012

* *The r_s is Spearman rank correlation coefficient.*

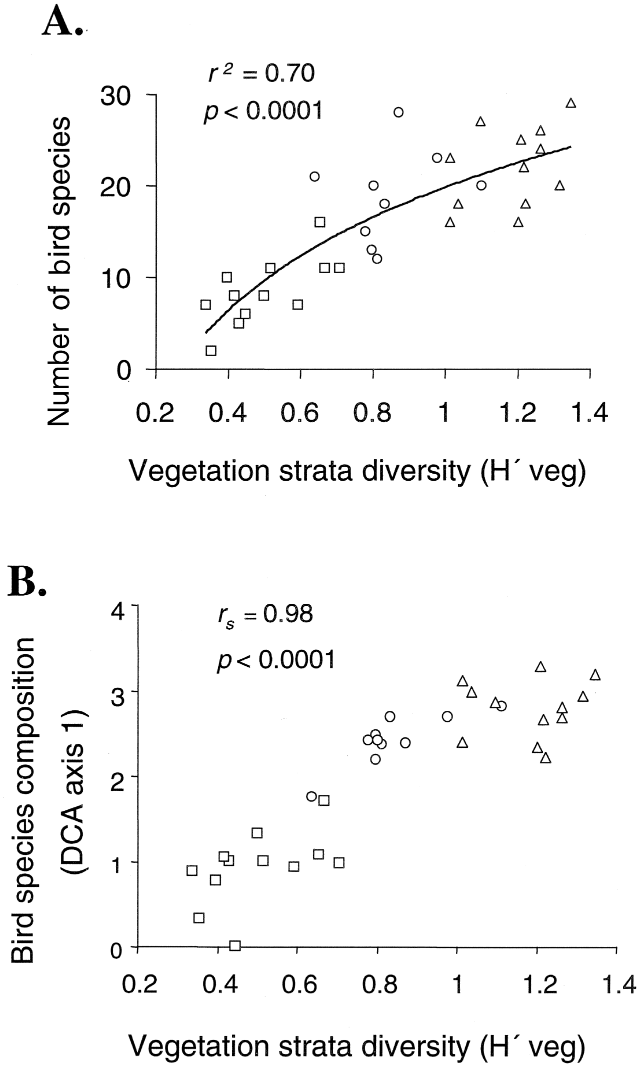

*Figure 1. Relation between (a) bird species richness and vegetation strata diversity (*H′ *veg) and (b) the detrended correspondence analysis (DCA) axis 1 gradient in bird species composition and vegetation strata diversity. The DCA site scores are given in units of average standard deviation of species turnover; four units is about one complete turnover. Cottonwood-shrub patches are denoted by triangles, cottonwood patches by circles, and shrub-steppe patches by squares.*

ated with cottonwood-shrub patches, spanning several taxonomic groups including warblers and sparrows and representing seven foraging microhabitat guilds (aerial insectivores, foliage gleaners throughout the shrub and canopy layers, and trunk insectivores). Six species from four guilds were significantly associated with the open tree canopies in the cottonwood patches, including the canopy-foraging Bullock's Oriole (*Icterus bullockii*) and forest generalist Common Grackle (*Quiscalus quiscula*; Table 3). Two ground foragers and two aerial insectivores (kingbirds) were also more abundant in the cottonwood patches. Three species, the Western Meadowlark (*Sturnella neglecta*), Red-winged Blackbird (*Agelaius phoeniceus*), and Rock Wren (*Salpinctes obsoletus*), were significantly associated with treeless shrub-steppe patches. Additional grassland or shrub-steppe birds recorded in grassland embedded within cottonwood and cottonwood-shrub sites included the Killdeer (*Charadrius vociferus*), Horned Lark (*Eremophila alpestris*), Chipping Sparrow (*Spizella passerina*), Clay-colored Sparrow (*S. pallida*), Brewer's Sparrow (*S. breweri*), Vesper Sparrow (*Pooecetes gramineus*), and Lark Sparrow (*Chondestes grammacus*).

Three of eight foraging guilds were significantly associated with the extent of cover of the vegetation strata to which the guild was most strongly tied (Table 2). The canopy-foraging guild, including Yellow Warblers, was significantly more abundant in patches with greater cover of trees and tall shrubs (Table 2 and Fig. 2a). Members of the tall shrub foraging guild, including American Goldfinches, Yellow-breasted Chats (*Icteria virens*), and Common Yellowthroats (*Geothlypis trichas*), also were significantly more abundant in patches with greater cover of their foraging substrate (Table 2; Fig. 2b). The forest-generalist guild, notably the Common Grackle, was negatively associated with tree cover (Table 2). There were no relationships between the abundances of the remaining five tested guilds (aerial and trunk insectivores, ground and low-shrub foraging guilds) and vegetation structure.

Density estimates were determined for 15 bird species. Table 3 reports densities in the habitat patch for which the association was strongest. Overall densities of these species were greater in cottonwood-shrub than in cottonwood patches (208.4 birds/10 ha [8.3% CV] and 140.5 birds/10 ha [7.3% CV], respectively; $t_{744} = 4.089$, $p < 0.001$). Densities of three individual species were significantly greater in cottonwood-shrub than in cottonwood patches (Yellow Warbler, 39.9 vs. 20.6 birds/10 ha, $t_{35} = 2.250$, $p < 0.05$; American Goldfinch, 22.5 vs. 6.4 birds/10 ha, $t_{24} = 2.106$, $p < 0.05$; Yellow-breasted Chat, 13.3 vs. 1.7 birds/10 ha, $t_{24} = 2.075$, $p < 0.05$).

Geomorphic Change, Vegetation Establishment, and Grazing History

Forest patches were restricted to alluvial surfaces, including channel islands, narrow flood deposits between the channel and adjacent upland, and tributary fans. Half of all cottonwood-shrub patches and one cottonwood patch were located on channel islands. The remaining forest patches were on flood deposits, except for site 210.9, which was located on a tributary fan. Shrub-steppe patches included narrow alluvial surfaces and adjacent uplands.

Table 3. Bird species with strong association to specific habitat patches.[a]

		Importance value (IV) for analysis of all habitats				Importance value (IV) for analysis of forest habitats			
Habitat type and bird species	Foraging guild[a]	shrub-steppe	cotton-wood	cotton-wood-shrub	p[b]	cotton-wood	cotton-wood-shrub	p[b]	Density[c] (% CV)
Cottonwood-shrub									
Yellow-breasted Chat (*Icteria virens*)	5	0	7	75	0.00	7	76	0.00	11.3 (16.7)
Cedar Waxwing (*Bombycilla cedrorum*)	4	0	4	66	0.00	4	66	0.01	10.8 (30.3)
American Goldfinch (*Carduelis tristis*)	5	2	25	62	0.00	26	67	0.01	22.5 (17.4)
Yellow Warbler (*Dendroica petechia*)	4	1	38	59	0.00	39	61	0.01	39.9 (11.0)
Black-capped Chickadee (*Poecile atricapilla*)	4	0	8	55	0.00	8	55	0.06	—
House Wren (*Troglodytes aedon*)	5	0	39	52	0.00	39	52	>0.10	18.1 (19.1)
American Redstart (*Setophaga ruticilla*)[d]	4	0	0	50	0.00	0	50	0.01	—
Common Yellowthroat (*Geothlypis trichas*)	5	13	17	50	0.02	22	64	0.04	13.1 (14.7)
American Robin (*Turdus migratorius*)	9	0	30	50	0.01	31	51	>0.10	12.0 (20.0)
Downy Woodpecker (*Picoides pubescens*)[d]	8	0	4	48	0.00	4	48	0.05	—
Brown-headed Cowbird (*Molothrus ater*)	7	0	11	47	0.01	11	47	>0.10	—
Least Flycatcher (*Empidonax minimus*)[d]	3	0	24	45	0.02	24	45	>0.10	14.5 (26.5)
Spotted Towhee (*Pipilo maculatus*)	6	4	30	45	0.03	35	52	>0.10	8.5 (21.5)
Lazuli Bunting (*Passerina amoena*)	6	9	8	42	0.06	10	51	0.08	8.6 (30.3)
Song Sparrow (*Melospiza melodia*)[d]	6	0	1	38	0.01	1	38	0.07	—
Black-headed Grosbeak (*Pheucticus melanocephalus*)	4	0	8	37	0.02	8	37	>0.10	—
Red-eyed Vireo (*Vireo olivaceus*)[d]	4	0	0	25	0.09	0	25	>0.10	—
Cottonwood									
Bullock's Oriole (*Icterus bullockii*)	4	0	65	26	0.00	65	26	0.01	12.7 (25.4)
Common Grackle (*Quiscalus quiscula*)	8	1	59	7	0.00	63	7	0.01	8.8 (38.2)
Mourning Dove (*Zenaida macroura*)	7	1	57	20	0.00	61	22	0.07	12.2 (35.1)
Northern Flicker (*Colaptes auratus*)	7	1	51	35	0.02	54	37	>0.10	8.1 (31.0)
Eastern Kingbird (*Tyrannus tyrannus*)	3	5	50	29	0.01	57	33	>0.10	9.8 (29.0)
Western Kingbird (*Tyrannus verticalis*)	3	0	33	2	0.05	34	2	>0.10	—
Shrub-steppe									
Western Meadowlark (*Sturnella neglecta*)	6	54	33	4	0.01	70	9	0.01	—
Red-winged Blackbird (*Agelaius phoeniceus*)	7	41	13	8	0.07	30	17	>0.10	—
Rock Wren (*Salpinctes obsoletus*)	1	34	1	4	0.06	2	13	>0.10	—

[a] *Foraging guilds correspond to those listed in Methods.*

[b] *The* p *represents the probability that the IV of a randomized trial equals or exceeds the observed maximum. Species with* $p < 0.10$ *are considered significantly associated with habitat type.*

[c] *Densities of birds in associated habitat type (birds/10 ha [% CV]).*

[d] *Species of concern in Montana (Montana Partners in Flight 2000).*

Vegetation strata diversity (H' veg) was significantly greater in patches that had experienced geomorphic change over the last 35 years in the form of sediment accretion ($t_{33} = 3.31, p = 0.002$). Sediment accretion occurred in 8 of 12 cottonwood-shrub forest patches, 5 of 10 cottonwood patches, but none of 12 shrub-steppe patches. Vegetation strata diversity (H' veg) was also significantly greater in patches with recent woody vegetation establishment ($t_{20.7} = -3.63, p = 0.002$) and in ungrazed patches ($t_{19.6} = 3.75, p = 0.001$). Woody vegetation establishment was observed in 6 of 12 cottonwood-shrub patches and in 1 of 10 cottonwood patches. Five of 12 structurally complex cottonwood-shrub patches received no livestock grazing, whereas all cottonwood and shrub-steppe patches were grazed.

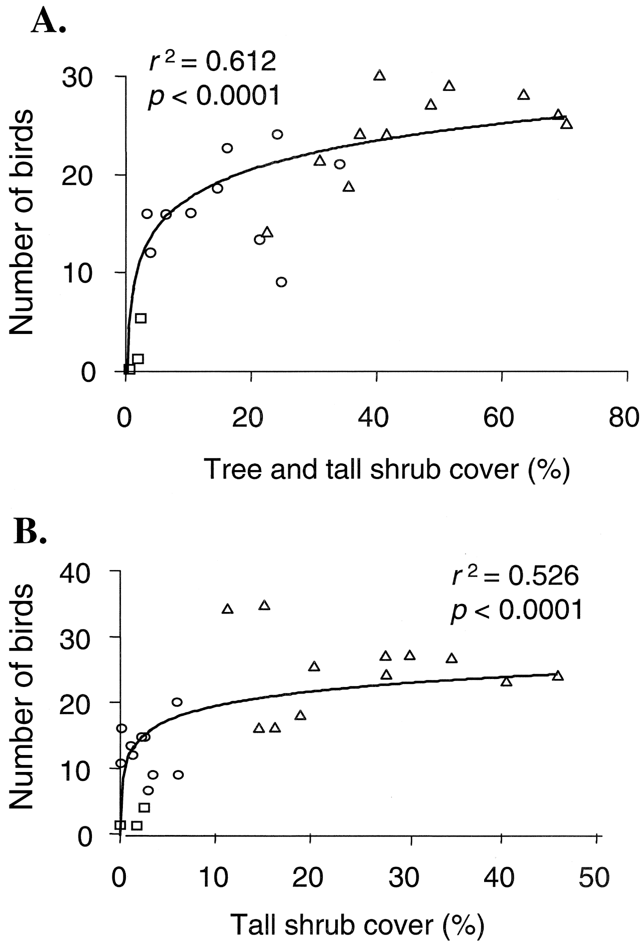

Figure 2. Relation between (a) bird abundance (number of birds) in the canopy foraging guild versus tree and tall-shrub cover and (b) bird abundance (number of birds) in the tall-shrub foraging guild versus tall-shrub cover.

Discussion

Conservation of terrestrial birds depends on a clear understanding of their habitat requirements and the physical and biotic processes that create and maintain those habitats (Askins 2000). Riparian or bottomland forests provide particularly important habitat for birds. From humid to arid regions, bottomland forests typically support higher bird densities than adjacent uplands (Szaro & Jakle 1985; Lugo et al. 1990; Knutson et al. 1996). It is generally recognized that the biological diversity associated with such landscape features is in part a function of vegetation patch dynamics, driven by specific disturbance regimes (Meffe & Carroll 1997). Riparian forests are structured by the distinctive fluvial geomorphic processes and hydrologic conditions found on bottomlands. In response to temporally variable flows, streams move across their flood plains, removing existing plant and animal communities and initiating new ones. Infrequent, high-power floods create disturbance patches and topographic diversity through large-scale erosion and deposition of sediments. Against these larger-scale geomorphic features, more-frequent, low-power floods produce smaller-scale, spatially complex hydrologic gradients that control patterns of vegetation establishment and successional processes. The presence of water and nutrient-rich soils, and the interspersion of a diversity of successional aquatic and terrestrial biotic communities, make bottomland forests, particularly in arid regions, more productive and biologically diverse than surrounding uplands (Brinson 1990; Knutson et al. 1996).

In contrast to the positive role of fluvial geomorphic processes in supporting biological diversity in riparian ecosystems, some anthropogenic disturbance factors contribute to the decline or elimination of certain species. In the arid southwestern United States, extensive loss and ecological simplification of riparian ecosystems has resulted primarily from alteration of natural hydrologic regimes, forest clearing, and chronic livestock grazing. These changes have led to declines, endangerment, and loss of a wide array of riparian-dependent species, including a number of bird species (Askins 2000; Stromberg 2001). Thus, efforts to conserve, restore, and manage the distinctive biological diversity of riparian ecosystems must rest upon a clear understanding of the primary physical and biological processes that structure and maintain that diversity, as well as on the root causes of riparian degradation (Briggs 1996).

In our study, flow-related geomorphic change, subsequent establishment and succession of woody vegetation, and livestock grazing were all significantly related to differences in vegetation structure across riparian vegetation patches. Recent geomorphic change in the form of lateral and vertical sediment accretion, in conjunction with the establishment and succession of woody vegetation (primarily cottonwood and willow) on these new alluvial surfaces, was correlated with a higher structural complexity of vegetation. Correspondingly, the diversity and abundance of breeding bird communities increased significantly with increases in the structural complexity of habitat patches.

The initiation of riparian succession in arid environments of western North America typically begins with the establishment of species of cottonwood and willow on freshly deposited alluvial substrates (Johnson et al. 1976; Rood & Mahoney 1990; Scott et al. 1996; Merigliano 1998). In portions of the northern Great Plains, succession terminates in grassland in the absence of intervening fluvial disturbance (Hansen et al. 1991; Boggs & Weaver 1994; Friedman et al. 1997). The structural diversity of semiarid riparian forests reaches a maximum after approximately 90 years with the development of a mature cottonwood canopy and shrub understory. With the attrition of mature cottonwoods, structure declines as the stand gives way to shrubs and ultimately upland grasses (Boggs & Weaver 1994). A comparison of photographs within the study reach from 1903 and 2000 (Fig. 3a & 3b) illustrates the temporal changes in the pattern and extent of riparian forest patches resulting from geomorphic change and riparian succession. These photographs depict (1) the relocation and expansion of a channel island by lateral and vertical sediment accretion and development of a small cottonwood-shrub patch and (2) the reduction in the size of a cottonwood patch on a narrow, geomorphically inactive alluvial surface. The progressive loss of trees from portions of this surface represents succession from riparian forest to shrub and grassland (Boggs & Weaver 1994) in the absence of recent geomorphic activity and vegetation establishment.

Long-term grazing was correlated with lower structural complexity and lower bird diversity and abundance. Measured structural differences between cottonwood-shrub, cottonwood, and shrub-steppe patches were significantly related to grazing history. Studies from other riparian systems indicate that long-term overgrazing by livestock can alter riparian vegetation succession by limiting reproduction and simplifying vegetation structure and composition (Knopf & Cannon 1982; Kauffman & Krueger 1984; Taylor 1986; Schultz & Leininger 1990). Within the study reach, Auble and Scott (1998) documented short-term decreases in the survival of cottonwood and willow seedlings caused by grazing. Rood et al. (1999) observed an apparent lack of sandbar willow (*S. exigua*) reproduction in heavily grazed areas along the Bow River in southern Alberta. Further, grazing may accelerate the succession of riparian forest to shrub- or grass-dominated associations by reducing or eliminating the establishment of tree and shrub species such as cottonwood, willow, green ash, boxelder, and other associated woody species (Szaro & Pase 1983; Hansen et al. 1991; Boggs & Weaver 1994).

Statistical inferences regarding the extent to which interactions between geomorphic change and grazing influence patch structure were limited by sample size, but our data suggest the importance of such an interaction. For example, the sites with the most recent woody vegetation establishment were those that were geomorphically active and ungrazed. Geomorphically active sites that were grazed had an intermediate amount of woody vegetation establishment. Sites that were geomorphically inactive and grazed had no woody vegetation establishment, and six of these sites had lost tree cover over the last 35 years.

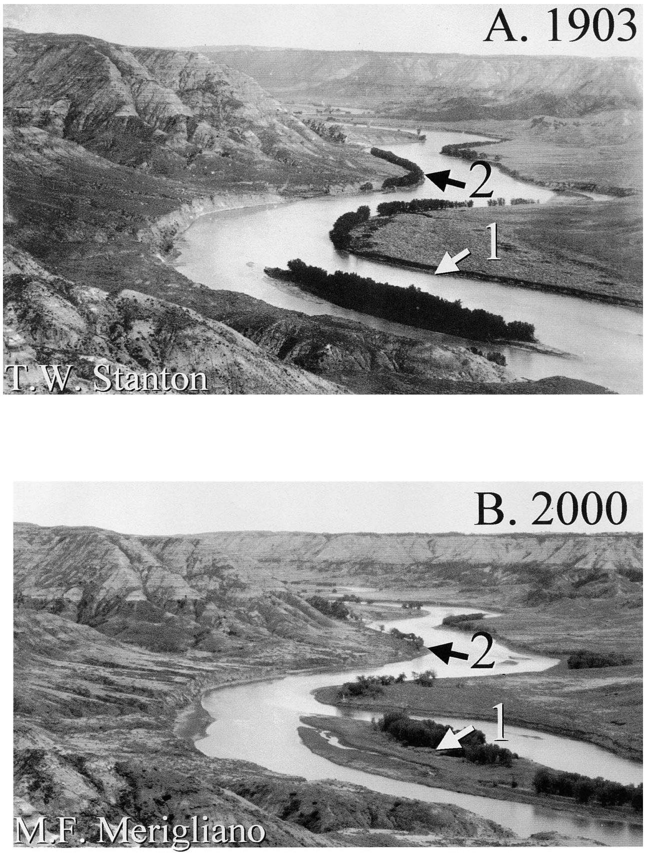

Figure 3. Paired photographs of sampled habitat patches from within the study reach along the upper Missouri River, Montana, from (a) 1903 and (b) 2000. The white arrow indicates the location of cottonwood-shrub patch in the 2000 photo at river kilometer 151.7, and the black arrows indicate a cottonwood patch present in both photos at river kilometer 153.3. The 1903 photo was taken by T. W. Stanton (U.S. Geological Survey photo archives), and the 2000 photo was taken by M. F. Merigliano.

The structural complexity of forests can have important influences on avian abundance and composition (MacArthur et al. 1962; Willson 1974; Brinson et al. 1981). In our study, structurally complex cottonwood-shrub forest patches hosted a more diverse community of birds at greater abundances than cottonwood forest or treeless shrub-steppe patches. These relationships held regardless of the bird metric used but were most striking for canopy and tall-shrub foraging guilds. Increased grazing pressure in riparian areas leads to decreased avian abundance and diversity (Taylor 1986; Ammon & Stacey 1997; Dobkin et al. 1998; Belanger & Picard 1999), but not all bird species are affected by grazing in the same way. Eastern Kingbirds may be found in greater densities in heavily grazed areas, whereas American Redstarts, Song Sparrows, Yellow-breasted Chats, and Common Yellowthroats are found in greater densities in ungrazed areas (Mosconi & Hutto 1982; Sedgwick & Knopf 1987; this study). Unlike landscape attributes of the Snake River in Idaho, which were influential in determining bird distributions (Saab 1999), the landscape surrounding the two forest patch types in our study was fairly uniform (Table 1) and therefore of no predictive value.

Conclusions and Conservation Implications

Our results reinforce the central importance of fluvial geomorphic processes to bird species diversity and abundance in riparian forests (Knutson & Klaas 1997; Lock & Naiman 1998) and begin to describe the specific mechanisms underlying these relationships. We suggest that structural differences between cottonwood-shrub, cottonwood, and shrub-steppe patch types reflect local geological controls on the frequency and extent of cottonwood and willow establishment, subsequent riparian vegetation succession, and grazing pressure. The development of these patch differences is presented conceptually in Figure 4. Cottonwood-shrub patches develop in less constrained, geomorphically active channel reaches, where cottonwood and willows establish and grow adjacent to existing stands on newly created alluvial surfaces formed by lateral and vertical accretion. Vegetation succession and additional vertical sediment accretion in the absence of grazing results in a structurally diverse habitat with a relatively diverse assemblage of birds (Fig. 4a). Cottonwood patches develop on elevated alluvial deposits in constrained channel reaches following infrequent large

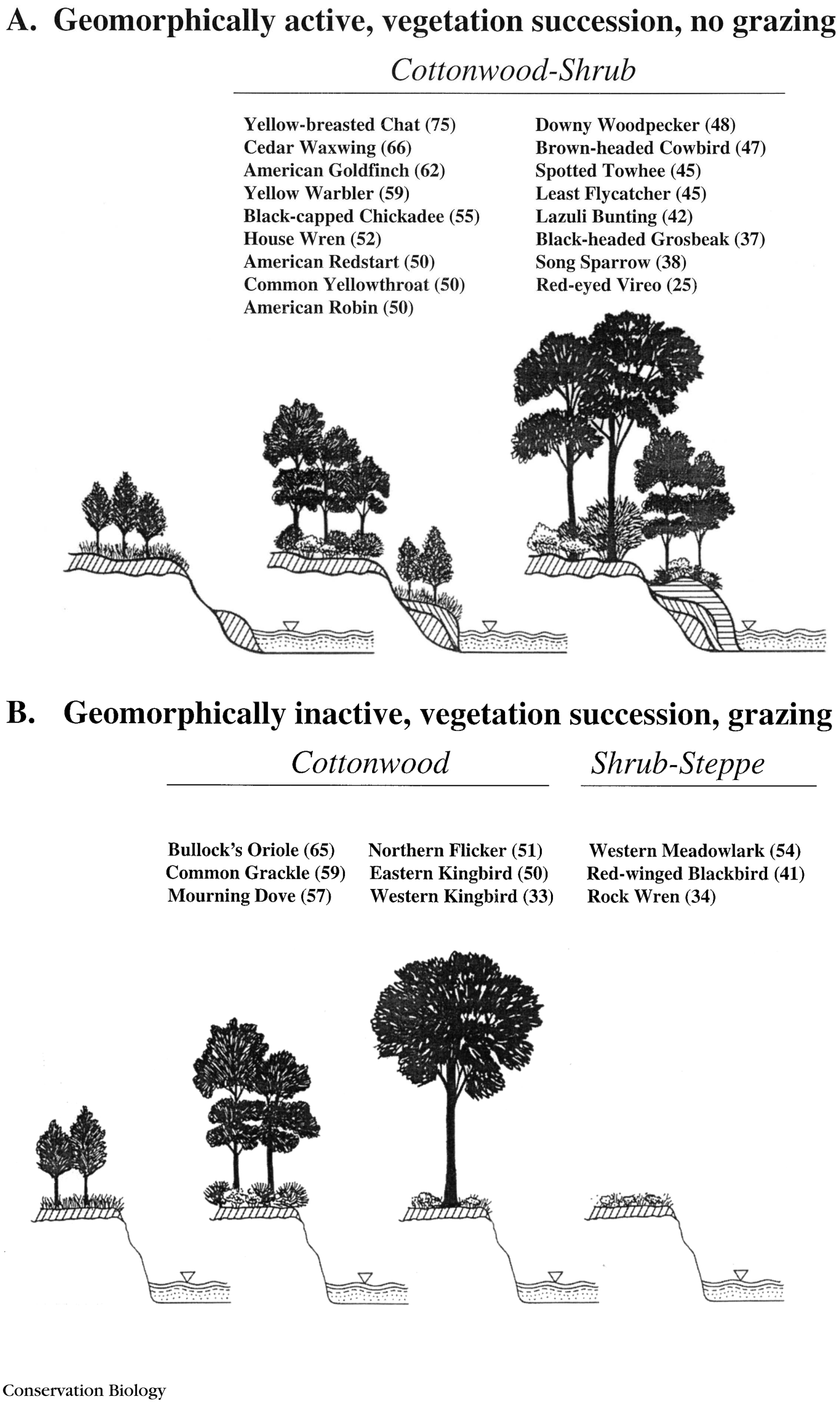

Figure 4. Conceptual diagram of the development of structurally distinct riparian habitat patches along the upper Missouri River, Montana. Following infrequent large floods, cottonwoods and willows initially become established on alluvial deposits (right oblique shading). (a) In geomorphically active reaches, vegetation succession in the absence of grazing and new cottonwood-willow establishment on adjacent accreting surfaces (additional shading) leads to the development of cottonwood-shrub patches. (b) In geomorphically inactive reaches, vegetation succession in combination with grazing leads to the development of cottonwood and ultimately shrub-steppe patches. For both (a) and (b), bird species (importance value) associated with the three patch types are listed, and inverted triangles indicate water-surface elevation.

floods. A lack of subsequent geomorphic change, in combination with vegetation succession and chronic livestock grazing, results in a structurally simplified habitat patch and reduced bird diversity. Finally, cottonwood patches succeed to shrub-steppe as mature cottonwoods are lost, without replacement, from long-stable alluvial surfaces. Loss of forest structure is accompanied by additional losses in bird diversity (Fig. 4b).

In their journey up the Missouri River in the spring of 1805, Lewis and Clark described the riparian forest patches in this region of the northern Great Plains as being "the haunts of innumerable birds" (Coues 1893). Their observations provide an important historical backdrop to the conservation implications of our work. Preserving the breeding bird abundance and diversity characteristic of riparian forests of this arid region will require the maintenance of flows and associated geomorphic processes responsible for the establishment and survival of woody vegetation (Scott et al. 1997; Bovee & Scott 2002) in combination with management of livestock grazing. Our conclusions are consistent with observations from rivers in the southwestern United States, where extensive modification of natural flow regimes, grazing, and forest clearing have led to the loss and simplification of native riparian forests and the decline and endangerment of riparian-dependent bird species (Briggs & Cornelius 1998; Askins 2000; Stromberg 2001).

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