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RECENT BIODIVERSITY PATTERNS IN THE GREAT PLAINS: IMPLICATIONS FOR RESTORATION AND MANAGEMENT

Carolyn Hull Sieg

USDA Forest Service, Rocky Mountain Research Station
501 E St. Joseph Street
Rapid City, SD 57701
csieg@fs.fed.us

Curtis H. Flather

USDA Forest Service, Rocky Mountain Research Station
21.50 Centre Ave., Bldg A, Suite 361
Fort Collins, CO 80526

and

Stephen McCanny

Parks Canada
Western Canada Service Center
Winnipeg, Manitoba R3B 3E8 Canada

ABSTRACT- Ecosystem, species and genetic dimensions of biodiversity have eroded since widespread settlement of the Great Plains. Conversion of native vegetation in the region followed the precipitation gradient, with the greatest conversion in the eastern tallgrass prairie and eastern mixed-grass types. Areas now dominated by intensive land uses are "hot spots" for exotic birds. However, species of all taxa listed as threatened or endangered are well-distributed across the Great Plains. These species are often associated with special landscape features, such as wetlands, rivers, caves, sandhills and prairie dog towns. In the long run, sustaining biodiversity in the Great Plains, and the goods and services we derive from the plains, will depend on how successfully we can manage to maintain and restore habitat variation and revitalize ecosystem functioning. Public policy and legislation played a significant role in the degradation of native habitats in the region. Both policy and legislation will be needed to reverse the degradation and restore critical ecosystem processes.

Introduction

The sustainability of the Great Plains can be assessed in many different ways. A focus on agricultural production may be adequate in some respects. However, this assumes that economic production is the only relevant indicator of environmental change on the Great Plains. A more inclusive approach, and one adopted for describing the sustainability of forest landscapes (Coulombe 1995), is to include measures of biodiversity. “Biodiversity” refers to “the variety of life and its processes,” and encompasses ecosystems, communities, species and genes (The Keystone Center 1991). Maintaining biodiversity is important, not only for aesthetic and cultural reasons but also for the goods and services that humans derive from ecosystems (Daily 1997; Pimentel et al. 1997). Rangelands, for example, play an important role in maintaining the atmospheric composition (Sala and Paruelo 1997) and filtering non-point source pollution (Shogren and Crocker 1995). Yet, most of the world’s mesic rangelands have been converted to agricultural land (Sala and Paruelo 1997).

In the USA, more than half of the ecosystems determined to be critically endangered (> 98% of the area1 extent of the ecosystem has been lost or ecologically degraded) are grasslands and an additional 24% are shrublands (Noss et al. 1995). In the Great Plains, the flat topography and nutrient-rich soils make these lands valuable for cultivation. Increasing settlement of the region, combined with public policies and legislation in the United States (e.g., Homestead Act of 1862) and Canada (Dominion Lands Act of 1908) that encouraged cultivation, accelerated the loss of native vegetation (Ostlie et al. 1997). In the late 1890s wetland drainage legislation in both countries encouraged the cultivation of additional acreages (Krenz and Leitch 1993). Until 30 years ago, laws and regulations governing development of streams and rivers favored flood control, power generation, navigation, and waste disposal, often to the detriment of maintaining functioning riverine systems (Rabeni 1996).

We define the Great Plains as the central North American grassland biome, extending from the boreal forests of Manitoba, Saskatchewan and Alberta south to the northern edge of the arid semi-deserts in southern Texas (Fig. 1). It is bordered by the foothills of the Rocky Mountains on the west and extends east to the tallgrass prairie of western Minnesota, Iowa and Missouri. In the USA portion of the region, rangeland comprises 42% of the land area, followed by croplands at 33%; most (95%) of the land is privately owned (Natural Resources Conservation Service 1992). In the Canadian

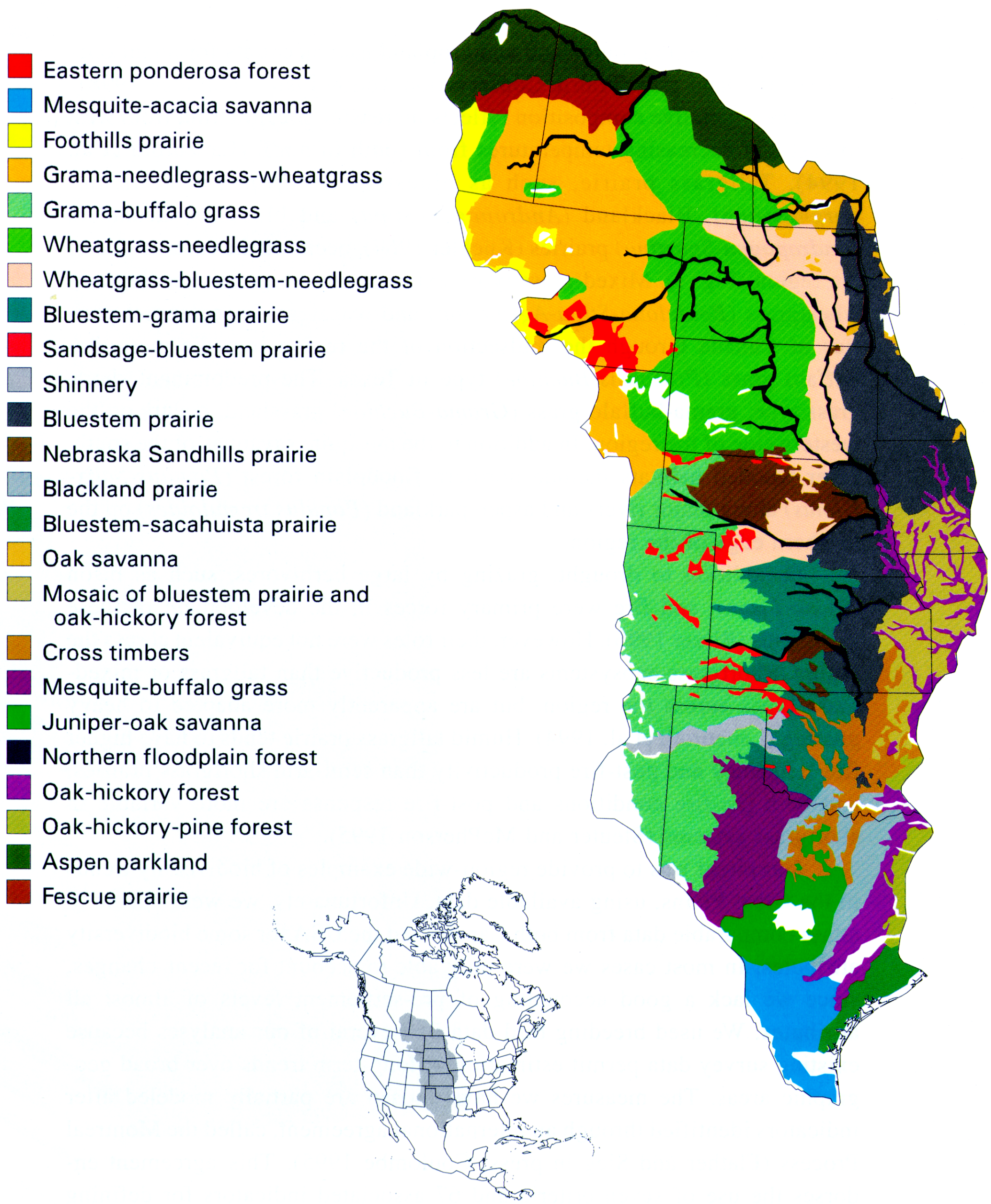

Figure 1. Major vegetation types (areal extent ≥ 20 thousand km²) within the Great Plains. Vegetation types within the USA are based on Küchler's 1966 map of potential natural vegetation (US Geological Survey 1970). Canadian vegetation types are based on Achuff (1994), Acton et al. (1998) and Canada (1974).

portion of the region, rangeland and cropland each accounts for about one-third of the land area (Prairie Conservation Action Plan Committee 1998).

The vegetative composition reflects increasing precipitation from west to east and decreasing temperatures from south to north (Lauenroth et al. 1994). Tallgrass prairie, such as bluestem *(Andropogon-Panicum-Sorghastrum)*, Blackland *(Andropogon-Stipa)* and bluestem-sacahuista *(Andropogon-Spartina)* (Küchler prairies 1964), occur on the eastern side of the region (Fig. 1). Mixed-grass types extend from the grama-needlegrass-wheatgrass *(Bouteloua-Stipa-Agropyron)* and wheatgrass-needlegrass prairies of Canada through the midsection of the region into the mesquite-buffalo grass *(Prosopsis-Buchloe)* type in Texas. The predominant shortgrass type, grama-buffalo grass *(Grama-Buchloe)* grassland, occurs on the western side of the region. In addition to the mesquite savannas of the south, other wooded habitats include northern floodplain forest *(Populus-Salix-Ulmus)* along major rivers and aspen parkland *(Populus tremuloides)* on the northern edge of the region.

In addition to drought, grazing by large herbivores, such as bison *(Bison bison)*, and fire were primary forces in the development of these grasslands (Risser 1996). However, their roles were not equivalent across the region. Shortgrass ecosystems are less productive than tallgrass or mixed-grass types across the region, but are apparently more adapted to heavy grazing (Lauenroth et al. 1994). Humid tallgrass prairie tends to have higher fire frequency and post-fire productivity than semi-arid shortgrass prairies, and both pre-fire conditions and post-fire response are more variable in shortgrass systems (Steuter and McPherson 1995).

Our intent was to provide region-wide examples of biodiversity trends in the Great Plains, using available data. Unfortunately, we were unable to attain comparable data from both Canada and the USA for some biodiversity attributes. In most cases we were only able to account for recent changes, since we lack a good accounting of pre-settlement, levels of almost all attributes. We used breeding bird data for several of our analyses because existing survey data permit estimation of long-term trends over broad geographic areas. The measures we have chosen are partially modeled after indicators identified through an international agreement, called the Montreal Process (Flather and Sieg in press; Coulombe 1995). This agreement endorses the use of seven criteria and 67 associated indicators for defining sustainable management of forests at a national scale. The biodiversity criterion identifies three aspects as being important to sustainability: ecosystem, species and genetic diversity. The ecosystem measures we selected include area of vegetation types, and two measures of fragmentation: patch size and amount of edge. We also discuss the ability of remaining patches of native vegetation to support biodiversity. For species diversity measures we selected: species richness of breeding birds, proportion of bird species that are exotic, and the geographic distribution of all taxa of threatened and endangered species. For genetic diversity, we based our examples on surrogate measures proposed by the Montreal Process (see Coulombe 1995): species whose ranges have been greatly reduced, and proportion of breeding bird species with declining populations.

Ecosystem Diversity

Ecosystem diversity is often measured by the area1 extent of various vegetation types in a given region (Hunter 1991). By tracking the remnant area of specific vegetation types, we can get a coarse indication of the variety of habitats encountered by Great Plains species. Maintaining enough area of each vegetation type is critical to sustaining the complex of communities, the number and kinds of organisms supported, the movement of those organisms, and the pattern of disturbances (Saunders et al. 1991).

Area of Vegetation Types

The most recent comprehensive assessment of the loss of natural vegetation since European settlement within the United States was done by Klopatek et al. (1979a). Their analysis compared county-by-county landuse in the "Conservation Needs Inventory" 1967 database (USDA 1971) with Küchler's 1966 map of potential natural vegetation (US Geological Survey 1970). Native vegetation in Great Plains counties has been converted to other land uses to a high degree (Fig. 2). The losses of native vegetation of this region were highest in tallgrass types, such as bluestem and bluestem-sacahuista prairie (Table 1, also see Fig. 1). Losses of eastern mixed-grass types, such as wheatgrass-bluestem-needlegrass and bluestem-grama, plus northern floodplain forests were also high. Nebraska Sandhills prairie and eastern ponderosa forest had conversion rates of less than 10%.

Although not well quantified, there is evidence that additional hectares of many Great Plains types have been converted to other uses since Klopatek et al.'s (1979a) assessment. The Prairie Conservation Action Plan Committee (1998) estimates that two-thirds of the Canadian prairie has been converted to cropland. For the tallgrass prairie, Loveland and Hutcheson (1995)

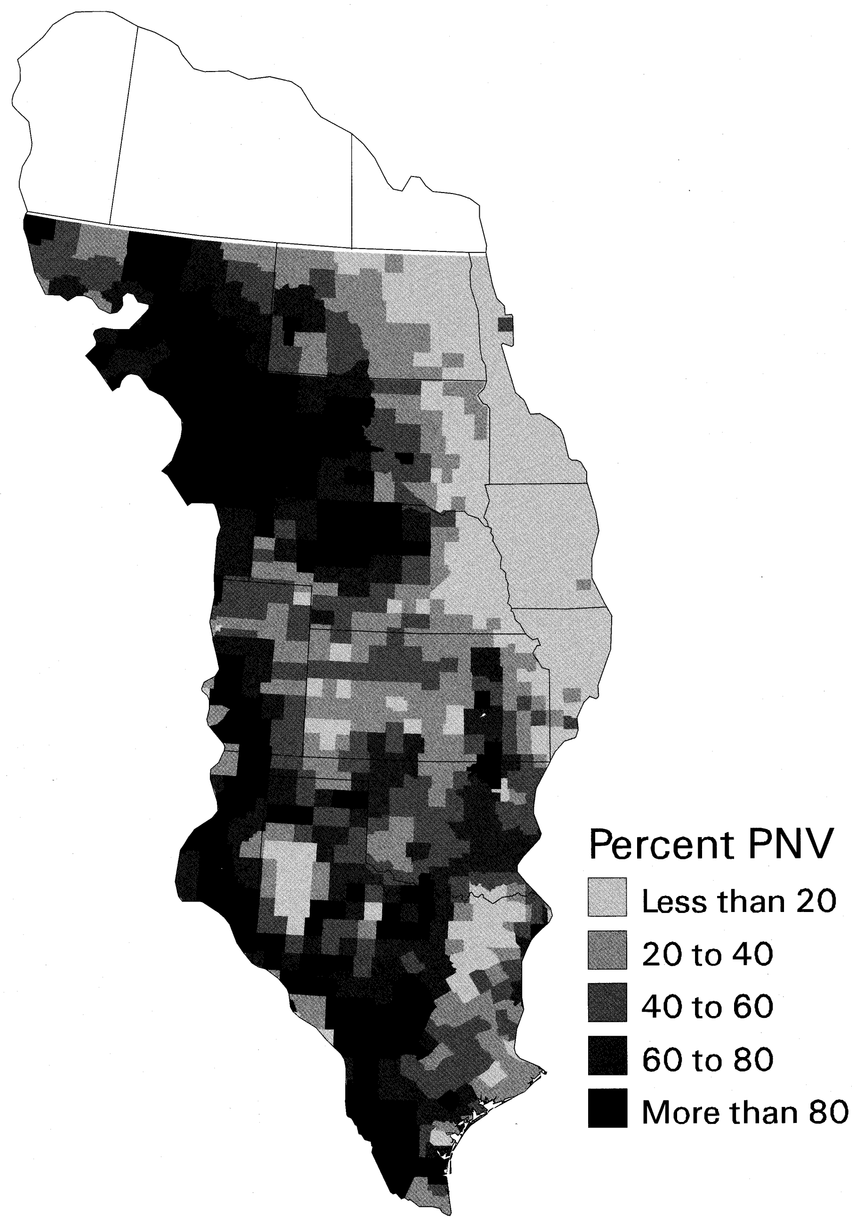

Figure 2. Percent potential natural vegetation (PNV) remaining within counties comprising the Great Plains. Adapted from Klopatek et al. (1979b).

TABLE 1

ESTIMATED LOSSES OF SELECTED VEGETATION TYPES IN THE GREAT PLAINS, BASED ON KLOPATEK ET AL.'S (1979A) ASSESSMENT IN THE USA, PLUS MORE RECENT ESTIMATES.

Biome	Estimated loss (%)	
Potential natural vegetation type	Klopatek et al. (1979a)[a]	Other estimates
Tallgrass Prairie		
bluestem prairie	85%	90% [b]
bluestem-sacahuista prairie	76%	
sandsage-bluestem prairie	58%	
Mixed-grass and transitional types		76%[b]
mesquite-buffalo grass	27%	42%[c]
wheatgrass-bluestem-needlegrass	69%	83 %[c,d]
bluestem-grama prairie	65%	76%[d], 92%[c]
wheatgrass-needlegrass	36%	39%[c], 33%[d]
grama-needlegrass-wheatgrass	24%	7%[d]
Nebraska Sandhills Prairie	6%	28%[c], 72%[d]
fescue prairie		95%[b]
Shortgrass		
grama-buffalo grass	45%	26%[d]
Forested types		
northern floodplain forest	69%	
eastern ponderosa pine	4%	

[a]Estimates are based on a comparison of “Conservation Needs Inventory” landuse data from 1967 with Küchler's 1966 map of potential natural vegetation types in the USA (US Geological Survey 1970).
[b] Gauthier and Henry (1989), for Canada.
[c] Bragg and Steuter (1996), estimates based on land-cover characteristics database (US Geological Survey 1993) by Küchler (1964) potential natural vegetation types in the USA.
[d] Loveland and Hutcheson (1995), estimates based on US Geological Survey land-cover data (Loveland et al. 1991) by Küchler (1964) potential natural vegetation types in the USA.

estimated a notable reduction in bluestem type (Table 1), using remotely sensed land-cover data collected in 1990 (Loveland et al. 1991). For states containing the majority of the remnant tallgrass prairie, the amount of remaining native vegetation varies from <1% in North Dakota to 15% in South Dakota (Samson and Knopf 1994) In Canada, the bluestem prairie has been almost completely eradicated (Gauthier and Henry 1989). The remaining prairies contain a smaller proportion of typical vegetation types and a larger proportion of atypical types (Ostlie et al. 1997).

For mixed-grass prairie, Samson and Knopf (1994) estimated declines ranging from 60-99% for the Canadian provinces and states for which statistics were available. Fescue (*Festuca*) prairie from the Aspen parkland region on the northern edge of the Great Plains has been nearly eradicated (Gauthier and Henry 1989) (Table 1). Other mixed-grass types in Saskatchewan and Alberta fared better (Gauthier and Henry 1989). Bragg and Steuter (1996) used remotely sensed land-cover data of mixed-grass types, employing techniques similar to Loveland and Hutcheson's (1995). Both of these 1990 assessments suggest that especially eastern mixed grass types have declined (Table 1). However, the contrasting estimated losses of Nebraska Sandhills prairie, 28% by Bragg and Steuter's estimate and 72% according to Loveland and Hutcheson (1995), point out the problem of smaller tracts being masked at the 1-km2 resolution that these more recent analyses used (Bragg and Steuter 1996). In contrast to the point-based estimates Klopatek et al. (1979a) used, the larger scale assessments involve categorizing grids with intermingled cropland and rangeland as one type or the other, and invariably lead to different estimates.

For shortgrass prairie, more recent estimates indicate that these arid types remain among the region's most intact. However, the problem associated with using a 1-km^2 scale is apparent in Loveland and Hutcheson's (1995) estimate that 26% of the grama-buffalo grass type has been converted, compared to Klopatek et al.'s (1979a) county-by-county estimate of 45%. Weaver et al. (1996) estimated that cultivation has claimed 40% of the shortgrass type; however, their definition of shortgrass included the grama-needlegrass-wheatgrass type, which other authors classify as mixed-grass.

Fragmentation

Decreasing patch size and increasing edge habitat are indications of fragmentation, and they affect many ecological processes (Forman 1995). Thus, we quantified patch size and rangeland edge, using digital Land Use and Land Cover data from the US Geological Survey (1987). We centered a circle with a radius of 19.7 km on each Breeding Bird Survey route (area ~ 1200 km^2 per route) within the USA portion of the Great Plains (Breeding Bird Survey described below). We chose a radius of half the length of a Breeding Bird Survey route to insure that each circle would contain the whole route. We used high-altitude aerial photographs, most at scales less than 1:60,000 to digitize and transfer land use and land cover data to 1:250,000 base maps in grid format (US Geological Survey 1987). Each of the grid cells (200 X 200 m) was classified into one of nine cover classes: urban/built-up land, agricultural land, rangeland, forest, water, wetlands, barren land, tundra and perennial snow/ice, using the criteria of Anderson et al. (1976). Field verifications indicated that these major land uses were interpreted with >95% accuracy (Fitzpatrick-Lins 1980). We measured average patch size as a weighted mean with area of the patch serving as the weights (see Turner et al. 1996). Total edge was measured as the length of the edges between non-converted types (rangeland, forest or wetlands) and all converted land types (urban or agricultural land) in each circle.

These analyses substantiated that the conversion of native rangeland to agricultural land has resulted in a gradient of rangeland patch size in the USA portion of the Great Plains that parallels the moisture gradient (Fig. 3). The largest remaining tracts of rangeland are in the west, with smaller patches in the east. Because intermediate levels of conversion are associated with maximum edge, the amount of rangeland edge was greatest in the central portion of the region (Fig. 4).

The size of an area can have a pronounced effect on the viability of species and on ecological processes. In most cases, representation of ecosystem types in small units cannot be considered adequate to preserve the functioning of those systems (Noss et al. 1995). Processes that are affected by habitat fragmentation include: dispersal, pollination, exotic species invasion, spread of fire, predation rate, and adaptation to climate changes (Saunders et al. 1991; Peters 1992; Rathcke and Jules 1993; Arenz and Joern 1996; Steinauer and Collins 1996; Robinson 1998). Fragmentation *per se*, however, is not necessarily associated with decreased biodiversity. Since some fragmentation increases the area of ecotones, it may actually contribute to higher species diversity (Hobbs and Huenneke 1992). Therefore, species richness may increase initially as a consequence of fragmenting large grasslands (Simberloff and Gotelli 1984). Further, by spreading the risk associated with environmental disturbances among subdivided populations, population persistence may actually increase under some level of fragmentation (Fahrig and Paloheimo 1988; Hof and Flather 1996).

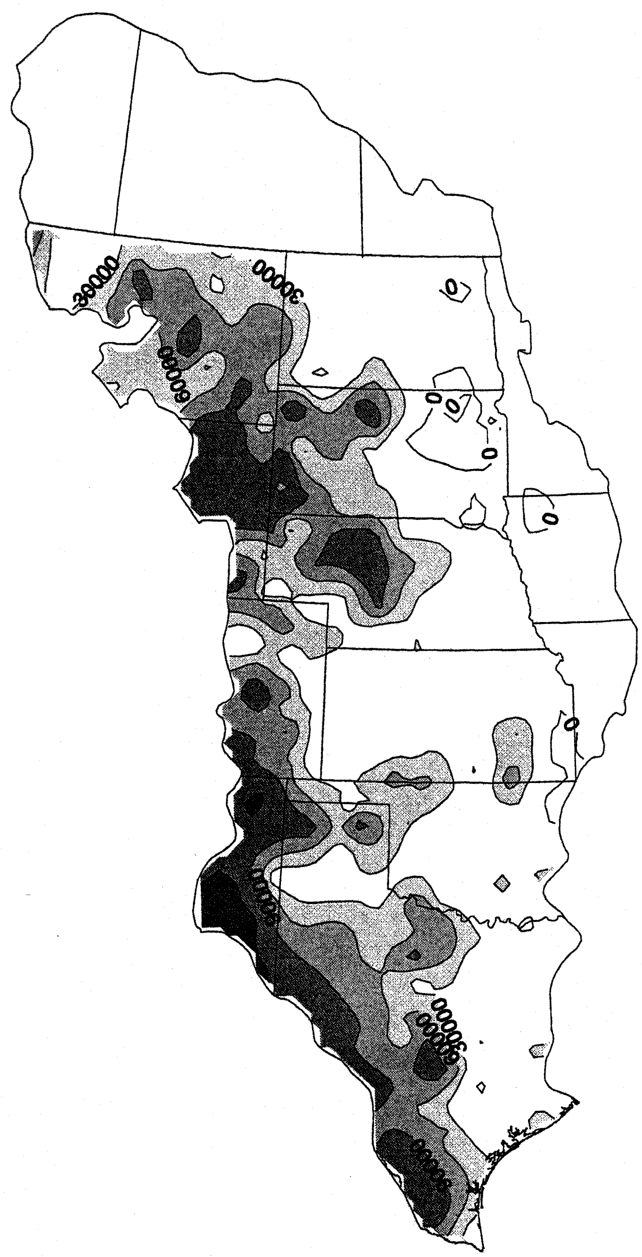

Figure 3. Weighted mean patch size (ha) calculated from Land Use Land Cover data centered on Breeding Bird Survey routes. Plots were generated by kriging (Cressie 1991) mean patch size estimates across all Breeding Bird Survey routes in the USA portion of the Great Plains.

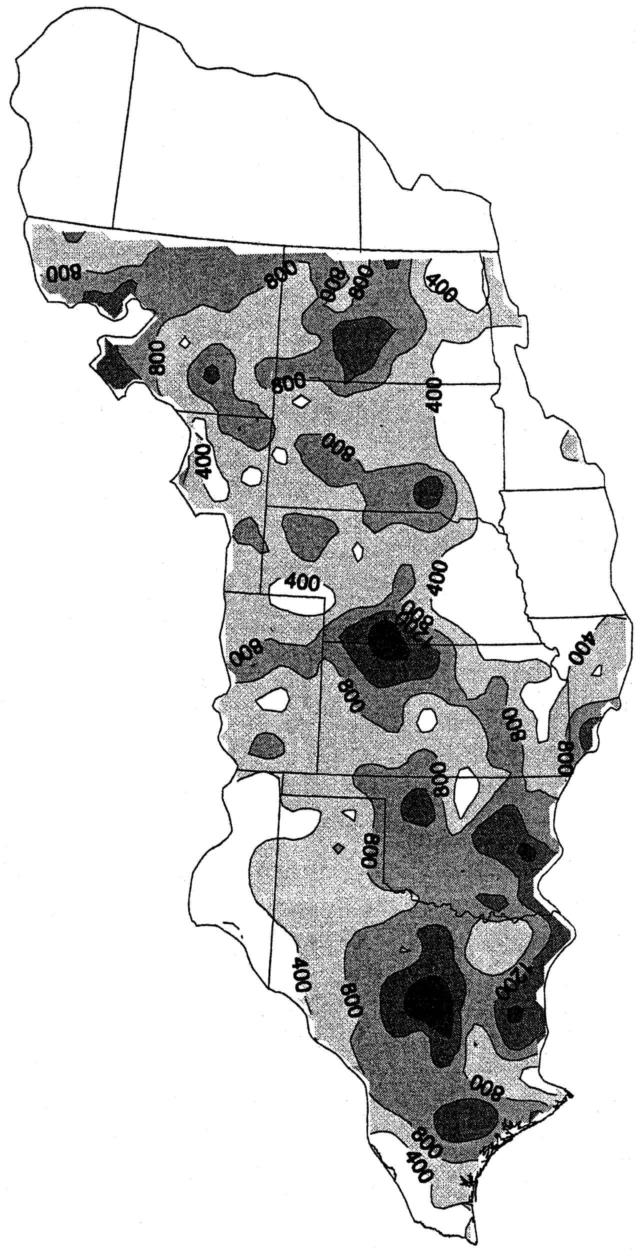

Figure 4. Rangeland edge (km) calculated from Land Use Land Cover data centered on Breeding Bird Survey routes. Plots were generated by kriging (Cressie 1991) total rangeland edge across all Breeding Bird Survey routes in the USA portion of the Great Plains.

Ability of Remaining Patches to Support Biodiversity

Several factors other than fragmentation degrade the capacity of remaining rangeland tracts to support biodiversity. One set of these factors, called "qualitative losses" by Noss et al. (1995), involve a change or degradation in the structure, function, or composition of an ecosystem. These "qualitative losses" include the loss and degradation of special landscape components, such as wetlands, free-flowing rivers, and riparian corridors. In addition, the increasing numbers and extent of invasive species reduce the capacity of remaining rangelands in a region to support biodiversity (Wilcove et al. 1998).

Special landscape components in the Great Plains identified by Noss et al. (1995) include large streams, rivers, wetlands, and glacial pothole ponds. These are endangered ecosystem components, based not only on decreases in land area, but also on the evidence of severe degradation. For example, Dahl (1990) estimated that by the 1980s, wetland losses in Great Plains states since settlement ranged from 27% in Montana to 52% in Texas (Table 2). Currently, less than 10% of the original wetlands in the Rainwater Basin area of south-central Nebraska have been drained, but nearly 50% of the wetlands in the Cheyenne Bottoms in central Kansas have been drained since 1950 (Batt 1996). In Canada, wetland losses in the Great Plains have been estimated to be 44% in rural areas and 88% in urban areas (Rubec et al. 1988). In addition to wetland drainage, a large number of remaining wetlands in the region have been altered. For example, playa lakes (or wind-deflated depressions in the southern Great Plains) surrounded by agricultural land, are threatened by sedimentation rates higher than those reported for any other wetland system (Luo et al. 1997).

Flows in most of the two dozen major stream systems of the Great Plains have been drastically reduced by dams for agricultural purposes in the last 150 years (Rabeni 1996). For example, by 1965, the Missouri River contained 107 major reservoirs and 1,387 minor reservoirs (Slizeske et al. 1982). Upstream water use and pumping of groundwater from the Ogallala aquifer were responsible for drying up 160 km of the Arkansas River and several tributaries in western Kansas (Cross and Moss 1987). The North and South Saskatchewan rivers had seven major water control structures on or upstream of the Great Plains, despite their modest flow rates (< 300 m^3 s^{-1}; Canada 1974). Stream flow alterations, coupled with changes in water temperature, turbidity and the introduction of non-native fish species better adapted to such conditions threaten several indigenous fish species (Fausch

TABLE 2

WETLAND LOSSES IN GREAT PLAINS STATES SINCE SETTLEMENT (DAHL 1990)

State	Estimated wetland hectares circa 1780s	% of wetlands lost by 1980s
Kansas	340,353	48%
Montana	464,191	27%
Nebraska	1,177,879	35%
North Dakota	1,994,159	49%
Oklahoma	1,150,400	67%
South Dakota	1,106,895	35%
Texas	6,475,079	52%

and Bestgen 1997). High flows are important in creating side-channels that native fish species, such as the endangered pallid sturgeon (*Scaphirynchus albus*), use for spawning (Hesse et al. 1993). Water regulation has also helped the spread of exotic saltcedar *(Tamarix ramosissima)* and Russian olive *(Elaeagnus angustifolia)*, to the detriment of native cottonwoods (*Populus* spp.) that prefer areas scoured by flooding (e.g., Friedman et al. 1997).

Remaining rangeland fragments also have been degraded through the accidental or purposeful planting of exotic plant species (Smeins 1999). After habitat loss, spread of alien species is considered the greatest threat to species listed as threatened or endangered (Flather et al. 1994) and to those classified as imperiled in the USA (Wilcove et al. 1998). These exotics include: species deliberately planted in road ditches or in pastures, such as smooth brome *(Bromus inermis);* accidentally introduced annual grasses, such as Japanese brome *(Bromus japonicus)* and cheatgrass (*B. tectorum*); and other invasive forbs, such as leafy spurge *(Euphorbia esula)* and spotted knapweed *(Centaurea maculosa)* (Roche and Roche 1991; Sieg and Bjugstad 1994; Laubhan and Fredrickson 1996; Weaver et al. 1996; Ostlie et al. 1997).

Furthermore, in some cases the quality of remaining remnants has been degraded by a disruption of ecological processes that are crucial for maintaining functioning ecosystems. The ecological impacts of bison or cattle *(Bos taurus)* may be more strongly associated with how they are managed than by functional differences between these two herbivores (Hartnett et al. 1997; Knapp et al. 1999). Sedentary herds negatively impact vegetation diversity and productivity when grazing is too intense, too frequent, too long, or occurs at inappropriate times of the year (Bragg and Steuter 1996). A recent Canadian study showed that the number of grazing animals had increased despite a continued decline in available rangeland acres (Coupland 1987). This trend, which effectively increases the stocking rate on remnant rangelands, has occurred throughout the Great Plains (Ostlie et al. 1997). However, the eastern tallgrass prairie is probably the most vulnerable to the effects of poor grazing management (Lauenroth et al. 1994). On the other end of the scale, total protection from grazing, especially for long periods, can also reduce habitat heterogeneity and species diversity of tallgrass types (Howe 1994; Bragg and Steuter 1996; Knapp et al. 1999).

Disruption of historic fire regimes has also influenced diversity of Great Plains habitats. Fire suppression has been linked to expansion of the aspen parkland in Canada (Archibold and Wilson 1980), woody plant encroachment in the eastern tallgrass prairie (Anderson 1990), expansion of eastern red cedar *(Juniperus virginianus)* in the Nebraska Sandhills prairie (Gehring and Bragg 1992), and increased density of honey mesquite *(Prosopsis glandulosa)* in the southern Great Plains (Archer 1989). Especially in the eastern portion of the region, but to a lesser extent in the drier portions of the prairie, fire suppression is related to changes in plant species composition, production and diversity (e.g., Steuter and McPherson 1995; Leach and Givnish 1996). However, the influence of fire needs to be viewed in the larger context of its interaction with other factors. For example, recently burned grasslands often attract grazers; yet, heavily grazed areas usually resist fire until dead litter reaccumulates (Steuter et al. 1990; Vinton et al. 1993). Therefore, the influences of grazing and drought must be a part of the discussion of historical fire effects.

Species Diversity

Species diversity refers to the variety and abundance of organisms that occurs in a given area. Reduction in species diversity is a widespread indication of ecosystem stress (Rapport et al. 1985). However, assessment of species diversity is difficult for at least two reasons. First, for most taxa, we do not have a complete accounting of species that occur in the Great Plains. Therefore, we are forced to rely on species lists for well-studied vertebrates, such as game animals or breeding birds. Second, since diversity embodies both species richness and distribution of individuals among species, its measurement is contentious (Huston 1994). We have chosen three elements to portray different aspects of species diversity: 1) the species richness of native breeding birds, 2) proportion of individual birds that are exotic and 3) the distribution of species in all taxa listed as threatened or endangered.

Species richness of native breeding birds

The North American Breeding Bird Survey provides information on the presence of bird species on over 4,000 routes in the USA and southern Canada beginning in 1966. Each route is composed of 50 stops, spaced at 0.8-km (½ mile) intervals. At each stop the species and number of birds seen or heard within 402 m (¼ mile) of the route are recorded (details in Droege 1990). We used data from 1980-1990 to examine average number of bird species across the Great Plains over the decade. A number of problems with these survey data have been identified, e.g., observer bias, start-up effects of new observers, and counts are biased indices of abundance. However, many of these issues can be accounted for by appropriate data analysis (Sauer et al. 1994; Barker and Sauer 1992). Further, the statistically-based survey design, standardized survey protocol, and the extensiveness of the survey in space and time make these data the best available for evaluation of broad scale trends in bird composition and abundance (Brown et al. 1995).

The pattern we observed is one of increasing richness of breeding birds from west to east (Fig. 5), similar to patterns observed in plant diversity across the region (Coupland 1979). This pattern is likely associated with increasing annual precipitation and net primary productivity (Raitt and Pimm 1976). The trend appears to contradict the prediction by Rapport et al. (1985) that species diversity should be reduced as land use intensification increases. We note, however, that the Rapport et al. prediction applies to diversity trends within a system rather than to comparisons across systems that may have inherently different capacities to support diverse communities. If we had historical estimates of species richness in these systems before land conversion, then we would be able to compare the proportionate loss in numbers of species across the rangeland types. Based on the observations above, the prediction would be that the loss of bird diversity has been greater in tallgrass prairie than in the shortgrass prairie.

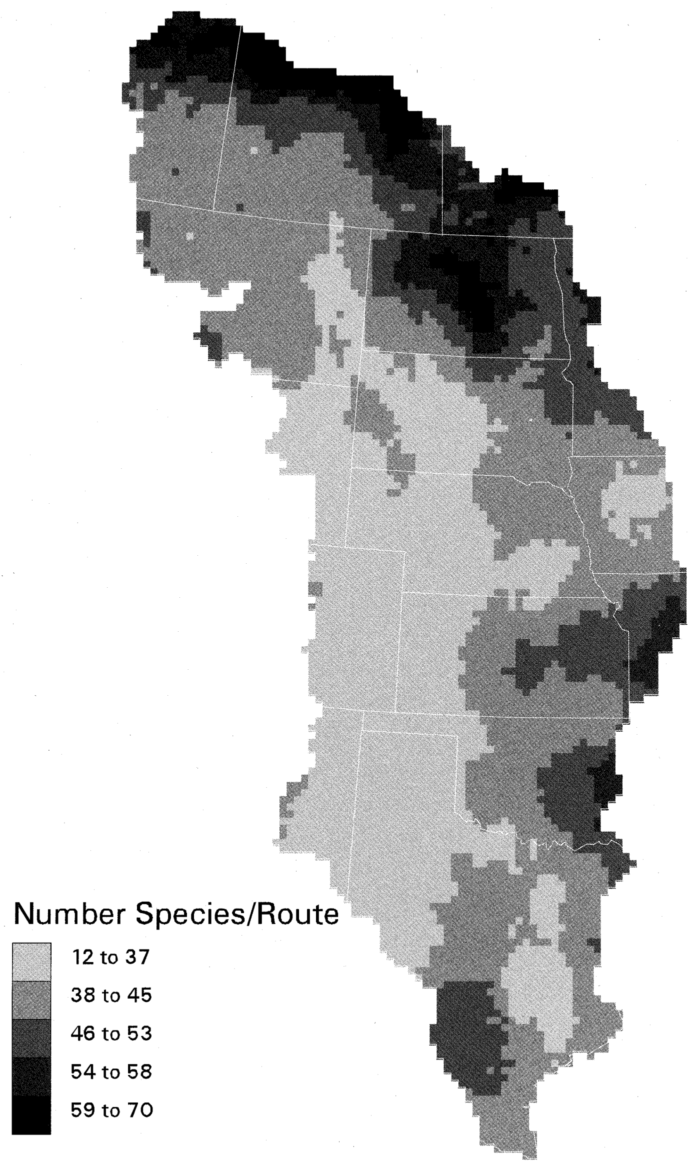

Figure 5. Breeding bird species richness based on the average number of species observed on Breeding Bird Survey routes over a decade, 1980-1990. Plots were generated by kriging (Cressie 1991) bird species richness across all Breeding Bird Survey routes in the Great Plains.

Proportion of exotic birds

Community structure can change dramatically without actually losing species from the regional pool. Thus, an evaluation of the status of biodiversity also requires examination of shifts in the relative abundance of species within the biota. One measure of fauna1 integrity is the prevalence of exotic species, or species not native to North America. We estimated the average percentage of the total number of individuals observed on a Breeding Bird Survey route classified as exotic over the 1980-1990 period. Non-native bird species constituted a high percentage of the total number of individuals in many locations throughout the region (Fig. 6). Concentrations of exotic bird species were often associated with areas of increased land-use intensification (Fig. 2). For example, the eastern edge of the Great Plains, as well as eastern and western Texas, have low proportions of potential natural vegetation remaining and high proportions of exotic bird species. Unfortunately, we lack site-specific information on levels of land-use conversion in the Canadian provinces to assess whether the concentrations of exotic birds in Canada are associated with areas of increased land-use intensification.

Other authors have suggested agricultural disturbances increase the invasibility of native habitats for exotic species. In a California study, the number of both exotic birds and mammals was highest in reserves surrounded by agriculture or human settlement, less in rangeland reserves, and least in reserves most removed from agriculture and human settlement (Smallwood 1994). In North Dakota, exotic bird species that increased in abundance 1967-1993 included species associated with agricultural lands (Johnsgard 1979), such as the gray partridge (*Perdix perdix*) and ring-necked pheasant (*Phasianus colchicus*), as well as species associated with human structures, such as house sparrows *(Passer domesticus)* (Igl and Johnson 1997). Increase of ring-necked pheasants is of special concern since there is evidence that they may have a detrimental effect on remnant populations of greater prairie chickens *(Tympanuchus cupido)* (Vance and Westemeier 1979).

Distribution of species in all taxa listed as threatened or endangered

Despite tremendous loss of habitat, relatively few species in the Great Plains, compared to other geographic areas of North America, have been listed as endangered or threatened (Ostlie et al. 1997). We examined distributions of species in all taxa listed as threatened or endangered in the USA

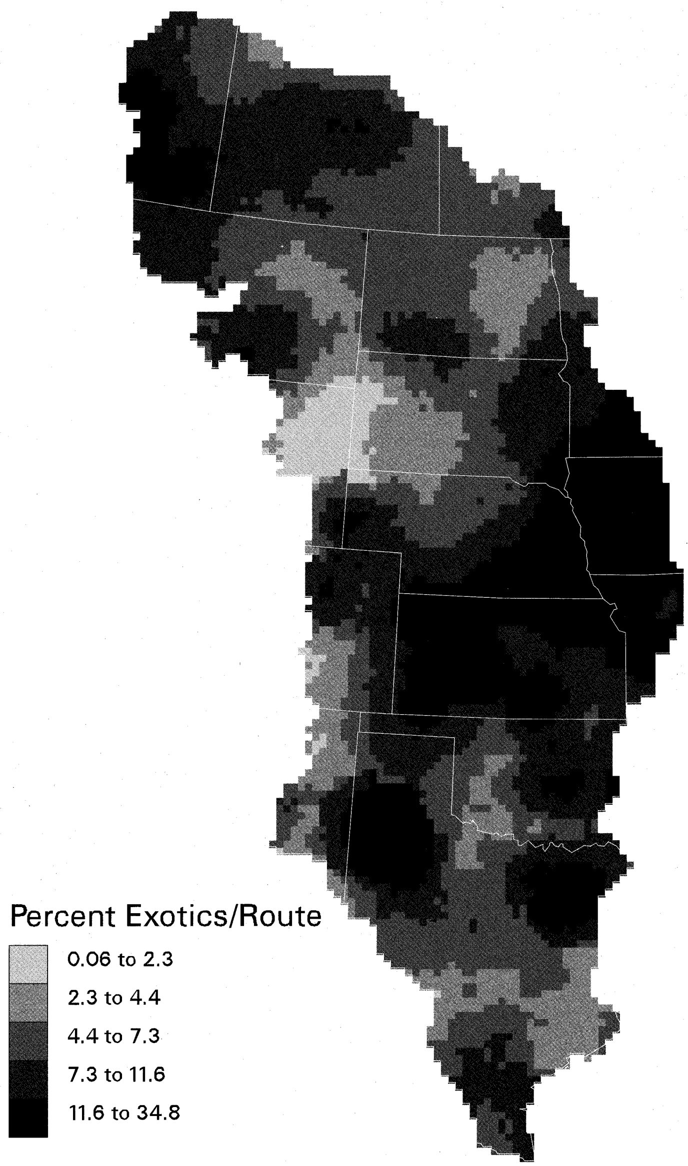

Figure 6. Average percentage of breeding birds that are exotic species. Plots were generated by kriging (Cressie 1991) percentage of exotic species across all Breeding Bird Survey routes in the Great Plains.

or Canada. We compiled distributions of threatened and endangered species as of November 1994 from: *Federal Register* final listings, US Fish and Wildlife Service *Endangered Species Technical Bulletins,* species recovery plans, environmental impact statements, federal and state agency reports, Heritage Program information, and consultation with US Fish and Wildlife Service regional and field biologists (see Flather et al. 1998). In Canada, we examined the distribution of species listed as threatened or endangered by the Committee on the Status of Endangered Wildlife (COSEWIC 1999). The number of threatened and endangered species in each rural municipality was compiled from information provided by provincial Conservation Data Centres.

The distribution of listed species in the Great Plains was relatively homogeneous (Fig. 7); and, at least for the USA, contrasts to the gradient of increased land use intensity west to east (Fig. 2). Counties in the Great Plains support up to 12 threatened or endangered species. The pattern is attributed at least partially to varying intensities of inventory across the region (Ostlie et al. 1997). Most of the tallgrass remnants have been thoroughly inventoried; however, other areas have received less attention. Notably, private lands in Texas have been exempted from inventory efforts (Ostlie et al. 1997).

The relatively low number and broad distribution of listed species in the region may also be related to the physiography and evolutionary history of the Great Plains. Contemporary Great Plains grasslands are thought to have evolved relatively recently, having formed approximately 12,000 years ago (Axelrod 1985). Further, the origins of the flora and fauna are diverse, and the lack of geographic barriers to dispersal likely contributed to low vertebrate and plant endemism (Risser 1996). The eastern portion of the Great Plains, in particular, is generally populated by relatively common species with broad geographic ranges (Risser 1988). Species characteristic of the western shortgrass ecosystem, for the most part, have more limited distributions (Weaver et al. 1996). Further, it is likely that the variable climate and disturbance regime under which Great Plains ecosystems evolved has resulted in high rates of adaptability in resident species (Cody 1985; Risser 1988).

The majority of the listed species in the Great Plains are vertebrates, with lesser numbers of plants and invertebrates (Ostlie et al. 1997). The domination of vertebrates on the list is explained, in part, by the fact that they are a relatively well-studied group that also engenders high public support for conservation. The identifiable “hot spots” of listed species in the

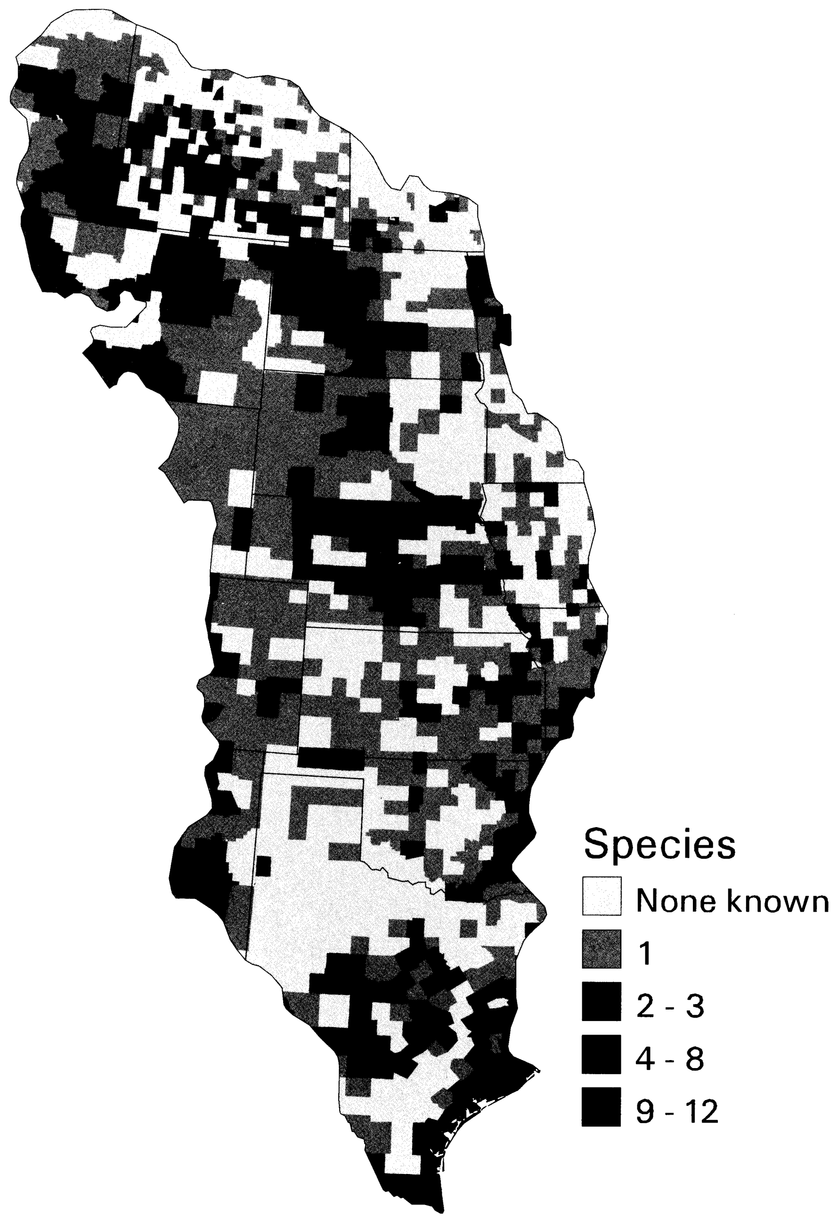

Figure 7. Numbers of threatened and endangered species, for all taxa, by county in the USA, and by rural municipality in Canada. USA data were taken from Flather et al. (1998); Canadian data were compiled from information provided by provincial Conservation Data Centres.

USA portion of this region are associated with bluestem prairie and Nebraska Sandhills prairie, as well as special landscape features, such as the coastal plain and caves in Texas, colonies of prairie dogs (*Cynomys* spp.), wetlands and riverine systems (Table 3). Special habitats that support threatened and endangered species in Canada include: wetlands, sandhills, and concentrations of Richardson's ground squirrels *(Spermophilus richardsonii).*

Another point is notable for listed species in the USA portion of the Great Plains. Only 19% of the occurrences of listed species in this region occur on federal land, compared to 36% nationally (Chaplin et al. 1995). In addition, 95% of the land area in the USA portion of the Great Plains is in private ownership (Natural Resources Conservation Service 1992). This makes private lands in this region particularly important to the conservation of imperiled species.

Genetic Diversity

Genetic diversity refers to the variability of genes among individuals in a species or population. A species' capacity to evolve depends on sufficient genetic diversity to maintain fitness and adaptability to changing environmental conditions (Pimm and Gilpin 1989). Risser (1988) suggested that, in spite of low levels of endemism, grassland species in the Great Plains tend to be characterized by high amounts of ecotypic differentiation. Therefore, the high rates of loss of native rangelands in this region has likely resulted in a reduction of genetic diversity - declines that are not represented in simple measures of species diversity (Risser 1988). Since it is nearly impossible to measure genetic diversity for more than just a handful of species, we examine two surrogate measures as proposed by the Montreal Process (Coulombe 1995): the number of species that occupy only a small portion of their former range, and the number of bird species whose population levels have declined significantly.

Species occupying a small portion of their former range

We do not have a complete accounting of species that now occupy a small portion of their former range. However, three better known examples of such species are the black-tailed prairie dog (*C. ludovicianus)*, the black-footed ferret *(Mustela nigripes)*, and the western prairie fringed orchid *(Platanthera praeclara).* Reductions in the historic ranges of these species

TABLE 3

EXAMPLES OF HABITATS SUPPORTING "HOT SPOTS" OF SPECIES LISTED AS THREATENED OR ENDANGERED IN THE GREAT PLAINS

Landscape feature	Associated listed species
Texas coastal plain	piping plover *(Charadrius melodus)*[a]
	Attwater's prairie chicken *(Tympanuchus cupido attwateri)*[a]
	nesting marine turtles [a]
	green sea turtle *(Chelonia mydas)*
	hawksbill sea turtle *(Eretmochelys imbricata)*
	Kemp's Ridley sea turtle *(Lepidochelys kempii)*
	loggerhead sea turtle *(Caretta caretta)*
Texas caves	tooth cave spider *(Neoleptoneta mypica)*[a]
	tooth cave pseudoscorpion *(Tartarocreagris texana)*[a]
	San Marcos salamander *(Eurycea nana)*[a]
sandhills	blowout penstemon *(Penstemon haydenii)*[a]
prairie dog colonies	black-footed ferret *(Mustela nigripes)*[a]
wetlands	western prairie fringed orchid *(Platanthera praeclara)*[ab]
	sand verbena *(Abronia micrantha)*[b]
tallgrass prairie	prairie bush-clover *(Lespedeza leptostachya)*[a]
riverine systems	piping plover [a] *(Charadrius melodus)*
	least tern *(Sterna antilarum)*[a]
	pallid sturgeon *(Scaphirynchus albus)* [a]
colonies of Richardson's	swift fox [b] *(Vulpes velox)*
ground squirrel colonies	burrowing owl [b] *(Athene cunicularia)*

[a] listed in USA

[b] listed in Canada

likely resulted in a loss of genetic diversity (Soulé and Mills 1998; Westemeier et al. 1998). Prairie dog towns in North America decreased from approximately 41 million ha in 1919 to < 1 million ha by 1960 (Summers and Linder 1978). The range of the black-tailed prairie dog continued to shrink after 1960, and there is evidence that the eastern boundary of their distribution may be receding toward the west (Mulhern and Knowles 1997). Prairie dog population declines have also contributed to range reductions of other species, such as the black-footed ferret (Hillman and Clark 1980). The range of the western prairie fringed orchid has receded to only three known metapopulations in the northern part of its range and scattered smaller populations in southern tallgrass prairie (US Fish and Wildlife Service 1996). Although unquantified, reductions in the ranges of these species undoubtedly represent significant declines in their genetic diversity, and therefore in their ability to adapt to environmental change.

Number of birds with decreasing population trends

Trend data for populations of breeding bird species are more prevalent than those for any other taxon (Droege 1990). We used Breeding Bird Survey data (see Droege 1990) to examine the 30-year trend in Great Plains species. We estimated the number of species whose population numbers have declined significantly between 1966 and 1996 (see Sauer et al. 1997) in the Canadian province and each of the six states constituting the majority of land area in the Great Plains. We limited our analysis just to those species observed on at least 15 routes. Species were counted as having a decreasing trend if the slope of the regression line was negative and differed from zero ($P \leq 0.1$) (details in Geissler and Sauer 1990; Link and Sauer 1994).

The 30-year trend for breeding birds in the Great Plains suggests that an average of 19% of the species declined in states and provinces in the region (Table 4). It is likely that those species whose population levels declined significantly have lost genetic diversity as well. We categorized declining species by breeding habitat (grassland, wetland, woodland, xeric scrub, and other), using the designations of Johnsgard (1979) when given and Ehrlich et al. (1988) for species not listed by Johnsgard. Grassland nesting birds had the highest overall rate of loss (36%), and the proportion of grassland species that declined was greatest (>44%) in the southern plains states and in Saskatchewan (Table 4). In addition, an average of 9% of the wetland bird species have declined across the region between 1966 - 1996. The decline in breeding bird species associated with grasslands and wet-

TABLE 4

TOTAL NUMBER OF NATIVE BREEDING BIRD SPECIES, AS WELL AS THE PERCENTAGE THAT DECREASED (P ≤ 0.1) 1966-1996, BY BREEDING HABITAT (JOHNSGARD 1979). DATA ARE FROM BREEDING BIRD SURVEY ROUTES IN THE CANADIAN PROVINCE AND 6 STATES THAT REPRESENT THE MAJORITY OF THE LAND AREA IN THE GREAT PLAINS. TRENDS ARE BASED ON SAUER ET AL.(1997) AND ARE ONLY GIVEN FOR THE SPECIES ENCOUNTERED ON AT LEAST 15 ROUTES WITHIN A STATE OR PROVINCE.

	Canada province	USA state						Overall
	SK	KS	ND	NE	OK	SD	TX	average
All Species (no.)	96	75	97	65	85	77	130	
% Decreasing	22%	13%	9%	26%	26%	7%	24%	19%
Grassland Species (no.)	18	11	24	14	11	16	11	
% Decreasing	44%	45%	17%	43%	55%	6%	45%	36%
Wetland Species (no.)	34	6	33	7	9	19	16	
% Decreasing	21%	17%	9%	0%	11%	0%	6%	9%
Woodland Species (no.)	40	50	34	40	57	37	73	
% Decreasing	15%	12%	6%	25%	26%	11%	22%	17%
Xeric Scrub Species (no.)	0	0	0	0	1	0	13	
% Decreasing	--	--	--	--	0%	--	46%	7%
Other Species (no.)	4	8	6	5	7	5	17	
% Decreasing	0%	12%	0%	20%	0%	0%	18%	7%

lands in the region has been noted by others (McNicholl 1988; Langner and Flather 1994; Knopf 1994; Igl and Johnson 1997). These declines are important, in that many of the endemic bird species of the region fall into grassland or wetland categories (Knopf 1996).

Population levels of a number of woodland-dependent species have declined in the region as well. An average of 17% of the bird species that breed in woodlands have declined over the last 30 years. Proportionate declines of woodland species were over 20% in southern plains states and Nebraska. In addition, nearly half of the birds that breed in xeric scrub habitats in Texas declined (Table 4).

Restoration and Management of Biodiversity in the Great Plains

There is much uncertainty associated with plans designed to restore and maintain biodiversity of the Great Plains. For most biodiversity dimensions, we lack a comprehensive understanding of past, or even current, status (Flather and Sieg in press). Even the relatively extensive data of the Breeding Bird Survey only allow us to assess trends over the last 30 years or so. We have a relatively poor understanding of the role that stochastic disturbances, such as drought, fire, grazing and flooding played in shaping various prairie types and their distinct landscape components, such as wetlands (Leach and Givnish 1996). We know less about how to incorporate these disturbances into a landscape vastly altered by intensive landuse, fragmentation, and the introduction of dozens of exotic species. Given this high level of uncertainty, adaptive management may offer a reasonable planning framework within which to incorporate uncertainty in the decision making process (see Walters 1986). The elements of adaptive management include: 1) stating an objective, 2) choosing management actions, 3) monitoring and assessing the outcome of these choices, and 4) using the monitoring and assessment data in making future decisions (Walters and Holling 1990; Nichols et al. 1995). The following suggestions relative to restoring and maintaining biodiversity are offered in light of this uncertainty as possible objectives that could be addressed in an adaptive management approach.

Maintenance of biodiversity, especially for the eastern tallgrass prairie and northern fescue grasslands, will require active preservation and restoration. Remaining patches are small and isolated, so they present challenging management issues. Restoration of dominant prairie species may be used to expand and buffer natural remnants (Morse 1996). However, the small size of most tallgrass and fescue prairie remnants makes the restoration of fully functioning landscapes, complete with the range of historic disturbances, unlikely (Steinauer and Collins 1996). Furthermore, recovering the reservoir of biological diversity that has been depleted by cultivation will be slow, or may never occur. Recovery depends on the size of the disturbed area (Sala and Paruelo 1997) and on our ability to overcome the reduced soil fertility caused by farming practices (World Resources Institute 1992).

Restoration of ecological processes in other vegetation types besides tallgrass is important, as well. Grassland species have evolved tolerances (Lauenroth et al. 1994) and even dependencies on grazing (Knapp et al. 1999; Collins et al. 1998). Therefore, properly planned grazing regimes are appropriate components of a strategy to restore biodiversity throughout the region (e.g., Bragg and Steuter 1996). To diversify habitats and increase the species that can be supported, grazing systems should be tailored to a particular ecosystem, and include variation in grazing duration and intensity (Saab et al. 1995). Restoring fire in management plans is also appropriate, but it should be based on historical patterns, including burning at varying intervals and in different seasons (Howe 1994; Sieg 1997). Additionally, both grazing and fire management programs must be adapted to the landscape patterns imposed by: geographic fragmentation (McPherson 1997); species changes, such as the introduction of exotic species and the rarity of others (e.g., Hobbs and Huenneke 1992); and, limitations imposed by management unit boundaries (Steuter 1988).

Management designed to conserve biodiversity of the Great Plains should focus on providing a diversity of habitats with varying successional and structural stages. Habitat requirements of species that depend on extremes of the vegetative continuum may be especially important to incorporate into management plans (Renken and Dinsmore 1987). Landscape features that support many of the threatened and endangered species of the region should receive priority in conservation plans. We also need to pay attention to the exotic species that threaten native flora and fauna (Wilcove et al. 1998). We need to better understand which exotic species are truly invasive (West 1993), actively manage these species, and prevent the introduction of new exotic species.

Success in restoring biodiversity in the Great Plains will be enhanced by regional planning and by collaboration between landowners. Conservation planning by The Nature Conservancy has identified landscapes of biological significance to target for protection (Chaplin et al. 1995). Collaborative efforts will also help recover imperiled species. For example, restoration of black-footed ferret populations will require providing an adequate number, size and proximity of black-tailed prairie dog town complexes (Biggins et a1.1993; Bevers et al. 1997). Regional plans and collaborative efforts among federal, state and private landowners are particularly critical in the Great Plains, given the high percentage of non-federal land in the region.

Our ability to monitor and assess the success of restoration efforts and biodiversity trends in the region will depend on the acceptance of an agreed upon system for classifying vegetation and for addressing ecosystem changes since settlement (National Research Council 1994). There is also a need to develop systematic schemes to monitor other taxa, similar to the Breeding Bird Survey (Solbrig 1992). The development of such inventory and assessment techniques will not allow us to account for past losses, but it will be critical in assessing future trends. These types of data, combined with other monitoring efforts, will be critical in developing future management options and the framework of public policy changes needed to restore biodiversity of the region.

Passage of the Endangered Species Act of 1973 (US Fish and Wildlife Service 1988) and the North American Wetlands Conservation Act (US Fish and Wildlife Service 1993) are positive steps towards reversing biodiversity degradation. In addition, several plains states have adopted “instream flow” regulations designed to maintain water in rivers at times and at levels sufficient to protect aquatic life (Rabeni 1996). Set-aside programs for marginal lands offer opportunities to restore grassland cover to areas where sustainability of crop production is particularly questionable. Such programs presently include: the Permanent Cover Program of Agriculture Canada, Prairie Care by Ducks Unlimited Canada under the North American Waterfowl Management Plan (Baydack et al. 1996), and the Conservation Reserve Program in the USA (Mitchell 1988). In the long run, however, sustaining biodiversity in the Great Plains, and the goods and services that we derive from it, will depend on how successfully we can restore ecosystem function. Therefore, public policies that focus on ecosystem protection (Noss et al. 1995) and provide private landowners with incentives to manage their property to meet biodiversity objectives (Wilcove et al. 1998) will be needed to maintain biodiversity and assure the long-term sustainability of North America’s heartland.

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