Yellowstone Bioregional Assessment

Understanding the Ecology and Land Use of Greater Yellowstone

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Thomas Moran, *Grand Canyon of the Yellowstone*, 1872. Department of the Interior Museum, Washington, D.C.

Prepared for the Gallatin National Forest, Bozeman, MT.

Technical Report #2, Landscape Biodiversity Lab, Montana State University, Bozeman

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Landscape Biodiversity Lab. Directed by Andrew Hansen, the Landscape Biodiversity Lab at Montana State University studies interactions between abiotic factors (climate, soils, topography) human land use, and biodiversity. By integrating field studies, remote sensing, spatial analysis, and statistics, we are able to quantify these interactions across spatial scales from landscapes to continents. Our findings from Greater Yellowstone have lead to studies across the Pacific and Inland Northwest, the Yellowstone to Yukon region, North America, and six comparative greater ecosystems around the world. These studies are designed to aid natural resource managers in implementing more ecologically-based management strategies. See http://www.homepage.montana.edu/~hansen/ for more information.

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Introduction

Yellowstone National Park and the surrounding lands include many federal, state, and private jurisdictions and ownerships. This area is called the Greater Yellowstone Ecosystem in recognition of strong connections across these multiple ownerships. Ecosystem processes such as wildfire and organisms such as elk move across the GYE connecting public and private lands. Tight socioeconomic linkages also characterize the GYE, with the economies of local cities and towns heavily influenced by proximity to national parks and other public lands. The six national forests within Greater Yellowstone (Gallatin, Custer, Shoshone, Bridger Teton, Caribou-Targhee, and Beaverhead-Deerlodge) are in the process of revising their forest plans. In recognition of their roles as components of the larger greater ecosystem, the forests have unified in supporting this single bioregional assessment. This assessment summarizes historic ecological patterns and human land uses as a context for forest planning on biodiversity.

The biodiversity goals of the upcoming decadal revision of forest plans are in transition. A new set of forest planning rules were enacted during the writing of this assessment. The previous rules focused on the maintenance of viable populations of species and functional communities and ecosystems. A five-step process was used for viability analysis. These steps were: bioregional assessment, coarse-filter evaluation of habitats and ecosystems, fine-filter evaluation of species at risk, analysis of alternative management scenarios, and inventory and monitoring. The bioregional assessment set the context for the course- and fine-filter analyses. These assessments were designed to characterize the historic and current conditions of plant and animal resources and help identify species, communities and ecosystems at risk at spatial scales beyond the national forest. The new forest planning rules place greater emphasis on sustaining social, economic, and ecological systems (Federal Register 2005). The rules specify that forest plans will include the following five components: desired conditions, objectives, guidelines, suitability of areas, and special areas. The directives that guide the planning process are still under review and are not final at this time. This bioregional assessment was formulated under the old planning rules, but is also relevant to identifying desired conditions and other components of the new planning rules.

The broad scale ecological and human patterns of the GYE are relatively well understood due to various previous assessments. Keiter and Boyce (1991) placed ecological processes and organisms in Yellowstone National Park in the context of the broader GYE. Glick et al. (1991) focused on the interplay between natural resources and local economics. Clarke and Minto (1994) explored how government and social institutions influence management of the GYE. Hansen et al. (2002) quantified change in land cover and use over the GYE for 1975-1995 and examined consequences for biodiversity and socioeconomics of local communities. Noss et al. (2002) rated ecological importance across the area based on several ecological and land use factors. Finally, Gude et al. (in press) evaluated the consequences of past, present, and possible future land use on several indices of biodiversity.

These assessments and other studies have identified several successes and challenges in maintaining viable species, communities, and ecosystems across the GYE. The remaining challenges stem largely from the fact that GYE is, on the one hand, a highly connected ecosystem undergoing rapid human growth and land use intensification. On the other hand, it is composed of multiple private and public ownership types and management jurisdictions that sometimes do not correspond well to ecological boundaries. Many of the success stories involve cooperative management of ecological processes and organisms across ownership and jurisdictional boundaries. Management of elk populations, recovery of the threatened grizzly bear, and reintroduction of wolves have each been highly successful. Each involved both large complex landscapes and extensive collaboration in research and management among federal and state agencies, private land owners, and nongovernmental organizations.

Some of the current challenges involve management of fire, the spread of weeds and disease among natural and human components of the system, and loss of key low elevation habitats due to rural and urban development on private lands. These changes have been vexing to managers because of the large spatial scale over which they occur and need for coordinated management among many stakeholders. Potential emerging management issues include threats to wildlife from expanding backcountry recreation (such as elevated grizzly bear mortality) and climate-induced changes in habitat and water. Dealing with these current and emerging management issues requires an understanding of the spatial patterning of the GYE and dynamics over time and coordinated management across ownerships.

The goal of this paper is to assess the major factors that influence species and ecosystem viability across the GYE as a context for the analysis and management of biodiversity by the US Forest Service. Specific objectives are:

1. Characterize the historic and current spatial patterns and conditions of terrestrial plant and animal resources at the spatial scale of the GYE;
2. Synthesize current knowledge of the species, communities, and ecosystems at risk across the ecosystem.
3. Derive guidelines to enhance the management of viability of these at-risk elements across the GYE.

The paper first examines historic to present interactions in climate, geomorphology, vegetation, disturbance, wildlife, and land use as a context for management. Current knowledge of biodiversity elements that are at risk is then summarized. Thirdly, ecological theory is used as a basis for deriving guidelines to aid the management of biodiversity.

The Interplay of Physical, Ecological, and Human Systems Past, Present, and Future

Greater Yellowstone has a rich ecological history. Knowledge of past and current patterns and dynamics provides a context for future land planning and management. As we shall see, much of the ecology and human use of GYE stems from its topography, climate, and parent materials. These abiotic factors shape the distributions and growth rates of plant communities, drive fire and flooding regimes, influence the population dynamics of animals, and contribute to where humans live and how they use the land. While topography and parent materials are relatively fixed on ecological time scales, climate has varied in important ways from past to present and is projected to continue to change in coming decades. Knowledge of past and present interactions between abiotic factors, the ecological system, and the human system is critical to effective management today and in the future. This section reviews these interactions as they have played out from the Holocene to present and examines potential future patterns.

Boundaries of Study Area

Centered on the Yellowstone Plateau, the Greater Yellowstone Ecosystem (GYE) was originally defined as the range of the Yellowstone grizzly bear (*Ursus arctos*) (Craighead 1991). Subsequently, Keiter and Boyce (1991) and Hansen et al. (2002) expanded the boundary to include the highlands of the region and the surrounding plains to better account for ecological processes and organism movements. For socioeconomic considerations, Rasker (1991) and Gude et al. (2006) considered a still larger area which included the 20 counties within Montana, Wyoming and Idaho that overlap the GYE. We use this expanded boundary in recognition of the strong ecological and socio-economic linkages across the public and private lands of this region (Figure 1).

Of the 145,635 square kilometers that make up the 20 counties of the GYE, public and tribal lands comprise 68% (98,386 km^2) of the region. Land ownership is divided between private land owners (32%), the USDA Forest Service (32%), the USDI Bureau of Land Management (19%), Yellowstone and Grand Teton National Parks (7%), Tribal Lands (5%), and state lands, wildlife refuges and other federal lands (5%).

Physical Factors

Geomorphology. The GYE is centered on the Yellowstone Plateau and the surrounding mountain ranges (Absaroka, Wind River, Overthrust, Teton, Centennial, Gravely, Tobacco Root, Madison, Gallatin, and Bridger). These mountains were formed by the Laramide orogeny, which uplifted the Rocky Mountains between 100 and 50 million years ago as the North American and Pacific crustal plates collided (Meagher and Huston 1998). The Yellowstone plateau was formed by the North American plate moving southwest over a hotspot in the earth's crust. Over the past two million years, collapsing crust and volcanic flows built up the current plateau. Consequently, the higher elevations of the GYE represent a horseshoe centered on the hotspot. The path of the crustal hotspot forms a ramp ascending from the Snake River Plains northeast onto the higher elevations of the Yellowstone Plateau. The major mountain ranges surround the path of the hotspot. Seven major rivers flow off the Yellowstone Plateau and mountains and onto the surrounding plains. These include the Yellowstone, Clark's Fork, Wind, Snake, Henry's Fork, Madison, and Gallatin Rivers. Elevations across the GYE range from 1150 – 1700 m on the plains to the northwest and 1700-2300 m on the plains to the south and east, to 2300 – 2700 m on the Yellowstone Plateau, and up to 3000 - 4200 m for maximum elevations for the mountain ranges.

The Pindale Glaciation covered nearly 90% of YNP at its maximum about 30,000 years ago. The ice was more than 1000-1200 m thick over the plateau and flowed down the major drainages to the high plains. The ice was largely gone by 14,000 years ago. It left high sculpted mountain cirques, lakes, and scoured rocks and deposition of till and moraines.

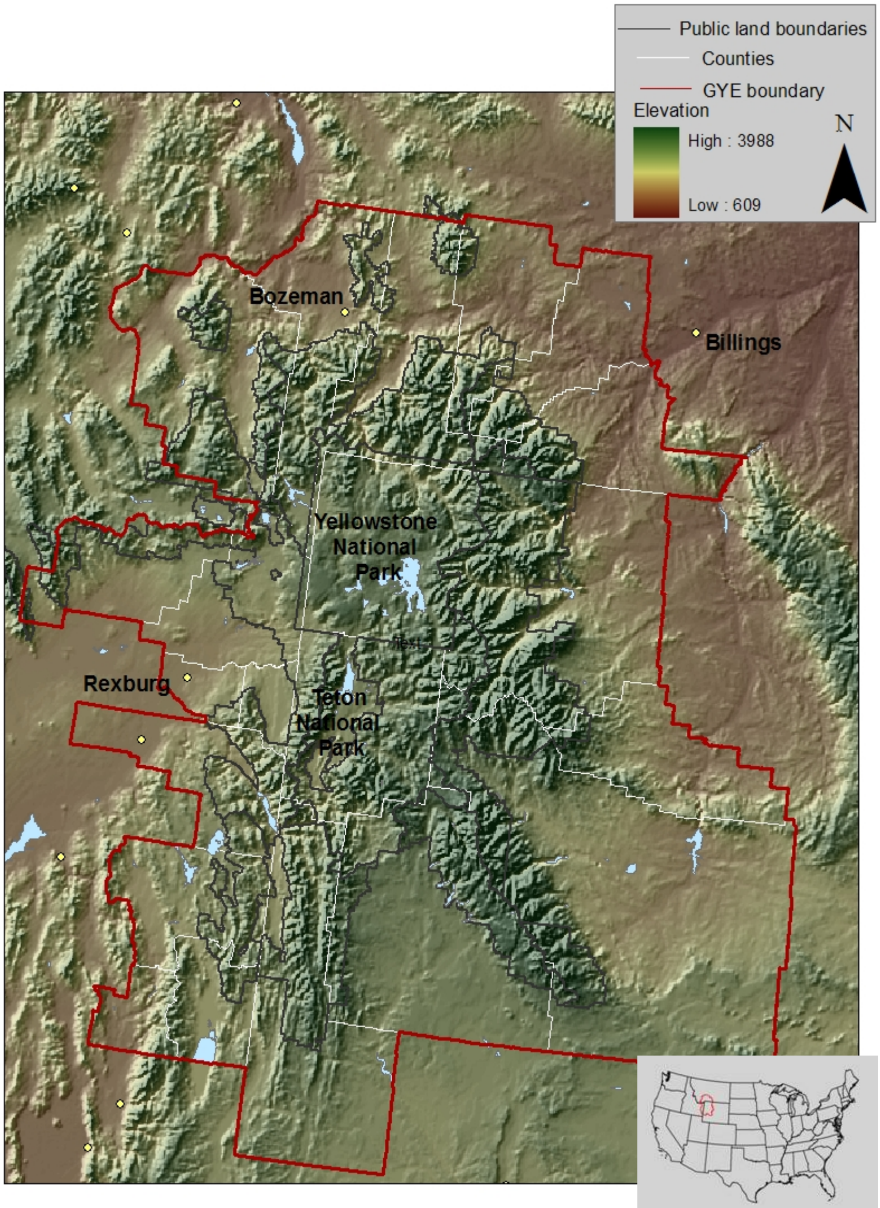

Figure 1. The Greater Yellowstone Ecosystem as defined by Rasker (1991) and Gude et al. (2006).

Parent material. Soils across the GYE are important to vegetation communities in influencing nutrient and moisture availability. While there are many soil types here, their properties for plant growth derive from smaller number of types of parent material. Precambrian granitic rock forms the basement rock for many mountain ranges in the GYE. These rocks weather to fine to medium textured soils moderately high in nutrients and water holding capacity. Granitic outcrops are found in the Crazy, Bridger, Madison, and Absaroka mountain ranges (Davis and Shovic 1996). Parent rock of the study area includes Paleozoic and Mesozoic limestones, sandstones, and shales (Rodman et al.

1996). These sedimentary rocks weather to soils with a high clay content and good water-holding capacity. Mineral nutrient levels are relatively high, providing good plant growth. These sedimentary rocks are found primarily across the Gallatin, Absaroka, and Overthrust Ranges.

Volcanic activity in the Eocene buried much of the Yellowstone Plateau in thick deposits of andesite lava. This was overlain in the Quaternary with flows and ash of rhyolites. These two volcanic rock types differ considerably in suitability for plant growth. Rhyolitic soils are low in nutrient content and are coarse textured resulting in low water holding capacity. Andesitic soils are higher in clay content and differ in nutrient composition. They have about four times the calcium, organic carbon, and other nutrients than rhyolitic soils and water holding capacity is considerably higher (Despain 1990). Andesitic soils are found primarily in the Gallatin and Absarokee Ranges while rhyolytic soils occur across the central and southwestern Yellowstone Plateau. Ash and loess from the Snake River Plains blew onto the rhyolites in the southwest side of the Yellowstone Plateau and this has increased total nutrients and water holding capacity by about 50% (Bowerman et al. 1997).

Glacial processes caused mixing and redistribution of these parent materials to valley bottoms and glacial moraines. Such areas include the valleys of the Lamar River and the lower Yellowstone River in YNP, the Madison Basin near West Yellowstone, the Snake River Valley through Grand Teton National Park, and most of the major river valleys through the high plains. These tills vary from low in nutrient content and water holding capacity (e.g., the Madison Basin) to relative high in these factors (the Lamar Valley) depending on parent material and soil texture. Some of the lower river valleys (particularly the Snake River Plain and the Gallatin River Valley) have received considerable loess deposits, resulting in very deep and fertile soils.

<u>Current Climate</u>**.** The GYE region is characterized as cold continental climate. However the area has considerable variation in climate as influenced by elevation, latitude, and broad-scale air masses. The area includes places that are very cold and snowy, places cold and dry, and relatively warm, moist locations suitable for agriculture. This variation in climate strongly influences ecological processes such as plant succession, distribution of organisms, and human land use.

Climate here varies most predictably with elevation. Valley bottoms and high plains are relatively warm and dry. Spatial extrapolations from meteorological stations (Thornton et al. 1997) indicate annual average temperatures are 6-7^0 C (43-45^0 F), length of growing season is in excess of 5 months (e.g., sum of growing degree days >2500), and average annual precipitation is 24-48 cm (10-20 in). Solar radiation is relatively high here due to lower cloud cover and vapor pressure deficit is high due to low humidity and high temperatures. Hence, plants frequently undergo drought stress in the absence of irrigation. The Yellowstone Plateau and mid elevation mountains are cold and wet, average annual temperatures are 0^0 C (32^0 F), growing seasons are 2-3 months limited both by cold temperatures and by summer drought in some areas, annual precipitation is 72–170 cm (28-66 in) and snow covers the ground for 210-250 days per year with an average snowmelt date of July 1. The highest mountain areas are very cold and wet with average annual temperatures of -6 to -1^0 C (21-30^0 F), annual precipitation of 170 – 204 cm (66-80 in), and less than 30 snow free days per year.

Overlain on these elevational influences on climate are effects of topography, latitude and longitude. A west to east precipitation gradient occurs over the GYE due to topography (Despain 1990, Knight 1994). The high levels of precipitation on the west side of the Yellowstone Plateau, up to 170 cm (66 in) per year, result from moist air masses off the Pacific being forced up over the plateau. The cooler, drier air descends on the east side of the Yellowstone Highlands resulting in desert conditions in the Big Horn Basin, with annual precipitation about 12 cm (5 in) per year. GYE also has a north to south gradient in solar radiation. The ecosystem is some 280 km (175 mi) from north to south. Consequently, growing season solar radiation increases from 20 MJ/m^2 day on the high plains to the north to 23 MJ/m^2 day at similar elevations to the south. Predominant aspects also differ across the GYE resulting from it being centered on the Yellowstone Plateau and surrounding mountains. Northerly and easterly aspects are more common on the north and east sides of the region and southerly and westerly aspects are more common on the south and west sides of the system. All else being equal, this results in cooler, moister conditions on slopes to the north and east and warmer, drier conditions on slopes to the south and west.

A third factor influencing the climate of GYE is its position at the transition between major continental air masses (Despain 1990, Whitlock 1993, Mock 1996). The western portion of the ecosystem is within the domain of the Pacific air mass which delivers high precipitation primarily in winter. Summers tend to be relatively dry as is typical of the Mediterranean climate of the Pacific and Inland Northwest. Some 75-80% of the precipitation here falls as snow. Monsoonal storms from the Gulf of Mexico and Gulf of California dominate the Great Plains. These storms push up to the Yellowstone highlands from the south and east. Consequently, the southern and eastern portions of the ecosystem tend towards higher precipitation in summer and some 35-55% of the precipitation falls as rain. Hence, the west central Yellowstone Plateau has been characterized as a "summer dry" climate and the eastern portion of GYE from the east side of the Overthrust mountains, around the east side of GYE, to the Yellowstone River Basin is characterized as a "summer wet" climate. There is uncertainty, however, about the strength of this effect in GYE due to the complicating effect of elevation on the seasonality of precipitation (more moisture falls in winter at higher elevations) and the relative lack of meteorological stations in this region. Data from meteorological stations for the high plains northeast of the Absaroka Mountains clearly show the summer wet pattern and the southwest Yellowstone Plateau shows the summer dry pattern. There is uncertainty about seasonality of precipitation around the southeast side of the ecosystem.

Past and Future Climate. While current climate strongly shapes the biota of GYE, the legacy of past climate continues to influence modern ecological patterns. Climate here has fluctuated on the scale of millennia since glaciation and on the scale of decades in recent centuries. This change is expected to continue in the future under the influence of human induced global warming.

Since the last glacial maximum some 20,000 years ago, solar radiation has varied due to the tilt of the earth and wobble on its axis (Whitlock 1993, Meagher and Houston 1998, Millspaugh et al. 2004). Temperatures were approximately 10-15 C^0 colder than today and there was less precipitation. Conditions became warmer and moister during the period 12,000 – 14,000 years before present. By 9,500 years ago, solar radiation in summer had increased to about 8.5% greater than today and temperatures were 1-2 C^0 (34-36^0 F) warmer. The summer dry regions of GYE became cooler and wetter starting about 5,000 years ago. The summer wet portions of the area became warmer and drier. Both regions warmed during the Medieval Warm Period, 1000 to 650 years ago. The Little Ice Age followed (1650-1890), with coldest, wettest conditions occurring from about 1860-1890. Rapid warming and drying has occurred in the last century with about a 1^0 C (1.8^0 F) rise since 1900. Hence, the period of European settlement in the GYE was the coldest and wettest in about 14,000 years and the current period of management is within a rapid warming phase.

Superimposed on this recent warming are 10-20 year cycles in temperature and moisture that result from changes in sea surface temperature in the Pacific. Yellowstone experienced cycles of high moisture during 1900-1950. Much of the time since 1950 has had below average moisture (Pederson et al. in 2006). The effects of warming since 1900 and the decadal cycles of precipitation have not been well integrated into thinking about ecosystem dynamics and management in the region.

The extent to which climate in the 20th century has been influenced by increases in greenhouse gasses due to human activities is under debate. Consensus among the scientific community is that humans have influenced global climate in recent decades and that this effect will intensify in the future (Houghton et al. 2001). Under the doubling of atmospheric CO_2 (expected in ca 100 years), the climate of Yellowstone is predicted to continue to warm. Both summer and winter temperatures are projected to increase by up to 10^0 C (18^0 F) (Bartlein et al. 1997). There is considerable uncertainty about future precipitation. Bartlein et al. (1997) project nearly a doubling of winter precipitation in the Yellowstone area. A more recent analysis by Schafer et al. (2001) suggested drier than present conditions for higher elevations and moister conditions for lower elevations.

A major conclusion is the climatic conditions across the GYE for the past 100 years are not representative of many earlier periods nor indicative of likely future conditions. Climate here has varied on millennial, centennial, and decadal scales. Current vegetation patterns were likely heavily shaped by the colder and wetter conditions of the Little Ice Age. The system has been on a trajectory of warming for the past century and this is likely to intensify in the future. Embedded within this change is decadal variation in moisture. Management regimes should be designed to be robust to such changes in climate.

Key Conclusions on Physical Factors.

1. GYE is centered on a plateau and mountain system, hence it includes high variation in elevation.
2. Geologic history of the area has lead to spatial patterning of soils, ranging from nutrient poor volcanic soils on the Yellowstone Plateau, to moderately fertile volcanic and granatic soils in some of the mountain ranges, to highly productive soils on some of the valley bottoms.
3. Climate is harsh over most of the GYE. Variation in climate is aligned with three major factors. Elevation – climate is most equitable in some low elevation settings. Latitude – the southwestern portion of GYE has higher solar radiation and more southerly aspects and hence has higher evaporative demand. Orography – Areas west of the continental divide receive primarily winter precipitation from the Pacific, while those east

of the divide have primary summer precipitation from the Gulf of Mexico and Gulf of California.
4. Climate has varied in GYE at decadal, centennial, and millennial time scales. The current period is one of particularly rapid flux, shifting, in the late 1800's, from the coldest period in 14,000 years to perhaps the warmest in that period in the coming century under increasing greenhouse gasses.

Vegetation and Natural Disturbance

The GYE lies within the temperate coniferous forest biome. Vegetation here is a mosaic of grasslands, shrublands, and forests from open savannas to closed dense stands. The distribution of vegetation types is heavily influenced by climate and parent materials (Despain 1990). The types of species actually found within a habitat type vary with disturbance history and rates of succession. Disturbances such as fire, flooding, avalanche, and earthquake vary among habitat types and with topography. Rates of forest growth and recovery also vary across these gradients. As with climate, vegetation varies spatially by elevation and by location within GYE. These spatial patterns responded over time to changing climate at decadal, centennial, and millennial time scales. The period of modern human intervention in the last century and a half is sufficiently different from previous times that "letting nature take its course" may not be a viable management strategy. Knowledge of the long term interplay between climate, soils, disturbance, and vegetation lays a basis for well-formulated management regimes to achieve natural resource objectives.

Current Natural Vegetation and Dynamics. Sagebrush steppe and grasslands occupy the lower and drier elevations within the GYE (Knight 1994). With increasing elevation and moisture, limber pine (*Pinus flexis*), ponderosa pine (*Pinus ponderosa*), and Douglas-fir (*Pseudotsuga menziesii*) savannas comprise the lower forest ecotone (Figure 2). Closed-canopy forest occupies intermediate elevations grading from Douglas fir to lodgepole pine (*Pinus contorta*) (on rhyolitic soils) to Englemann spruce (*Picea engelmannii*), subalpine fir *(Abies lasiocarpa*), and whitebark pine (*Pinus albicaulis*) at higher elevations. Whitebark pine dominates the upper forest ecotone, with alpine vegetation at still higher elevations.

The flood plains of the major rivers lay within the sagebrush steppe zone. These floodplains support complex riparian communities that are products of local environmental gradients and flooding (Knight 1994, Merigliano 1998). River reaches constrained by valley walls tend to have narrow riparian communities. It is where these rivers are not constrained by topography that braided channels wander across the floodplain creating extensive riparian habitats and the full suite of seral stages. Snowmelt from the Yellowstone highlands results in annual floods in the lower rivers. The magnitude of the flooding varies with winter snowpack and spring melting conditions. Large floods with about a 100-year periodicity (depending on river system) cause dramatic changes in the floodplain, cutting new channels and destroying some of the old riparian forests. These floods reinitiate succession. The resulting bare gravel bars are

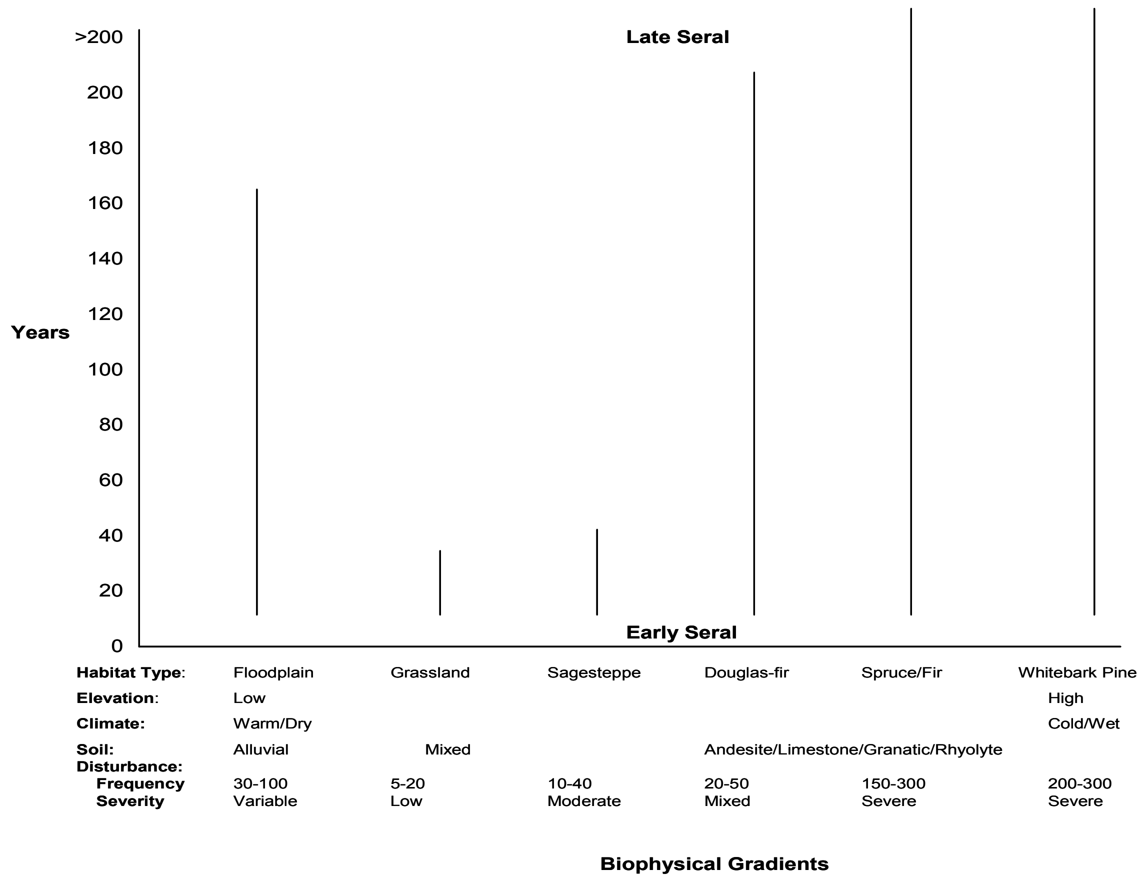

Figure 2. Major habitat types, biophysical attributes, and successional paths of vegetation in the GYE organized along major biophysical gradients.

often colonized by annual plants, willow (*Salix*), cottonwood (*Populus*), and aspen (*Populus tremuloides*). These sandbar meadows succeed to young, mature and eventually old-growth cottonwood forests (Figure 2). Without renewed flooding, the senescing old-growth cottonwood communities may succeed to grassland or shrublands. Also, some locations on the flood plain with fine soils may remain in grasslands or herbaceous swamp for extended periods. Thus, flooding causes these braided floodplains to be dynamic mosaics of varied seral stages. The variety of seral stages of riparian habitat, fertile soils, and high primary productivity support high numbers of shrubs, trees, and vertebrates (Hansen et al. 1999, Hansen et al. 2003).

The lower forest ecotone is a complex mix of grasslands to dense forest depending upon aspect, elevation, and fire history (Fischer and Clayton 1983, Barrett 1994, Bowerman et al. 1997). Dry soils and fire with a 10-20 year return interval maintain valley bottom grasslands. Upland meadows with slightly longer fire frequencies (20-40 years) may support sagebrush and be invaded by juniper, ponderosa pine, flex pine, and/or Douglas-fir. On wetter sites with more clay soils at this elevation, aspen may be the dominant early successional species, with Douglas-fir in the understory. After about 60 years post fire, Douglas-fir may replace aspen and dominate the stand until the next stand-replacement fire.

The increasing moisture in the lodgepole pine and fir zones leads to less frequent (100 to 250 year return intervals) and more severe fire (Bowerman et al. 1996, Romme 1982). Lodgepole pine dominates after fire until replaced by subalpine fir, Englemann Spruce, and whitebark pine some 80 to 120 years post fire.

While elevation dictates perhaps the primary pattern of vegetation in the region, there are additional spatial patterns. The rain shadow effect of the Yellowstone Highlands creates a desert in the Big Horn Basin. Vegetation here is dominated by sparse saltbrush (*Atriplex*), greasewood (*Sarcobatus*), and winterfat (*Krascheninnikovia*) mixed with bluebunch wheatgrass (*Agropyron*) and prairie junegrass (*Koeleria*) (Noss et al. 2002). Ponderosa pine is rare in the GYE, occurring in small areas in lower treeline in the eastern portion of the ecosystem (Knight 1994). It occurs in relatively warm areas with higher summer precipitation and on more fertile soils. Within the mid-elevation belt of GYE, the distributions of Douglas-fir and lodgepole pine vary largely with parent material. Lodgepole pine is found primarily on gravely soils, particularly rhyolites and on coarse glacial till. Thus, it is abundant on the Yellowstone Plateau. Douglas-fir occurs on andesites, granitics, and limestone soil types. Finally, aspen is found primarily in the southern portion of the GYE (Brown et al. in press). It occurs in relatively large patches in the Overthrust Belt south of the Tetons and in lower treeline of the Gros Ventre and Wind River Mountains. The factors explaining this prevalence to the south are not well understood. Hypotheses include increased summer precipitation, higher solar radiation due to latitude and southerly aspects, and more frequent fire (Brown in press, Noss et al. 2002).

The productivity of vegetation also varies with biophysical gradients and vegetation type (Hansen et al. 2000, Turner et al. 2004). Above ground net primary productivity (ANPP) is highest in riparian woodlands, Douglas-fir forests, and aspen stands. It is intermediate in lodgepole pine forests, and lowest in grassland and sagesteppe cover types. Within lodgepole pine forests, ANPP varies with parent material: rhyolites with ash/loess are more productive than rhyolites alone. ANPP decreases with increasing elevation in most cover types, possibly because low temperatures limit plant growth at higher elevations in the study area. As a consequence of these biophysical controls, areas high in ANPP are relatively rare. Only 6.5% of the northwest portion of the GYE had relatively high ANPP (upper quartile of values) (Hansen et al. 2000). These locations were primarily in low elevation forests and in floodplains with fertile soils.

<u>Natural Landscape Dynamics</u>. These patterns of natural disturbance and succession within stands merge to define the dynamic properties of landscapes. The temporal pattern of disturbance and subsequent recovery determine the "natural range of variation" (NRV) (Landres et al. 1999). This is the extent of variation in seral stages and vegetation conditions that occurs across multiple disturbance cycles. NRV in GYE is expected to vary with the succession sequences depicted in Figure 2. In the lodgepole pine zone, for example, stand replacing fires likely reoccur at 150-250 year intervals, resulting in the succession sequences from seedling/sapling through old-growth. Native organisms are

thought to be well adapted to the NRV. Hence, land managers have embraced the concept of NRV as a guide to managing disturbance to maintain biodiversity.

In landscapes that are large relative to the size of disturbances, the timing of disturbance is typically out of phase among patches. While some locations are being disturbed, others are recovering from disturbance. A landscape in a "dynamic steady-state equilibrium" is one where individual patches are out of phase in succession, but the landscape as a whole maintains a constant proportion of seral stages (Bormann and Likens 1979). This landscape dynamic is especially important because the full range of seral stages is maintained across the landscape over time. Hence, both early and late seral organisms are able to persist on the landscape. "Minimum Dynamic Area" (Pickett and Thompson 1978, Baker 1992) is a landscape of a size large enough to maintain this steady-state equilibrium.

It is unclear to what extent GYE approximated a dynamic steady-state equilibrium in pre-European settlement times. Analyses by Romme (1982) within a 7300 ha study area in the subalpine fir zone in YNP suggested a non-equilibrium distribution of seral stages as driven by large crown fires at about a 300-year return interval. This same conclusion was drawn for a larger 130,000 ha study area (15% of YNP) by Romme and Despain (1989). However, it is unknown if the entire subalpine fir zone of GYE, which is substantially larger, might have maintained a dynamic steady state. The lower elevation forests in GYE with smaller, more frequent fires would have an increasing possibility of approximating a steady-state equilibrium. Thus, at the scale of GYE it is likely that both early and later seral species continuously had habitat present.

Change in Vegetation Dynamics: Past, Present, Future. The current vegetation patterns are set within a long-term context of flux as driven by changing climate. Following retreat of the glaciers, the region was predominately tundra. Vegetation differed thereafter between the summer wet and summer dry regions of GYE (Millspaugh et al. 2004).

Some spruce established in the summer wet region during the period 12,000 – 14,000 years ago creating a spruce parkland with birch (*Betula*) in the riparian areas. After about 11,000 years ago, the parkland was replaced by a pine and juniper (*Juniperus*) forest and after 7000 years ago a parkland of Douglas-fir and aspen developed. Fire frequency was some 6-10 events per 1000 years during the mid Holocene, and increased during the late Holocene to approximately 12-17 events per 1000 years.

In the summer dry portions of the region, lodgepole pine became widespread after 11,000 years ago. This likely resulted both from climate and by the presence of the relatively infertile rhyolitic soils in this area. Fire frequency was some 5-7 events per 1000 years during much of the Holocene. In the last 2000 years, fire frequency has been about 3 events per 1000 years, the lowest at any time since the establishment of the lodgepole pine forest.

On finer time scales, variations on these trends in fire are apparent. Fire was especially frequent in both the summer wet and summer dry regions during portions of the Medieval Warm Period, especially during 500-1000 years ago. During the Little Ice Age of 500-100 years ago, in contrast, fire frequency was substantially reduced due to the cooler wetter weather.

The period of European settlement (1870 to present) largely coincides with the end of the Little Ice Age and the subsequent warming and drying. This period is characterized by an almost complete absence of fire, until the large fires of 1988. This was documented for the summer dry area of YNP by Romme (1982) and Romme and Despain (1989) who found that large fires occurred in the early 1700s and not again until 1988. In the summer wet regions of YNP, Barrett (1994) and Littell (2002) documented fire return intervals of 20-50 years prior to about 1860, and virtually no fires thereafter until 1988. The lack of fire in the Douglas-fir zone has been attributed to domestic livestock grazing reducing fuel loads and to fire suppression (Powell et al. in press). The additional effect of the climate of the Little Ice Age has not been fully considered.

Another change in the last century is the expansion of conifer forests and the contraction of grasslands, sagesteppe, and aspen stands. Photo sequences from 1880 and 1990 indicate substantial expansion of conifer into non conifer habitats and increases in density of open savanna-like conifer forests (Meagher and Huston 1999). A recent quantitative analysis by Powell (2003) found that 38.3% of samples not logged or burned increased in conifer cover during 1971-99. The average rate of increase was 0.22%/yr, which would be equivalent to 22% over 100 years. Change in conifer presence was not even across the landscape. It was most rapid in the lower elevation Douglas-fir and limber pine zones, where 48% of samples increased in conifer cover. The rate of increase in this zone was equivalent to 55-72% over 100 years. In contrast, changes in the upper forest elevation zone have been minimal. Projected over Powell's GYE study area, some 16% of the landscape experienced an increase in conifer cover during 1971-99, with the majority of this change in the lower forest zone. This change in conifer may be due to fire exclusion, livestock grazing, climate change, and/or increasing CO_2 in the atmosphere.

This expansion of conifer is occurring at the expense of other habitat types including grasslands, sagesteppe, and aspen. Across the GYE aspen cover declined by more than 20% in 34% of samples over the past 50 years (Brown in press). Most of the samples experiencing loss of aspen were in locations that were relatively cool and had higher winter precipitation, conditions that favor conifer growth. Within the East Beaver Creek Watershed in the Centennial Mountains, an area primarily in the Douglas-fir habitat type, area in aspen declined by 75% since the mid 1800s (Gallant et al. 2003). This rapid change was primarily due to absence of fire and succession to Douglas-fir.

How might these changes in vegetation over the last century influence fire regimes? The fires of 1988 burned some 1,405,775 ha, largely within YNP. Based on the longer term fire record for the higher elevation forests, Romme and Despain (1989) concluded that this event was typical of the longer-term fire regime for the higher elevation forests in the summer dry portion of the park and not influence by human fire suppression during the 1900s. This conclusion is supported by Powell's (2004) finding of little change in conifer cover in unburnt forests in this elevation zone since 1970. The dramatic increase in conifer cover and biomass, and thus fuel loading, in lower elevation forests, however, may set the stage for larger, more severe fires in this zone that has been documented since preEuropean settlement times (Powell et al. in press). This hypothesis is supported by the occurrence of fairly large crown fires in the Douglas-fir zone since 2000.

The concept of NRV as a guide to management needs to be considered in light of millennial and centennial fluctuations in climate, vegetation and fire. The concept may be applicable in the higher elevation forests that have experienced large, infrequent fires for much of the Holocene. However, the patterns of disturbance and succession in the lower elevation forests in the summer wet region have changed substantially with climate in recent millennia. The 300-year period prior to European settlement is often taken as a bench mark for establishing NRV (Romme and Turner 2004). However, this period coincides with the Little Ice Age, which was anomalous over the Holocene and fell immediately after the Medieval Warm Period of frequent fire. The colder, wetter conditions of the Little Ice Age reduced fire, and likely led to more expansive late seral forests across the region than in previous years. The warmer temperatures and forest expansion of the last century has likely put these forests on a new trajectory towards larger more severe fire in these forests. The distribution of seral stages in this zone has likely been in flux during the last several centuries, shifting from more early seral stages in the Medieval Warm Period, and more late seral stages during the Little Ice Age and last century of European settlement. Hence, there is no clear "natural condition" on which to base current management.

These dynamics are likely to continue to change, and even accelerate, in the coming century (Bartlein et al. 1997, Millspaugh et al. 2004). The simulated future climate in much of the Yellowstone region under the doubling of atmospheric CO_2 expected in the next 100 years (mild wet winters and warm dry summers) is similar to the present climate of northwestern Montana and northern Idaho, a region some 500 km to the northwest. In general, high-elevation habitats are projected to become restricted or even eliminated as warming occurs, while low-elevation habitats expand and move to middle elevations. Subalpine species such as whitebark pine and subalpine fir may be lost entirely. Ponderosa pine is projected to expand in lower elevations. Douglas-fir is projected to increase at middle elevations. Lodgepole pine is projected to continue to occupy current locations and to expand in the nonrhyolitic soils at higher elevations. Importantly, habitats are projected to become suitable for species not currently located in the GYE. These include gambel's oak (*Quercus gambelii*), western juniper (*Juniperus occidentalis*), and bigtooth maple (*Acer grandidentatum*), which are now found in Utah and Colorado. Species now found in the warm, moist environments of northwest Montana are projected to have suitable habitats in GYE, including western larch (*Larix occidentalis*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*). In total, these projected changes in floristics are greater than have occurred in the 14,000 years since deglaciation.

The required dispersal rates for tree species currently outside of GYE under this scenario are considerably faster than occurred in the Holocene. Hence, weeds and other fast-dispersing species may invade and become dominant in the newly created habitats of GYE. This is especially likely with an increase in fire frequency as is expected due to drier summer conditions.

These changes in climate and vegetation are likely to have substantial effects on several aspects of ecosystem function including rates of primary productivity, decomposition, snow distribution, and water yield. Unfortunately, how these factors may change is poorly known.

Key Conclusions on Vegetation and Disturbance

1. The current distribution and dynamics of vegetation is heavily influenced by biophysical factors including climate, soils, and topography and natural disturbance such as fire and flooding.
2. Changing climate during the Holocene drove substantial change in fire regimes and in vegetation composition and dynamics.
3. These dynamics differed between the summer wet and summer dry regions of the GYE.
4. Recent climate shifts on the scale of centuries (such as from the Medieval Warm Period and the Little Ice Age) and resulting changes in fire regime raise question about the validity of using the past few centuries as a benchmark for establishing a NRV, especially in lower elevation forests.
5. Fire was largely absent from the GYE from the mid 1800s until 1988 due to cold wet climate at the end of the Little Ice Age and/or human fire exclusion. Consequently, conifer forests have expanded and aspen, grassland, and sagestepe have contracted, especially at lower treeline.
6. The resulting high fuel loads may have shifted the fire regime in lower elevation forests to larger, more severe fires.
7. Vegetation change in the coming century under global warming is projected to be greater than at any time in the last 14,000 years. Subalpine tree species are projected to be greatly reduced or lost from GYE, while habitats are expected to become suitable for species from other places in the Rocky Mountains. Rates of dispersal of native tree species may be inadequate to reach the new climates of GYE leading to more rapidly dispersing weeds becoming more dominant in the ecosystem.

Terrestrial Vertebrates

The fauna of the GYE is unique primarily in its completeness. Unlike nearly any other location in the 48 contiguous US, all species of birds and mammals present in pre-European settlement times are currently present and all are thought to have viable populations. The remote location of the GYE, the harsh climate and terrain, and the early establishment of Yellowstone National Park, slowed human development and allowed for the persistence and restoration of species such as bison (*bison bison*), elk (*Cervus canadensis*), grizzly bear (*Ursus horribilis*), wolverine (*Gulo luscus*), whooping crane (*Grus americana*), and trumpeter swan (Cygnus buccinator) that were pushed to extinction in most places by European expansion in the 1800s. The only species to become extinct in the GYE, the gray wolf (C*anus lupis*), was successfully reintroduced in 1995.

The completeness of the community allows us to draw generalizations about behavior and habitat use across species that are highly relevant to forest management. The community is characterized by a high degree of adaptation for coping with environmental heterogeneity in space and time. Also, some species of wildlife exert strong influence on ecosystem processes and on other wildlife species. These generalizations are important considerations in management strategies to maintain population viability.

Habitat Use. Most species of wildlife are not distributed evenly across GYE. Rather many species specialize on particular habitat types and biophysical settings. A study of birds across the major habitats on the northwest portion of the GYE, for example, found some species were statistically associated with each of the major habitat types (Hansen et al. 1999). Examples are: sagebrush habitats – brewer sparrow (*Spizella breweri*) and green-tailed towhee (*Pipilo chlorurus*); grassland – vesper sparrow (*Pooecetes gramineus*), grasshopper sparrow (*Ammodramus savannarum*); Douglas-fir – ruby crowned kinglet (*Regulus calendula*); and riparian deciduous woodland – American redstart (*Setophaga reticilla*), willow flycatcher (*Empidonax traillii*). Ungulates such as elk (*Cervus canadensis*) are tied to grasslands for foraging and coniferous forests for cover. An important implication is that each habitat is critical to maintaining biodiversity in the GYE because some species are dependent upon each habitat.

Such habitat specialization by species is also true for seral stages. Some species of birds and small mammals require the high light levels, herbaceous understory, and standing and fallen woody debris found in recently burned areas. For example, Hutto (1995) found 15 species of birds significantly associated with recently burned habitats. Mid seral stages are heavily used by leaf-foraging birds and understory feeders that require a dense overstory such as swainson's thrush (*Cartharus ustulatus*). Old growth seral stages with their multiple canopy layers, large trees with thick bark, and abundant standing and fallen woody debris support species such as American marten (*Martes americana*) and the southern red-backed vole (*Clethrionomys gapperi*) that forages among down woody debris, and brown creepers (*Certhia americana*) that feed on thick bark. Similarly, individual species are uniquely associated with each seral stage resulting from flooding and succession along major river systems (Hansen et al. 2003).

An important consequence is that the maintenance of appropriate disturbance regimes is necessary to provide habitats for both early and late seral species. With the reduced fire frequency in lower elevation forests of GYE over the past century, there is likely a reduced area of early seral habitats. The decline of aspen in parts of GYE is likely due to lack of fire. There is also concern about loss of population viability of species like black-backed woodpecker (*Picoides arcticus*) and three-toed woodpecker (*Picoides tridactylus*) that may be dependent upon the habitats produced by recurrent fires across the landscape. Similarly, flood control is curtailing the availability of early seral riparian habitats along some GYE rivers (Merligliano 1998). Early seral species in the Northern Rockies are likely highly adapted to moving across the landscape to find and colonize new disturbance patches. However, some minimum frequency of disturbance is necessary to maintain such species.

At the landscape level, total area of habitat and spatial configuration may influence wildlife species. The size of most vertebrate populations is related to the aerial extent of suitable habitats. Thus, likelihood of extinction increases below some threshold area and some minimum population size (Pimm et al. 1988). The minimum habitat area required for population viability has been quantified for few if any species in the GYE. However, habitat reductions in recent decades have raised concern about inadequate area of habitat for pronghorn antelope (*Antilocapra americana*), grizzly bear, sage grouse (*Centrocercus urophasianus*), amphibians, trumpeter swans, mountain plovers (*Charadrius montanus*), some riparian birds, and some cavity nesting birds in portions of the GYE (Koch and Peterson 1995, Yellowstone National Park 1997, Hansen et al. 2002, Noss 2002).

The size and shape of patches of suitable habitat within landscapes also influences vertebrates in some ecosystems, with species specializing on either edge or interior habitats. This is especially true in ecosystems with naturally large continuous habitat such as the North American prairie or the Eastern Deciduous forest. In the Rocky Mountains, however, habitats tend to be patchy due to biophysical gradients and natural disturbance. Thus, some ecologists have speculated that species in the Rockies are well adapted to variable patch size and shapes. This view was largely supported by a synthesis effort for the Rocky Mountains centered on Colorado and Wyoming (Knight et al. 2000). No bird or mammal species was identified as being strongly associated with the cores of large forest patches. A comparison of life history traits among bird species in the Rockies with those in the Eastern deciduous and Pacific Northwest forests revealed many fewer species in the Rockies with traits associated with sensitivity to patch size or edge effects (Hansen and Rotella 2000). Overall, Romme et al. (2000) concluded that "It appears that no vertebrate or vascular plant species has yet been extirpated from the Southern Rocky Mountains by the effects of forest fragmentation, although the lynx is a possibility".

Perhaps more important to wildlife in the Rockies than patch size and edge effects are biophysical gradients. Because of the limiting effects of climate and soils, many wildlife species are more abundant and have higher reproduction and survival in lower elevation and more productive landscape settings (Hansen and Rotella 2002). Community diversity is also highest in such settings (Hansen et al. 2003). For example, the American robin was found to have substantially higher population viability in low elevation riparian habitats than in high elevation riparian habitats, likely due to a longer breeding season and higher food availability (Hansen and Rotella 2002). Such low elevation productive settings are relatively rare in the GYE. Hansen et al. (unpublished data) found for example, that hot spots for bird diversity covered less than 7% of the GYE, while such hotspots covered nearly 70% of the more mesic coastal ecosystems in the Pacific Northwest. Even within a habitat type like lodgepole pine, bird species richness was higher where rhyolitic soils with ash allowed higher net primary productivity than rhyolitic soils without ash (Hansen et al. 1999). These findings suggest that identification and judicious management of low elevation and productive habitats is critically important to wildlife conservation in the GYE.

<u>Seasonal Movements</u>. Many species in GYE cope with seasonal variation in climate and food availability through short or long distance movements. The ungulate species follow increasingly well known migration routes between summer and winter range. Most of the ungulate species use higher elevation habitats in summer because the higher summer moisture allows good forage production. In winter, these species move to lower elevations where energetic costs are less severe and shallower snow cover allows better access to forage. The migrations of elk, deer, bison, are on the order of 10s of kilometers from summer to winter range. The longest migration is that of pronghorn antelope. Antelope from Grand Teton National Park move up to 225 km south into the Green River Basin (Berger 2004). These mammal migrations in GYE are the most pronounced in North America south of central Canada. Omnivores such as grizzly and black bear also

show seasonal movements based on phenology of plant foods and movements of prey. Most bird species migrate out of the GYE during the nonbreeding season to avoid the harsh winter conditions. Maintaining these migration pathways for mammals is an important management challenge in GYE. Berger (2004) estimated that about 75% of the migration routes for elk, bison, and pronghorn in GYE have been lost since presettlement times.

Wildlife Dispersal. Movements of individuals among subpopulations within the GYE and among populations across the Northern Rockies may be an important limiting factor for some GYE wildlife. The patchiness of habitats in the GYE leads to some species being distributed as subpopulations connected by some level of emigration. Such movements among subpopulations may be important for maintaining population viability (Hansen and Rotella 2002). Subpopulations in harsh biophysical settings, for example, may be sink populations in some years, where reproduction does not offset mortality. Emigration from source populations (where births exceed deaths) may increase persistence of sink populations and reduce risk of extinction of the overall metapopulation across GYE.

There is also speculation that some species such as grizzly bear disperse from GYE to other large wilderness areas in the Northern Rockies and vice versa (Craighead 1994). Such exchange of individuals would increase genetic variation and population viability (Shaefer 1991). While evidence for such long distance movement is not well developed, considerable attention has been paid to mapping and conserving potential movement corridors. Forested mountain ranges such as the Bridgers and the Centennials are thought to be such movement corridors. Maintenance of such dispersal within the GYE and with other ecosystems is an important management concern.

Wildlife Influence on Ecosystems. A subset of wildlife species in GYE may exert strong influence over ecosystem function and composition. Beaver are widely known as ecological engineers that can convert an incised stream into a large, complex wetland, improve trout habitat, and stimulate growth of riparian vegetation to the benefit of other riparian invertebrate and vertebrate species. Ungulates may change the biomass, productivity, and species composition of forage species. In grazing adapted systems, the productivity and species diversity of forage often increases with grazing intensity up to a threshold in grazing intensity, and then decreases at higher levels of grazing. In GYE, elk are known to strongly influence herbaceous and/or woody plants, often increasing diversity of herbaceous plants, but decreasing abundance of wood plants (National Research Council 2002). The roles of birds and invertebrates in driving ecosystem processes in GYE are not well studied. However, they are likely important vectors for seed dispersal, pollination, and in influencing pest outbreaks. Finally, evidence is emerging in GYE that top predators may dramatically influence the ecosystem through trophic cascades. The restoration of wolves in GYE may be: reducing mid-sized carnivores such as coyote; allowing expansion of scavenging species such as ravens; reducing the density and altering the behavior of prey species, especially elk; resulting in release of deciduous wood plants such as willow, aspen, and cottonwood; and stimulating riparian and bird and invertebrate communities (Ripple and Beschta 2003, Smith 2005).

The important conclusion is that the management of such keystone species as beaver and ungulates may have large consequences for many aspects of the ecosystem.

Key Conclusions on Wildlife Habitat and Dynamics.

1. The wildlife community of GYE is unique in that all species are present. This allows for understanding of natural interactions among species and with the ecosystem. It also presents a management challenge to maintain these species and processes.
2. Many species specialize on particular habitat types and seral stages. Maintenance of adequate area of suitable habitat and disturbances to initiate succession are management concerns.
3. Landscape settings with mesic climate, water, and high primary productivity are rare in GYE and support high species abundances and high species richness. They may also be population source areas necessary for the viability of GYE-wide populations of some species.
4. Many resident species cope with the high level of spatial and temporal heterogeneity of the GYE through seasonal movements.
5. Dispersal among subpopulations within GYE and between GYE and other ecosystems is likely important for population viability for some species.
6. Keystone species such as elk, wolves, and beaver shape ecosystem function and composition and the population dynamics of other species. Management of such species cascades through the ecosystem.

Human Land Use and Influences on Wildlife

Types and Rates. Although 68% of the GYE is publicly owned, critical resources and habitats are under-represented within the protected lands. This is because the public lands in the GYE are relatively high in elevation, harsh in climate, and are low in primary productivity, whereas the private lands are primarily in valley bottoms and floodplains with longer growing seasons, and higher plant productivity (Hansen et al. 2000). Consequently, hot spots for biodiversity and many ungulate winter ranges are largely on private lands (Hansen et al. 2002). Land use varies with ownership. Agriculture, range, rural residential development, and urban are common land use types on private lands. The GYE has 370,000 residents, most living in small cities. The national forests provide for multiple use of natural resources including recreation, forest products, forage, and minerals. The national parks serve both as nature reserves and as sites for public recreation.

The GYE is undergoing a transition in demography and land use. The population has grown about 60% since 1970, fueled partially by wealthy in-migrants that are attracted by the natural amenities. Some counties in GYE are in the upper 90% of growth rates across the US. The dominant change in land use is from natural and agricultural land uses to urban and exurban development (defined as 1 home per 0.4 to 16.2 hectares). Developed land is increasing faster than the rate of population growth. While the GYE experienced an increase in population of 58% from 1970 to 1999, there was a 350% increase in the area of rural lands supporting exurban development (Gude et al. 2006).

Some 11% of the total land area of the GYE and 43% of the unprotected land area are subject to intense land use (Hansen unpublished data). Of the many miles of river flowing through private lands in the area, only 11 % of the streamsides are not near homes, farms, or cities. Among aspen and willow habitats on private lands, critical for wildlife, only 51% of those in the Greater Yellowstone area are free from intense human land use (more than 1.6 km [1 mile] from agriculture, rural homes, or urban areas).

Major land uses on the national forests include livestock grazing, logging, mining, and motorized and nonmotorized recreation. A comprehensive assessment of rates and locations of logging has not been done across the GYE. It appears that rates of logging vary among national forests and time periods. In general, large-scale commercial logging was more widespread in the 1970's and 1980's and has been substantially scaled back. During these years, staggered-setting clearcutting over large portions of the Targhee National Forest and in portions of the Gallatin National Forest occurred. Less extensive timber harvesting was done on the Shoshone, Custer, and Bridger Teton National Forests. More recently, timbering operations have focused on smaller sales of house logs, fuels reductions projects, and salvage logging of burned areas. Extensive road systems were created in association with the logging and major road closure programs have been in place during the past decade. Livestock grazing is extensive on the National Forests of the GYE. However, historic and current levels of livestock use and effects on the ecosystem are not well known.

Public recreation has likely increased dramatically on the National Forests in recent decades. Use in winter by snowmobiles and in summer by ATVs and motorcycles is extensive and increasing. Similarly, use of backcountry area by hikers, skiers, fisherman, and campers appears to be rapidly increasing. Comprehensive data on these motorized and nonmotorized have not been compiled across the public lands of the GYE. However, travel management is currently receiving much attention across the region.

Effects on Wildlife. Land use intensification exerts influences on wildlife both in and near sites of logging, agriculture, and human settlements as well as in remaining natural parts of an ecosystem. Changes in land use influence biodiversity by altering habitat, ecological processes, biotic interactions and human disturbance (Marzluff 2001, Hansen et al. 2005). These factors act on the population dynamics of individual species via changes in rates of birth, death, and movements. The aggregate responses of individual species define patterns of community diversity.

Perhaps the most obvious repercussions of land use change are loss, fragmentation, and degradation of habitat. Conversion of natural habitats to agriculture or other intensive human land uses causes these areas to become inhospitable for many native species. This conversion also reduces the area of natural habitats. Established theories in island biogeography and empirical evidence indicate that community diversity declines as habitat area is reduced as a function of the well-known species area relationship. Smaller habitats can support fewer individuals within a population, hence rates of extinction increase with habitat loss. The spatial pattern of habitat also influences biodiversity potential. Habitats with small patch sizes, increased edge to area ratios, and increased distance among patches fail to support habitat interior specialists and species with poor dispersal abilities. Within forest stands, logging and other vegetation modifications may simplify the number of canopy layers and other elements of forest structure, reducing the microhabitats available to organisms and limit biodiversity (Hunter 1999). Habitat destruction has apparently not been a major issue in the GYE. Logging rates have declined in recent decades. Rural development has been increasing rapidly. However, the area of native habitats converted to lawns and homes and driveways is generally small relative to the remaining habitat.

Human land use can have repercussions on ecological processes. For example, agriculture and urbanization in western Colorado have altered climate and nutrient deposition in Colorado Rockies, with negative consequences for biodiversity in Rocky Mountain National Park. Natural disturbances such as wildfire are also altered by human land use. Consequently, species dependent upon early seral habitats may be lost if disturbance is suppressed or species specializing on late successional habitats may be lost if disturbance frequency and severity are increased. Natural processes likely altered by humans in the GYE include altered water quantity and quality in some rivers and streams and reduced natural disturbance. Irrigation leads to unnaturally low summer stream flows in some dry years with likely consequences for aquatic and riparian species. Also, water pollution levels are likely increasing in some rivers due to effluent from rural homes. Flooding and fire are the primary natural disturbances altered by humans in the GYE. Many of the rivers of the region are dammed or channelized, resulting in loss of or reduced flooding, riparian succession, and riparian habitat diversity (Merigliano 1998, Hansen et al. 2003). Fire suppression by humans in lower elevation forests has likely lead thus far to reduced initiation of succession, loss of early seral habitats, and reductions in wildlife species dependent upon these early seral habitats (Litell 2002). In the longer term, human fire exclusion will likely lead to unnatural levels of fuel accumulation, and large and severe fires that may be outside the range to which native species are adapted.

Some of the consequences of land use change are much less visible, because they involve not habitats but the organisms within habitats. Human activities often result in changed numbers and distributions of native species, as well as the introduction of alien species and pathogens. As a result, biotic interactions among species are changed, and ecosystem traits are altered. Exurban and agricultural development in the Rockies has been shown to lead to increases in mesopredators such as coyotes, skunks, and corivids and decreases in reproductive success of prey species such as neotropical migrant birds (Odell and Knight 2001). Rural development and agriculture in and near floodplains in the GYE has resulted in increased predators and brood parasites on native birds and reduced reproduction by some neotropical migrant birds which may be putting regional populations at risk (Hansen and Rotella 2002). Invasive plants are able to spread from rural homes and agricultural fields into adjacent natural habitats. The number of documented exotic plants in Yellowstone National Park has increased from 85 known in 1986 to over 185 today (Olliff et al. 2001), possibly due in part to human development on surrounding private lands. Also, exchange of disease among wildlife, domestic livestock and pets is a growing concern in the GYE. For example, several native wildlife species contracted Brucellosis, likely from domestic livestock, and are now managed to minimize risk of transmission back to livestock (Yellowstone National Park 1997). Similarly, whirling disease has been introduced to local rivers and streams, likely due to a human vector, causing substantial reductions of rainbow trout populations.

Humans also interact directly with native species through exploitation and inadvertent disturbance. Domestic pets may range considerable distances from rural homes and displace and kill wildlife. Bird feeders and other food sources may attract wildlife to rural homes, leading to the need to control or destroy unwanted or dangerous wildlife. Increases in roads and vehicle usage escalates the potential for roadkill. Finally, backcountry recreation such as hiking and off-road vehicle use is increasingly popular in an around natural habitats and can act to displace wildlife, influencing reproduction, survival, and population dynamics. Such human activities in the GYE have lead to increasing levels of grizzly bear mortality, raising concern about the viability of the population under continued human expansion and land use intensification.

Most of the human activities above are centered on private lands. Land use intensification in private lands may have substantial influence on public lands. This is because public lands are often parts of larger ecosystems, and are connected to private lands through flows of energy, materials, and organisms. Consequently, land use and land cover change occurring in unprotected areas of the larger ecosystem can influence park resources. Hansen and DeFries (in press) outlined four general mechanisms through which land use change on private lands may impact biodiversity on public lands (Table 1). First, land use may destroy natural habitats and reduce the effective size of the larger ecosystem which can: simplify the trophic structure as species with large home ranges are extirpated; cause the area of the ecosystem to fall below that needed to maintain natural disturbance regimes; and reduce species richness due to the loss of habitat area. Second, land use may alter characteristics of air, water, and natural disturbance moving through the public lands. Third, land use may eliminate or isolate crucial habitats, such as seasonal habitats, migration habitats, or habitats that support source populations. Fourth, land use may increase human activity along public land borders and result in the introduction of invasive species, increased hunting and poaching, and higher incidence of wildlife disturbance.

<u>Current and Potential Future Effects of Private Lands Development in the GYE.</u>
Globally, land use is on a trajectory of change that is much faster than human induced climate change and this is certainly the case in GYE. Management of public lands will be most effective if done in the context of potential future land use. Gude et al. (in press) recently used simulation modeling to project rural home density and location across the GYE under alternative scenarios. The scenarios were: continuation of current growth rates; slower growth than present; and faster growth than present. The model predicted by 2020 an increase in rural homes of 82%, 27% and 234% for these scenarios, respectively. Impacts on wildlife are presented in the next section on biodiversity elements at risk. The results make evident that private land use will substantially challenge the ability of public land managers to maintain some elements of biodiversity within the time frame of the next round of national forest plans.

Table 1. General mechanisms by which land use surrounding national parks may alter ecological processes and biodiversity within reserves. From Hansen and DeFries (in press).

Mechanism	Type	Description
Change in effective size of ecosystem	Minimum dynamic area	Temporal stability of seral stages is a function of the area of the park relative to the size of natural disturbance.
	Species Area Effect	As natural habitats in surrounding lands are destroyed, the functional size of the park is decreased and risk of extinction in the park is increased.
	Trophic structure	Characteristic spatial scales of organisms differ with trophic level such that organisms in higher levels are lost as ecosystems shrink.
Changes in ecological flows	Initiation and runout zones	Key ecological processes move across landscapes. "Initiation" and "run-out" zones for disturbance may lie outside park.
	Location in air- or water-shed	Land use in upper watersheds or airsheds may alter flows into reserves lower in the water- or air-shed.
Loss of crucial habitat	Ephemeral habitats	Lands outside of park may contain unique habitats that are required by organisms within park.
	Dispersal/ Migration habitats	Organisms require corridors to disperse among parks or to migrate from parks to ephemeral habitats.
	Population source-sink habitats	Unique habitats outside of parks are population "source" areas required to maintain "sink" populations in parks.
Increased exposure to human impacts	Edge effects	Negative human influences from the park periphery extend some distance into park.

Key Conclusions on Land Use.

1. While private lands comprise only 32% of the GYE, they are located disproportionately in the low-elevation productive habitats that are important to wildlife.
2. Human population density is increasingly rapidly in the GYE and rates of rural home development are even faster.
3. On public lands, large-scale logging has declined in recent decades, while motorized and nonmotorized recreation has likely increased substantially.
4. Intense land use can exert strong influence on wildlife by altering habitat, ecological processes, interactions among wildlife species, and human disturbance.
5. These effects can radiate considerable distances from the sites of intense land use.
6. The current challenge of maintaining wildlife on public lands will be increased in coming decades under the projected rapid intensification of human use of private lands and increased recreation on public lands.

Species, Communities, Ecosystems Most at Risk

Limited resources dictate that focus be placed on the elements of biodiversity that are the highest priority for management. This includes elements that are both at risk and likely to be responsive to USFS management actions. The current National Forest regulations specify the goal of sustaining biodiversity and ecosystem services. This goal involves levels of organization from individual species, to habitats, to communities of species and the ecological process that link them. Here we highlight some of the elements at risk across these levels of organization, with an emphasis on legal requirements, elements most important to biodiversity and ecosystem function, those most at risk due to human activities, and those that management has the best chance of success. We start with species that have been identified as at risk by the National Forests of the GYE under the previous planning rules. We then draw on the earlier GYE assessments (Hansen et al. 2002, Noss et al. 2003, Gude et al in press) to identify high priority habitat types, communities, and indices of biodiversity. This effort should be considered preliminary and be the basis for more rigorous efforts during the USFS planning process. This is especially important because the criteria for identifying species at risk will likely change under the new planning rules (Fred Samson, personal communication).

Species

Species of terrestrial mammals and birds that have been identified as at risk by the national forests of the GYE (under the previous planning rules) are listed in Table 2. Omitted are aquatic species (outside the scope of this review) and species less amenable to USFS management strategies. Many of the species considered at risk by the USFS in the GYE require the natural habitat conditions and ecological processes described above.

Management to maintain these habitats and ecological processes should help to retain many of these species. Large tracts of late seral coniferous forests are required by Canada lynx, fisher, wolverine, American marten, and northern goshawk, boreal owl and three-toed woodpecker (see Table 2 for scientific names). Black-backed woodpecker is dependent upon such forests that are recently burned. Ponderosa pine with large trees and open canopies as produced by frequent fire are key habitats for Lewis's woodpecker and flammulated owl. Species dependent upon riparian habitats include bald eagle, yellow-billed cuckoo, and river otter. Vigorous sagebrush habitats are required by pygmy rabbit, brewer's sparrow, burrowing owl, Columbian sharp-tailed grouse, and sage grouse. Grasslands, often in large tracts, and maintained in adequate condition by fire or grazing support black-footed ferret, black-tailed prairie dog, Baird's sparrow, grasshopper sparrow, and Sprague's pipit. In contrast to these species that are mostly dependent upon habitats and processes, both grizzly bear and wolf are currently most limited by interactions with people and livestock. Management of animal human conflicts may be required to maintain these species.

The list of species described above represents one iteration of species at risk as was done by national forests of the GYE under the previous forest regulations. Forest planners indicated that the list is likely to change under the new regulations. New assessments of species at risk should be done rigorously, with well formulated and objective criteria. They should draw on other high quality national and regional efforts such as those by NatureServe and Partners in Flight.

Table 2. Species of terrestrial mammals and birds identified as at risk by the national forests of the GYE (USDA 2004). Omitted are aquatic species and species not amenable to USFS management strategies. Threats and management strategies were derived from NatureServe (www.natureserve.org/explorer/servlet/NatureServe).

Species Common Name	Primary habitat	Key Threats	Key management strategies
Threatened, Endangered, or Candidate Species under the Endangered Species Act			
Gray wolf *Canus lupus*	General	Human-induced mortality	Manage human-wolf conflicts
Grizzly bear *Ursos arctos horribilis*	General	Large home range, loss of low elevation habitats, loss of whitebark pine, human-induced mortality	Reduce human-induced mortalities; provide low elevation habitats; restore whitebark pine
Canada lynx *Lynx canadensis*	Coniferous forest	Harvest, Large home range, fragmentation of coniferous forest habitats; loss of diverse age structure of habitat; loss of prey, unnatural fire frequency	Management of roads and human access; fire management to restore habitats; minimize human harvest
Bald eagle *Haliaeetus leucocephalus*	Riparian, costal	Recovered following pesticide effects and habitat loss	Maintain riparian and lacustrine habitats
Yellow-billed cuckoo *Coccyzus americanus*	Riparian	Edge of range; Loss of cottonwood and willow habitats	Maintain and restore riparian habitats
Black-footed ferret *Mustella nigripes*	Prairie	Loss of prairie, loss of prey; disease	Protect current populations, captive breeding and release
USFS Sensitive Species			
Fisher *Martes pennanti*	Coniferous forest	Harvest, fragmentation of old-growth coniferous forest	Maintain large tracts of old-growth forest, including low-mid elevations
North American wolverine *Gulo gulo*	Coniferous forest	Large home range, human encroachment, harvest	Maintain habitat for prey populations, including at low-mid elevations; minimize human harvest;
American marten *Martes Americana origins*	Coniferous forest	Harvest, fragmentation of old-growth coniferous forest	Maintain large tracts of old-growth forest, including low-mid elevations

Table 2 Continued.

Northern goshawk *Accipiter gentiles*	Coniferous forest	Harvest, fragmentation of old-growth coniferous forest	Maintain large tracts of old-growth forest
Boreal owl *Aegolius funereus*	Coniferous forests	Loss of prey due to timber harvest; large home range	Maintain large tracts of suitable habitat, large snags, aspen stands
Three-toed woodpecker *Picoides tridaclylus*	Coniferous forests	Loss of older forest	Maintain older seral stages and structural complexity
Black-backed woodpecker *Picoides arcticus*	Recently burned areas, old-growth coniferous forest	Fire exclusion; timber harvest	Maintain crown fire regimes, maintain structural complexity in timber and salvage units.
River otter *Lutra canadensis*	Riparian, lacustrine, coastal shores	Local trapping, loss of riparian habitat	Maintain riparian habitats
Flammulated owl *Otus flammulatus*	Ponderosa pine	Loss of large snags and forest structural complexity	Maintain large trees and structural complexity
Lewis's woodpecker *Malanerpes lewis*	Ponderosa pine; cottonwood	Loss of large snags; densification of open stands	Maintain large snags and open canopy with fire and silviculture
Black-tailed prairie dog *Cynomys ludovicianus*	Grasslands	Loss of prairie, disease	Maintain habitats
Baird's sparrow *Annodramus bairdii*	Grasslands	Loss and alteration of habitat due to agriculture and grazing.	Maintain medium-height grasslands, in large tracts
Grasshopper sparrow *Ammodramus savannarum*	Grassland	Loss of grassland habitats, alteration of natural fire	Maintain large tracts of grasslands; manage fire to produced relatively sparse cover
Sprague's pipit *Anthus spragueii*	Grasslands	Loss of grassland and wetland habitats	Maintain grassland and wetland habitats
Pygmy rabbit *Brachylagus idahoensis*	Shrubsteppe	Loss of shrub-steppe habitats	Protect shrubsteppe habitat, especially on floodplains

Table 2 Continued.

Brewer's sparrow *Spizella breweri*	Sagesteppe	Loss of sagebrush	Maintain vigorous sagebrush communities
Burrowing owl *Athene cunicularia*	Sagesteppe	Loss of sagebrush	Maintain sagebrush communities
Columbian sharp-tailed grouse *Tymphanuchus phasianellus columbianus*	Sagesteppe	Loss of sagebrush	Maintain sagebrush communities; manage grazing
Sage grouse *Centrocercus urophasianus*	Sagesteppe	Loss of sagebrush	Maintain sagebrush communities

Habitats

Terrestrial habitats identified as most at risk are identified on Table 3. These include habitats that are high in community diversity and energy production, support species that specialize on these habitats, are relatively low in aerial cover in the GYE, and/or are threatened by human activities such as fire exclusion. The importance of these habitats and their vulnerabilities vary across the national forests of the GYE. Thus each should be evaluated carefully in each forest's planning process.

Indices of Biodiversity

In addition to species and habitats, various methods are available to develop biodiversity indices that integrate across species, habitats, and other aspects of biodiversity. Two comprehensive efforts of this nature have been completed for the GYE. The results of both efforts are highly relevant to USFS planning.

Noss et al. (2002) performed a quantitative assessment of GYE aimed at prioritizing lands outside of protected areas for conservation value. The analysis considered several measures of biodiversity including: imperiled species, bird species, aquatic species, and rare plant communities; vegetative, abiotic, and aquatic habitat types; and high quality habitat for five focal mammal species (wolverine, lynx, grizzly bear, gray wolf, and elk). Units of land across the GYE were rated on these measures of biodiversity. The SITES selection algorithm was used to assemble and compare alternative portfolios of sites. SITES attempts to minimize portfolio "cost" in land area while maximizing attainment of conservation goals in a compact set of sites. The sites were evaluated for irreplaceability and vulnerability. Irreplaceability was a quantitative measure of the relative contribution different areas make to reaching conservation goals. Vulnerability was rated based on expert opinion with data on human population growth

Table 3. Habitats identified as at risk in the GYE. Aerial extent estimates are from Parmenter et al. (2003) and Powell (2004).

Habitats At Risk	Ecological Importance	Aerial Extent	Key Threats
Braided large river floodplains	High in species richness and NPP; seral stages support specialists species	Ca 1% of GYE	Inhibition of natural dynamics thru dams, bank stabilization, irrigation; exurban development
Other willow, cottonwood and riparian forests	High in species richness and NPP;	Ca 1% of GYE	Flood control; dewatering thru irrigation; livestock grazing; Exurban development
Grasslands	Specialist species	With sagesteppe - 35% of GYE	Exurban and urban development; agriculture; livestock grazing; alteration of fire regime; conifer encroachment
Sagesteppe	Specialist species	With grassland - 35% of GYE	Exurban and urban development; agriculture; livestock grazing; alteration of fire regime; exotic species; conifer encroachment
Aspen	High in species richness and NPP; several specialists species	Ca 1% of GYE	Lack of disturbance to reduce conifer competition and stimulate aspen regeneration; Excessive herbivory
Ponderosa pine	Specialists species	<1% of GYE	Alteration of fire regime; encroachment by other conifers; logging
Productive low elevation Douglas-fir forest	Moderately high in species richness and NPP	Ca 5% of GYE	Fire exclusion leading to densification, fuel build-up, and change to more severe fire regime; logging; exurban development
Early post-fire structurally complex coniferous forest	Specialist species	Highly variable in extent due to unpredictable crown fire	Fire exclusion in low to mid elevations
Mature and old growth coniferous forest	Specialist species	5% of GYE	Fragmentation by logging and roads
Whitebark pine	Food source for grizzly bear	5% of GYE	Climate change, disease

and land use. The analyses identified some 43 sites that best fulfilled the conservation objectives. Fifteen of the sites were identified as of greatest conservation importance because they were rated high in both irreplaceability and in vulnerability. For example, the Teton River Area near Jackson and the Henry's Fork near Island Park, ID had the highest scores. The resulting maps of the sites (e.g., Figure E10 in Noss et al. 2002) and tables of scores for irreplaceability and vulnerability offer guidance to USFS planners to locations of high conservation value.

The second assessment was by Gude et al. (in press). The focus was on the geographic overlap of biodiversity value and land use intensity past, present, and possible future. Historical land use maps were overlain on eleven biodiversity response variables. These biodiversity factors included the current ranges of four species of concern (grizzly bear, elk, pronghorn antelope, and moose), the distribution of four land cover types (Douglas-fir, grassland, aspen, riparian), and the occurrence of three different indices of biodiversity (bird hotspots, mammal migration corridors, and irreplaceable areas, from Noss et al. 2002). They found that exurban densities of rural homes occurred at higher proportions within most of these habitats than would be expected at random, indicating that these responses are at high risk to the negative impacts of development. Additionally, they integrated maps from 1980 and discovered that the percent area of currently occupied habitat that is impacted by homes has at least doubled for most variables over the past 20 years.

Based on these historical and current analyses of land use, Gude et al. (in press) projected rural home growth 20 years into the future and quantified potential impacts on biodiversity. They simulated five plausible scenarios of rural residential development for the year 2020. These scenarios ranged from low growth, to status quo (current rates of growth continue), to booming growth, and included two scenarios depicting development under growth management. These five maps depicting potential future land use scenarios were then each overlaid with each of the eleven ecological response maps used for historical analyses. Numbers of rural homes increased for all scenarios, ranging from 28% in the low growth scenario, to 234% in the boom scenario. Four of the responses were forecasted to experience degradation in at least 20% of their area under the status quo, and 30 to 40% under the boom scenario (Table 4). These were bird hotspots, riparian habitat, potential corridors, and irreplaceable areas. These elements of biodiversity should be considered especially at risk across GYE. Early warning of the vulnerability of these four habitats to land use change may help managers to develop strategies for mitigating future effects.

Context and Guidelines for Managing for Biodiversity

This review indicates that the GYE is a complex ecosystem with many ecological processes and organisms operating over very large spatial scales and the system is undergoing rapid change in climate and land use. Consequently, ecological management presents numerous challenges. Fortunately, the ecosystem has been less altered by human activities than most areas of the US and the opportunity remains to sustain ecological processes and native organisms under future global change. This section presents guidelines for management largely derived from the ecological review earlier in the paper.

Table 4. The percent of area impacted by exurban development is presented for each of twelve biodiversity response variables. The impacts of exurban development were assumed to extend into one neighboring section (1.61km). Table adapted from Gude et al. (in press).

			Growth Scenario			Growth Management Type	
Response	1980	1999	Status Quo 2020*	Low 2020	Boom 2020	Moderate 2020	Aggressive 2020
Pronghorn (Antilocapra americana) Range	2.00%	3.35%	5.83%	5.05%	7.58%	6.06%	4.73%
Moose (Alces alces) Range	2.73%	5.49%	7.96%	6.83%	11.11%	7.24%	6.26%
Grasslands	2.99%	5.57%	8.36%	7.02%	11.97%	8.01%	6.87%
Grizzly Bear (Ursus horribilis) Range	3.13%	5.98%	8.52%	7.68%	10.70%	7.74%	6.88%
Douglas-fir	2.91%	6.01%	8.85%	7.07%	13.31%	7.82%	7.09%
Elk (Cervus elaphus) Winter Range	2.36%	6.26%	9.98%	8.61%	13.47%	9.00%	7.23%
Aspen	5.55%	13.92%	19.53%	15.58%	28.39%	18.74%	17.60%
Bird Hotspots	8.42%	16.91%	23.20%	19.23%	34.36%	21.04%	20.23%
Riparian Habitat	10.22%	17.30%	23.64%	19.43%	31.27%	22.45%	18.77%
Potential Corridors	8.89%	18.79%	24.43%	20.83%	35.38%	22.96%	21.80%
Irreplaceable Areas[1]	11.41%	23.15%	29.61%	25.69%	40.08%	30.88%	26.92%
Integrated Index[2]	11.80%	23.24%	29.93%	25.84%	40.66%	29.28%	26.43%

* Responses are ranked by the proportion impacted in the Status Quo 2020 scenario; [1] Multicriteria assessment based on habitat and population data for GYE species (Noss et al., 2002); [2] Top 25% of lands important to the four responses most impacted by development under the Status Quo 2020 scenario, including bird hotspots, riparian habitat, potential corridors, and irreplaceable areas.

Spatial Scale

While the USFS is the largest land holder in the GYE, it is apparent that many ecological processes and organisms operate at spatial scales larger than the national forests and include the full suite of private and public lands of the GYE. USFS management will be most effective if it is done in full recognition of large spatial scaling of the system. Three scales of management are evident: within a national forest, across public lands, and among all ownerships of the GYE.

Most USFS employees have jurisdiction only within the boundaries of their national forest. Thus there is the temptation to ignore factors outside these boundaries and to focus on important challenges within the forest. In some cases, however, management within the national forest will be more effective if conducted within the context of broader spatial scales. For example, the presence of rural homes on the boundary of the forest may necessitate a more conservative prescribed fire regime within the forest to minimize threat to the homes. The presence of these homes on the forest boundary may also increase invasion of the forest by weedy plants, hence additional weed control measures may be needed in the forest. Knowledge of ecological connections across the broader ecosystem provides a basis for management within the portion of the ecosystem that is within the national forest.

Public lands comprise some 68% of the GYE. These national forests, national parks, and USFWS refuges often are similar ecologically and often share borders. Coordinated management and data sharing among these public land entities can be efficient and cost effective. In recognition of these advantages, the Greater Yellowstone Coordinating Committee was formed in 1986 as a vehicle for this integration and cooperation among federal agencies of the GYE. The GYCC has been successful in integrated research and management on whitebark pine, fire, and ungulates. Continuation and expansion of this cooperative effort can enhance integration of maps and data, development of decision support tools, inventory and monitoring, and other management activities.

Perhaps the most difficult level of management is between public and private entities. Considerable tension and even mistrust may exist between private land owners and federal personnel. Mutual benefits can ensue by information exchange and in some cases cooperative management. The USFS can provide a great service to county planners and private land owners by sharing maps and data on ecological processes and organisms that operate over larger scales. This can help local citizens better understand connections among lands across the GYE and to better prioritize the location and type of land use activities. Such cooperation can help the USFS by facilitating management on private lands that helps the USFS achieve is ecological objectives. Such management might include establishing conservation easements on important sites and/or land exchanges that promote public and private values. The Gallatin National Forest, for example, successfully concluded a major land exchange with a large private owner which reduced the pattern of checkerboard ownership in proximity to Yellowstone National Park. Positive interaction with private land owners and the public can also aid the USFS by helping to educate citizens on behavior and practices in the backcountry and at rural home sites that minimizes negative ecological impacts.

Goals for such regional-scale cooperative management can be derived from knowledge of the ways that use of private lands influences public lands. The ecological mechanisms linking public and private lands lead to design criteria for regional landscapes (Table 5). These include: maximize area of functional habitats; identify and maintain ecological process zones; maintain key migration and source habitats; and manage human proximity and edge effects. The USFS can help facilitate such regional scale management through the communication, cooperation, and incentives-based approaches described above.

Climate Change

Climate change presents an especially difficult challenge to forest managers. The rate of change in climate, while very rapid on the scale of millennia, is slow relative to the forest planning period of 10 years. Thus, more rapidly changing issues are often considered higher priorities. At the same time, natural variability combined with climate change can bring rapid extreme weather that leads to the ecological outcomes expected under climate change requiring management action. The extreme fires in the west under the drought conditions of the last five years are an example. Finally, there is considerable

Table 5. Criteria for managing regional landscapes to reduce the impacts of land use change outside of nature reserves on ecological processes and biodiversity within reserves. From Hansen and DeFries (in press).

Mechanism	Type	Design Criteria
Change in effective size of reserve	Species Area Effect Minimum Dynamic Area Trophic Structure	Maximize area of functional habitats
Changes in ecological flows into and out of reserve	Disturbance initiation and runout zones Placement in watershed or airshed	Identify and maintain ecological process zones
Loss of crucial habitat outside of reserve	Ephemeral habitats Dispersal or migration habitats Population source sink habitats	Maintain key migration and source habitats
Increased exposure to human activity at reserve edge	Poaching Displacement Exotics/disease	Manage human proximity and edge effects

uncertainty in our ability to predict future climate for a place or likely ecological responses. Thus, the form and outcome of human-induced climate change is difficult to anticipate.

As climate change is more fully manifest, forest managers will likely face substantial engineering of ecological systems (Hansen et al. 2001). For communities that are unlikely to reach suitable environments elsewhere (e.g., subalpine and alpine communities), for example, it may be appropriate to minimize change by manipulating vegetation structure, composition, and/or disturbance regimes to favor the current community. For communities that may be able to reach newly suitable habitats, a reasonable strategy may be to manage some of the current habitat as a reservoir until the community is reestablished in the new locations. Other portions of the current habitat may be managed to encourage change to the new species and communities more appropriate for the new environment. Global change could offer opportunities to restore communities that are now degraded. In this case, management to induce rapid change may allow for the establishment of more desirable species. Attempting to maintain connectivity among national forests and other wildlands is also important for allowing natural dispersal of organisms.

For the near future, forest managers may do best to conduct their activities in the context of a changing climate. This would include recognition that forest dynamics do operate on the time scale of the current climate change. Hence, the concept of NRV is of limited value as a guide to forest management because climate and forest response have been changing since pre-European settlement times. Similarly, we should not assume that forests will respond to a given treatment in future decades as they have in past decades because of the influence or changing climate. Forest managers can also anticipate and prepare for some of the ecosystem changes expected under climate change including reduced water yield, more severe fire, increased invasive weeds and diseases, and decline of sensitive species such as whitebark pine.

Disturbance and Vegetation Succession

Managing natural and human disturbance remains critically important in natural forests under the current regime of climate and land use change. Exclusion of fire, flooding, timber harvesting, and other natural and human disturbances leads to inadequate early seral conditions and loss of species associated with these conditions. Also, fuel loads may build, resulting in catastrophic fires that reset the system to a new, less desirable state.

While the concept of NRV may not longer be a direct guide for management, past successional trajectories and vegetation structures (Figure 2) provide the basis for setting management objectives. Forest managers should attempt to maintain the full range of seral stages and structural complexities. Means for accomplishing this include: natural and prescribed fire; timber harvest, thinning, and other silvicultural practices; livestock grazing; and maintenance of natural flooding regimes. These disturbances should occur across time and space so as to maintain a dynamic steady state mosaic of seral stages across the landscape and maintain the range of organisms dependent upon them.

Use of fire to accomplish these objectives is made difficult by risk to the increasing number of rural homes near forest boundaries. Landscape-level analysis and planning can be used to identify the locations in the landscape where each disturbance type should best be used. For example, natural fires may be allowed to burn in locations in the landscape distant from human dwellings. Prescribed fire during less risky times of year may best be used in zones closer to the urban interface. Fire may be too risky in close proximity to homes and here, thinning, timber harvest, and other fuels reduction efforts may be used.

In both burned and logged areas, attention to within stand structural complexity is important. Much progress has been made in designing timber harvest units to accomplish both economic and ecological objectives (Hunter 1999). Salvage logging of burned areas continues to be an important issue. Intensive salvage logging may substantially reduce structural complexity and habitat quality within burned areas and should be done in ways that promote biodiversity objectives (Hutto 1995).

Fire and silviculture may also be applied to restore early seral habitats that have been declining over the past century. Aspen, sage steppe, and grasslands may be restored from conifer encroachment by applying these disturbances. These efforts may be most successful if they are applied in places in the landscape where the target communities are most likely to have a positive response. Brown (in review), for example, identified the places in the GYE that have the biophysical conditions that favor aspen presence and growth. Restoration attempts within these locations should produce more rapid aspen response.

Flooding and channel migration are critically important disturbances in stream and riparian systems. The large river floodplains that support well-developed riparian forests are largely off USFS lands. Some impoundments and other water control structures are under USFS jurisdiction. Managing these to promote natural levels of flooding would contribute to maintaining ecologically-important flood plain dynamics.

Human Activities on USFS Lands

The rapid increase in outdoor recreation in the national forests causes this to be one of the major management issues faced by the forest service. Current data on rates and location are lacking for many forms of recreation and ecological impacts are not well understood. The national forests of the GYE would benefit by developing an integrated data base to document and analyze the spatial distribution and rates of camping, motorized use (on and off road), and nonmotorized backcountry hiking, skiing, boating, bicycling, and climbing. Studies of the ecological consequences of these activities are also needed. Such knowledge would provide a basis for developing access plans that best balance human and ecological objectives. The current access assessment on the Gallatin National Forest is an excellent example.

Biotic Interactions

Human activities often cause some species to become over abundant and others to become less abundant. As a consequence, interactions between these species and others in the community may be altered. While the USFS does not manage animal populations, the actions of the USFS may influence abundances and interactions of animals. Managing habitats to maintain viable populations of top carnivores such as grizzly bears and wolves promotes healthy trophic cascades through the ecosystem to the benefit of small carnivores, scavengers, wood plants, bird communities, and invertebrate communities. Managing campgrounds and livestock feed lots to reduce human provisioning of food to wildlife can help to reduce the expansion of native and nonnative mesocarnivores such as raccoons, skunks, opossums, magpies, and cowbirds, and reduce their devastating impacts on other native species. And, of course, management to reduce invasion by noxious weeds is critical for maintaining healthy ecosystems.

Summary of Management Guidelines

1. Biodiversity goals of the USFS will best be advanced through the USFS participating in management at multiple spatial scales including: within a national forest, among public lands of the GYE; and across the public and private lands of the GYE. At the regional scale, the USFS can help private land managers understand ecological connections, prioritize important places, and implement criteria for maintaining biodiversity across the GYE in the face of land use intensification. These efforts should be guided through a scientific assessment of the lands across the GYE that are most important for the maintenance of native biodiversity on public lands.
2. Human induced climate change will increasingly influence national forests and require management attention. In the coming decade, USFS managers should conduct their activities in the context of a changing climate, recognizing that current and future forest dynamics will likely differ from the past. In the longer term, ecological engineering may be required to maintain ecological values in the face of substantial climate change.
3. Careful management of disturbances such as fire, flooding, and timber harvest is needed to maintain the full suite of seral stages and structural complexities across the

GYE. In the face of climate and land use change, Natural Range of Variation is increasingly inappropriate as a guide for managing disturbance. Rather, managers should apply disturbance so as to achieve the dynamic steady state mosaic across the landscape that is required to maintain native organisms. This effort would be advanced through compilation of the wildlife species associated with each seral stage and structural configuration across the habitat types of the GYE and the landscape configuration of seral stages that best promotes maintenance of native species. Also, restoration of habitats now at risk due to lack of disturbance should be a high priority.

4. More scientific approaches are needed for effective management of recreation on national forests. Data systems are needed to monitor recreation type and intensity in a spatially-explicit manner. Research is needed on the effects of various types and intensities of recreation on biodiversity.

5. Changes in species abundances can cascade through ecosystems resulting in undesirable changes. The USFS can help to better maintain balanced wildlife communities through maintaining habitat for top carnivores, managing campgrounds and feed lots to reduce food provisioning to mesocarnivores, and controlling noxious weeds.

Literature Cited

Baker, W. 1992. The landscape ecology of large disturbances in the design and management of nature reserves. Landscape Ecology 7(3):181-94.

Barrett, S.W. 1994. Fire regimes on andesitic mountain terrain in northeastern Yellowstone National Park, Wyoming. International Journal of Wildland Fire 4:65-76.

Bartlein, P. J., Whitlock, C., and Shafer, S. 1997. Future climate in the Yellowstone National Park region and its potential impact on vegetation. Conservation Biology 11: 782-792.

Berger, J. 2004. The Last Mile: How to Sustain Long-Distance Migration in Mammals. Conservation Biology 18:320-331.

Bormann, F.H., and G.E. Likens. 1979. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York, New York, USA.

Bowerman, T.S., J. Dorr, S. Leahy, K. Varga, J. Warrick. 1997. Targhee National Forest Ecological Unit Inventory. USDA Forest Service, Targhee National Forest, St. Anthony, ID.

Brown, K., A.J. Hansen, R.E. Keane, L.J. Graumlich. In Press. Complex interactions shaping aspen dynamics in the Greater Yellowstone Ecosystem. Landscape Ecology.

Clark T.W, S.C. Minta. 1994. Greater Yellowstone's Future: Prospects for Ecosystem Science, Management, and Policy. Island Press, Washington DC.

Craighead, J.J. 1991. Yellowstone in transition. Pages 27–40 in R.B. Kieter, M.S. Boyce, eds. The Greater Yellowstone Ecosystem: Redefining America's Wilderness Heritage. Yale University Press, New Haven, CT.

Craighead, F.L. 1994. Conservation Genetics of Grizzly Bears. PhD dissertation. Montana State University, Bozeman Montana. 227 pp.

Davis, C., and H.F. Shovic. 1996. Soil Survey of the Gallatin National Forest, Montana. USDA Forest Service, Gallatin National Forest, Bozeman, MT.

Despain, D.G., 1990. Yellowstone Vegetation: Consequences of Environment and History in a Natural Setting. Roberts Rinehart Publishers, Boulder, CO.

Federal Register 2005.National Forest System Land and Resource Management Planning: Removal of 2000 Planning Rule. Federal Register 70:3.

Fischer, W.C. and G.D. Clayton 1983. Fire ecology of Montana forest habitat types east of the Continental Divide. US Forest Service General Technical Report INT-141.

Gallant, A.L. A.J. Hansen, J.S. Councilman, D.K. Monte, and D.W. Betz. 2003. Vegetation Dynamics under fire exclusion and logging in a Rocky Mountain watershed: 1856-1996. Ecological Applications 13(2):385-403.

Glick, D., M. Carr, and B. Harting. 1991. An Environmental Profile of the Greater Yellowstone Ecosystem. Bozeman, Montana, Greater Yellowstone Coalition.

Gude, P.H., A.J. Hansen, R. Rasker, B. Maxwell. 2006. Rate and drivers of rural residential development in the Greater Yellowstone. Landscape and Urban Planning 77:131-151.

Gude, P.H., A.J. Hansen, D.A. Jones. In press. Biodiversity consequences of alternative future land use scenarios in Greater Yellowstone. Ecological Applications.

Hansen, A.J., J.J. Rotella, and M.L. Kraska. 1999. Dynamic habitat and population analysis: A filtering approach to resolve the biodiversity manager's dilemma. Ecological Applications 9(4):1459–1476.

Hansen, A.J., J.J. Rotella, M.L. Kraska and D. Brown. 2000. Spatial patterns of primary productivity in the Greater Yellowstone Ecosystem. Landscape Ecology. 15:505-522.

Hansen, A.J. and J.J. Rotella. 2000. Bird responses to forest fragmentation. Pgs 202-221 in R.L. Knight, F.W. Smith, S.W. Buskirk, W.H. Romme, and W.L. Baker, (eds.) Forest Fragmentation in the Southern Rocky Mountains. University of Colorado Press, Boulder, CO.

Hansen, A.J., R.P. Neilson, V. Dale, C. Flather, L. Iverson, D. J. Currie, S. Shafer, R. Cook, P. Bartlein. 2001. Global Change in Forests: Interactions among Biodiversity, Climate, and Land Use. BioScience 51(9):765-779.

Hansen, A.J., R. Rasker, B. Maxwell, J.J. Rotella, A. Wright, U. Langner, W. Cohen, R. Lawrence, J. Johnson. 2002. Ecology and socioeconomics in the New West: A case study from Greater Yellowstone. BioScience 52(2)151-168.

Hansen, A.J., and J.J. Rotella. 2002. Biophysical factors, land use, and species viability in and around nature reserves. Conservation Biology 16(4):1-12.

Hansen, A.J., J. Rotella, D.A. Jones, L.P. Klaas. 2003. Riparian habitat dynamics and birds along the upper Yellowstone River. Technical Report #1, Landscape Biodiversity Lab, Montana State University, Bozeman, MT.

Hansen, A.J., R. Knight, J. Marzluff, S. Powell, K. Brown, P. Hernandez, and K. Jones. 2005. Effects of exurban development on biodiversity: Patterns, Mechanisms, Research Needs. Ecological Applications 15(6):1893-1905.

Hansen, A.J., DeFries, R., In Press. Ecological mechanisms linking nature reserves to surrounding lands: a conceptual framework for assessing implications of land use change. Ecological Applications.

Houghton, J. T., Y. Ding, D.J. Griggs, M. Noguer, P. J. van der Linden and D. Xiaosu (Eds.). 2001. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC). Cambridge University Press, Cambridge, UK. pp 944

Hunter, M.L., Jr. 1999. Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, Cambridge, UK.

Hutto, R.L. 1995. Composition of Bird Communities Following Stand-Replacement Fires in Northern Rocky Mountain (U.S.A.) Conifer Forests. Conservation Biology 9(5):1041-1058.

Keiter, R.B. and M.S. Boyce. 1991. The Greater Yellowstone Ecosystem: Redefining America's Wilderness Heritage. Yale University Press. New Haven.

Knight, D.H., 1994. Mountains and Plains: The Ecology of Wyoming Landscapes. Yale University Press, New Haven, CT.

Knight, R.L. F.W. Smith, S.W. Buskirk, W.H. Romme, W.L. Baker. 2000. Forest Fragmentation in the Southern Rocky Mountains. University of Colorado Press. Boulder, CO.

Koch, E.D and C.R. Peterson. 1995. The amphibians and reptiles of Yellowstone and Grant Teton National Parks. University of Utah Press, Salt Lake City, UT.

Landres, P.B., P. Morgan, and F.J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9:1179-1188.

Littell, J.S., 2002. Determnants of fire regime variability in lower elevation forests of the northern Greater Yellowstone Ecosystem. Thesis. Montana State University, Bozeman, MT.

Marzluff, J. M. 2001. Worldwide urbanization and its effects on birds. Pgs 19-48 in J.M. Marzluff, R. Bowman, and R. Donnelly, eds., Avian Ecology and Conservation in an Urbanizing World. Kluwer Academic Publishers, Boston.

Meagher, M., and D.B. Houston. 1998. Yellowstone and the Biology of Time: Photographs across a Century. University of Oklahoma Press, Norman, OK.

Merigliano, M.F. 1998. Cottonwood and willow demography on a young island, Salmon River, Idaho. Wetlands 18(4):571-576.

Millspaugh, S.H., Whitlock C. and Bartlein, P. 2004. Postglacial fire, vegetation, and climate history of the Yellowstone-Lamar and Central Plateau provinces, Yellowstone National Park. In After the Fires: The Ecology of Change in Yellowstone National Park (L. Wallace, ed.). Yale University Press. New Haven, CT.

Mock, C.J. 1996. Climatic Controls and Spatial Variations of Precipitation in the Western United States. J of Climate. 9(5):1111-1125.

National Research Council. 2002. Ecological Dynamics ON Yellowstone's Northern Range. National Academy Press, Washington, D.C.

Noss R.F., C. Carrol, K. Vance-Borland, G. Wuerthner. 2002. A multicriteria assessment of the irreplaceability and vulnerability of sites in the Greater Yellowstone Ecosystem. Conservation Biology 16(4)**:** 895-908.

Odell, E. A., and R. L. Knight. 2001. Songbird and medium-sized mammal communities associated with exurban development in Pitkin County, Colorado. Conservation Biology 15: 1143-1150.

Olliff, T., R. Renkin, C. McClure, P. Miller, D. Price, D. Reinhart, and J. Whipple. 2001. Managing a complex exotic vegetation program in Yellowstone National Park. Western North American Naturalist 61(3): 347-358.

Pederson, GT, S.T. Gray, D.B. Fagre, and L.J. Graumlich. In press. Long-Duration Drought Variability and Impacts on Ecosystem Services: A Case Study from Glacier National Park, Montana USA. Earth Interactions.

Pickett, S.T.A., and J.N. Thompson. 1978. Patch dynamics and the design of nature reserves. Biol. Conserv. 13:27-37.

Pimm, S.L., H.L. Jones, and J. Diamond. 1988. On the risk of extinction. American Naturalist 132(6):757-785.

Powell, S.L., 2004. Conifer cover increase in the Greater Yellowstone Ecosystem: Rates, extent, and consequences for carbon. Ph.D. dissertation, Ecology Department, Montana State University, Bozeman, MT.

Powell, S.L., A.J. Hansen. In press. Conifer cover increase in the Greater Yellowstone Ecosystem: Frequency, rates, and spatial variation. Ecosystems.

Rasker, R., 1991. Dynamic economy versus static policy in the Greater Yellowstone ecosystem. Pgs. 8–11 in Proceedings to the Conference on the Economic Value of Wilderness, Jackson, WY.

Ripple, W.J., and R.L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? BioScience 54:755-766.
Rodman, A., H. Shovic and D. Thoma. 1996. Soils of Yellowstone National Park. Yellowstone Center for Resources, Yellowstone National Park, Wyoming, YCR-NRSR-96-2.
Romme WH . 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs 52:199-221. Uses fire scars and tree ages to quantify the temporal and spatial patterns of fire and succession.
Romme, W.H. and D.G. Despain. 1989. Historical perspective on the Yellowstone fires of 1988. BioScience 39:695-699.
Romme, W.H., and M.G. Turner. 2004. Ten years after the 1988 Yellowstone fires: Is restoration needed? Pgs. 318-361. In L. Wallace, Ed, In After the Fires: The Ecology of Change in Yellowstone National Park. Yale University Press. New Haven, CT.
Romme, W.H., R.L. Knight, W.L. Baker, F.W. Smith, S.W. Buskirk. 2000. What have we learned about forest fragmentation in the southern Rocky Mountains? Pgs 423-430 in R.L. Knight, F.W. Smith, S.W. Buskirk, W.H. Romme, and W.L. Baker, (eds.) Forest Fragmentation in the Southern Rocky Mountains. University of Colorado Press, Boulder, CO.
Shafer, S.L., P.J. Bartlein, and R.S. Thompson. 2001. Potential changes in the distributions of western North America tree and shrub taxa under future climate scenarios. Ecosystems. 4:200-215.
Shaffer, M.L. 1991. Minimum population size for species conservation. BioScience 31:131-134.
Smith, D. W. 2005. Ten Years of Yellowstone Wolves, 1995-2005. Yellowstone Science 13(1)7-33.
Thornton, P.E., S.W. Running, and M.A. White. 1997. Generating surfaces of daily meteorology variables over large regions of complex terrain. Journal of Hydrology 190:214-251.
Turner, M.G., D.B. Tinker, W.H. Romme, D.M. Kashian, C. M. Litton. 2004. Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). Ecosystems 7:751-775.
USDA 2004. Grizzly bear conservation for the Greater Yellowstone Area national forests. Draft Environmental Impact Statement. Gallatin National Forest, Bozeman, MT.
Whitlock, C. 1993 Postglacial vegetation and climate of Grand Teton and southern Yellowstone National Parks. Ecological Monographs 63: 173-198.
Yellowstone National Park. 1997. Yellowstone's northern range: complexity and change in a wildland ecosystem. National Park Service, Mammoth Hot Springs, WY.

Annotated Bibliography of Key References

Baker, W. 1992. The landscape ecology of large disturbances in the design and management of nature reserves. Landscape Ecology 7(3):181-94.
Applies theory on natural disturbance to nature reserves.

Barrett, S.W. 1994. Fire regimes on andesitic mountain terrain in northeastern Yellowstone National Park, Wyoming. International journal of Wildland Fire 4:65-76.
Uses fire scars to reconstruct fire regimes in the Douglas-fir zone.

Bartlein, P. J., C. Whitlock, and S. Shafer. 1997. Future climate in the Yellowstone National Park region and its potential impact on vegetation. Conservation Biology 11: 782-792.
Uses climate predictions from global circulation models to protect future vegetation.

Berger, J. 2004. The Last Mile: How to Sustain Long-Distance Migration in Mammals. Conservation Biology 18(2)320-331.
Synthesizes knowledge on mammal migrations globally with emphasis on GYE.

Bormann, F.H., and G.E. Likens. 1979. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York, New York, USA.
Classic work on landscape-scale disturbance and succession patterns.

Bowerman, T.S., J. Dorr, S. Leahy, K. Varga, J. Warrick. 1997. Targhee National Forest Ecological Unit Inventory. USDA Forest Service, Targhee National Forest, St. Anthony, ID.
Maps and describes the soils, disturbances, and successional sequences for major habitat types in the Targhee National Forest.

Brown, K., A.J. Hansen, R.E. Keane, L.J. Graumlich. In Press. Complex interactions shaping aspen dynamics in the Greater Yellowstone Ecosystem. Landscape Ecology.
First GYE-wide quantification of aspen presence, growth rate, change in cover, and biophysical correlates.

Clark TW, S.C. Minta. 1994. Greater Yellowstone's Future: Prospects for Ecosystem Science, Management, and Policy. Washington (DC): Island Press.
Detailed overview of GYE natural resource policy issues.

Craighead, F.L. 1994. Conservation Genetics of Grizzly Bears. PhD dissertation. Montana State University, Bozeman Montana. 227 pp.
Evaluation of genetic make-up of the Grizzly.

Davis, C., and H.F. Shovic. 1996. Soil Survey of the Gallatin National Forest, Montana. USDA Forest Service, Gallatin National Forest, Bozeman, MT.
Detailed description of soils.

Despain, D.G., 1990. Yellowstone Vegetation: Consequences of Environment and History in a Natural Setting. Roberts Rinehart Publishers, Boulder, CO.
Current definitive work on biophysical setting, disturbance, and succession of vegetation organized by habitat type.

Fischer, W.C. and G.D. Clayton 1983. Fire ecology of Montana forest habitat types east of the Continental Divide. US Forest Service General Technical Report INT-141. Describes fire regimes and successional sequences for the major habitat types of this region.
Synthesis of disturbance and succession of major forest habitat types.

Gallant, A.L. A.J. Hansen, J.S. Councilman, D.K. Monte, and D.W. Betz. 2003. Vegetation Dynamics under fire exclusion and logging in a Rocky Mountain watershed: 1856-1996. Ecological Applications 13(2):385-403.
Uses simulation model to reconstruct vegetation composition, seral stage, and spatial distribution across a watershed in the Centennial Mountains.

Glick, D., M. Carr, and B. Harting. 1991. An Environmental Profile of the Greater Yellowstone Ecosystem. Bozeman, Montana, Greater Yellowstone Coalition.
Overviews social and natural resource patterns across the GYE.

Gude, P.H., A.J. Hansen, D.A. Jones. In press. Biodiversity consequences of alternative future land use scenarios in Greater Yellowstone. Ecological Applications.
Quantifies rural home development from 1860 to present, projects future homes to 2020 under five alternatives, evaluates overlap of rural homes with 11 indices of biodiversity.

Hansen, A.J., J.J. Rotella, and M.L. Kraska. 1999. Dynamic habitat and population analysis: A filtering approach to resolve the biodiversity manager's dilemma. Ecological Applications 9(4):1459–1476.
Provides a method for integrating habitat and population dynamics for prioritizing species and places for conservation.

Hansen, A.J., J.J. Rotella, M.L. Kraska and D. Brown. 2000. Spatial patterns of primary productivity in the Greater Yellowstone Ecosystem. Landscape Ecology. 15:505-522.
Estimates spatial patterns of aboveground primary productivity based on vegetation growth rates.

Hansen, A.J. and J.J. Rotella. 2000. Bird responses to forest fragmentation. Pgs 202-221 in R.L. Knight, F.W. Smith, S.W. Buskirk, W.H. Romme, and W.L. Baker, (eds.) Forest Fragmentation in the Southern Rocky Mountains. University of Colorado Press, Boulder, CO.
Compares bird communities from the Eastern Deciduous Forest, Rocky Mountains and the Pacific Northwest in response to habitat fragmentation based on life history characteristics.

Hansen, A.J., R.P. Neilson, V. Dale, C. Flather, L. Iverson, D. J. Currie, S. Shafer, R. Cook, P. Bartlein. 2001. Global Change in Forests: Interactions among Biodiversity, Climate, and Land Use. BioScience 51(9):765-779.
Projects response of biomes, vertebrate community richness, and individual tree species to alternative climate scenarios under a doubling of CO_2.

Hansen, A.J., R. Rasker, B. Maxwell, J.J. Rotella, A. Wright, U. Langner, W. Cohen, R. Lawrence, J. Johnson. 2002. Ecology and socioeconomics in the New West: A case study from Greater Yellowstone. BioScience 52(2)151-168.
Assesses interactions among land use, biophysical factors, biodiversity, and socioeconomics.

Hansen, A.J., and J.J. Rotella. 2002. Biophysical factors, land use, and species viability in and around nature reserves. Conservation Biology 16(4):1-12.
Evaluates population dynamics of two bird species and concludes that human land use on private lands influences population viability in Yellowstone National Park.

Hansen, A.J., J. Rotella, D.A. Jones, L.P. Klaas. 2003. Riparian habitat dynamics and birds along the upper Yellowstone River. Technical Report #1, Landscape Biodiversity Lab, Montana State University, Bozeman, MT.
Quantifies bird species abundances and community diversity across successional stages and river reach types.

Hansen, A.J., R. Knight, J. Marzluff, S. Powell, K. Brown, P. Hernandez, and K. Jones. 2005. Effects of exurban development on biodiversity: Patterns, Mechanisms, Research Needs. Ecological Applications 15(6):1893-1905.
Provides a broad synthesis of current knowledge on how rural homes influence biodiversity.

Hansen, A.J., R. DeFries. In press. Ecological mechanisms linking nature reserves to surrounding lands: a conceptual framework for assessing implications of land use change.
Synthesizes ecological theory to identify mechanisms by which land use around protected areas influences biodiversity within protected areas.

Houghton, J. T., Y. Ding, D.J. Griggs, M. Noguer, P. J. van der Linden and D. Xiaosu (Eds.). 2001. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC). Cambridge University Press, Cambridge, UK. pp 944
Provides primary conclusions on global climate change on this international panel of scientists.

Hunter, M.L., Jr. 1999. Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, Cambridge, UK.
Exhaustive text on the topic.

Hutto, R.L. 1995. Composition of Bird Communities Following Stand-Replacement Fires in Northern Rocky Mountain (U.S.A.) Conifer Forests. Conservation Biology 9(5) 1041-1058.
Summarizes patterns of bird abundance across the major succession gradients of the region.

Keiter, R.B. and M.S. Boyce. 1991. The Greater Yellowstone Ecosystem: Redefining America's Wilderness Heritage. Yale University Press. New Haven.
First comprehensive synthesis of ecological factors across the GYE.

Knight, D.H., 1994. Mountains and Plains: The Ecology of Wyoming Landscapes. Yale University Press, New Haven, CN. USA.
The major work on vegetation distribution and driving factors across Wyoming.

Knight, R.L. F.W. Smith, S.W. Buskirk, W.H. Romme, W.L. Baker. 2000. Forest Fragmentation in the Southern Rocky Mountains. University of Colorado Press.
Edited book synthesizing knowledge on the topic and effects on wildlife.

Landres, P.B., P. Morgan, and F.J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9:1179-1188.
Excellent overview on the concept of natural range of variation.

Littell, J.S., 2002. Determinants of fire regime variability in lower elevation forests of the northern Greater Yellowstone Ecosystem. Thesis. Montana State University, Bozeman, Montana, USA.
Uses tree age and fire scars to reconstruct fire patterns, especially over the last three centuries.

Marzluff, J. M. 2001. Worldwide urbanization and its effects on birds. Pgs 19-48 in J.M. Marzluff, R. Bowman, and R. Donnelly, eds., Avian Ecology and Conservation in an Urbanizing World. Kluwer Academic Publishers, Boston, USA.
Draws on international literature to develop conceptual models of bird response to the rural to urban gradient.

Meagher, M., and D.B. Houston. 1998. Yellowstone and the Biology of Time: Photographs across a Century. University of Oklahoma Press, Norman, OK.
Provides comprehensive set of photo retakes from 1880s, 1970s and 1990s and draws conclusion for ecological dynamics.

Merigliano, M.F. 1998. Cottonwood and willow demography on a young island, Salmon River, Idaho. Wetlands 18(4):571-576.
Field study of riparian forest response to flooding and flood control.

Millspaugh, S.H., C. Whitlock, and P.Bartlein. 2004. Postglacial fire, vegetation, and climate history of the Yellowstone-Lamar and Central Plateau provinces, Yellowstone National Park. In After the Fires: The Ecology of Change in Yellowstone National Park (L. Wallace, ed.). Yale University Press.
Contrasts vegetation, climate, fire for the NE part of YNP (summer wet) with the south and western part of YNP (summer dry) for the Holocene.

Mock, C.J. 1996. Climatic Controls and Spatial Variations of Precipitation in the Western United States. J of Climate. 9(5):1111-1125.
Describes the various climate systems across the western US with reference to GYE.

National Research Council. 2002. Ecological Dynamics on Yellowstone's Northern Range. National Academy Press, Washington, D.C.
Congressionally mandated synthesis of knowledge on ungulates effects on ecosystems in this area.

Noss R.F., C. Carrol, K. Vance-Borland, G. Wuerthner. 2002. A multicriteria assessment of the irreplaceability and vulnerability of sites in the Greater Yellowstone Ecosystem. Conservation Biology 16(4)**:** 895-908.
Rigorous bioregional assessment of highest priority unprotected lands in GYE.

Odell, E. A., and R. L. Knight. 2001. Songbird and medium-sized mammal communities associated with exurban development in Pitkin County, Colorado. Conservation Biology **15**: 1143-1150.
Unique field study of wildlife response to distance to rural homes.

Olliff, T., R. Renkin, C. McClure, P. Miller, D. Price, D. Reinhart, and J. Whipple. 2001. Managing a complex exotic vegetation program in Yellowstone National Park. Western North American Naturalist 61(3): 347-358.
Documents number of exotic plants in YNP and treatment efforts.

Pederson, GT, S.T. Gray, D.B. Fagre, and L.J. Graumlich. In press. Long-Duration Drought Variability and Impacts on Ecosystem Services: A Case Study from Glacier National Park, Montana USA. Earth Interactions.
Documents decadal to centennial variation in climate in the Northern Rockies.

Pickett, S.T.A., and J.N. Thompson. 1978. Patch dynamics and the design of nature reserves. Biol. Conserv. 13:27-37.
Applies theory on landscape dynamics to design of nature reserves.

Pimm, S.L., H.L. Jones, and J. Diamond. 1988. On the risk of extinction. American Naturalist 132(6):757-785.
Evaluates the characteristics of species most at risk of extinction.

Powell, S.L., A.J. Hansen. In press. Conifer cover increase in the Greater Yellowstone Ecosystem: Frequency, rates, and spatial variation. Ecosystems.
Uses aerial photos to quantify change in conifer cover and biophysical correlates.

Powell, S.L., 2004. Conifer cover increase in the Greater Yellowstone Ecosystem: Rates, extent, and consequences for carbon. Ph.D. dissertation, Ecology Department, Montana State University, Bozeman, MT.
Maps change in conifer cover in recent decades using Landsat satellite imagery and quantifies consequences for carbon budgets.

Rasker, R., 1991. Dynamic economy versus static policy in the Greater Yellowstone ecosystem. Pgs. 8–11 in Proceedings to the Conference on the Economic Value of Wilderness, Jackson, WY.
Defines boundaries of Greater Yellowstone based on socioeconomic factors and describes links between natural amenities and economics.

Ripple, W.J., and R.L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? BioScience 54:755-766.
Rigorous literature review on how predators can elicit a trophic cascade across ecosystems.

Rodman, A., H. Shovic and D. Thoma. 1996. Soils of Yellowstone National Park. Yellowstone Center for Resources, Yellowstone National Park, Wyoming, YCR-NRSR-96-2.
Describes soil types within YNP.

Romme WH . 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs 52:199-221.
Uses fire scars and tree ages to quantify the temporal and spatial patterns of fire and succession.

Romme, W.H. and D.G. Despain. 1989. Historical perspective on the Yellowstone fires of 1988. BioScience 39:695-699.
Draws on earlier studies to interpret if the 1988 Yellowstone fires were within the natural range of variation.

Romme, W.H., and M.G. Turner. 2004. Ten years after the 1988 Yellowstone fires: Is restoration needed? Pgs. 318-361. In L. Wallace, Ed, In After the Fires: The Ecology of Change in Yellowstone National Park. Yale University Press. New Haven, CT.
Comprehensive review of the impacts of the 1988 fires on the Yellowstone ecosystem.

Romme, W.H., R.L. Knight, W.L. Baker, F.W. Smith, S.W. Buskirk. 2000. What haave we learned about forest fragmentation in the southern Rocky Mountains? Pgs 423-430 in R.L. Knight, F.W. Smith, S.W. Buskirk, W.H. Romme, and W.L. Baker, (eds.) Forest Fragmentation in the Southern Rocky Mountains. University of Colorado Press, Boulder, CO.
Summary chapter of this book on fragmentation.

Shafer, S.L., P.J. Bartlein, and R.S. Thompson. 2001. Potential changes in the distributions of western North America tree and shrub taxa under future climate scenarios. Ecosystems. 4:200-215.
Uses change during the Holocene as basis for predicting vegetation response to future climate change.

Shaffer, M.L. 1991. Minimum population size for species conservation. BioScience 31:131-134.
Pioneering paper on the concept of minimum viable population size.

Smith, D. W. 2005. Ten Years of Yellowstone Wolves, 1995-2005. Yellowstone Science 13(1)7-33.
Reviews the history of wolves in GYE since reintroduction and ecological consequences.

Thornton, P.E., S.W. Running, and M.A. White. 1997. Generating surfaces of daily meteorology variables over large regions of complex terrain. Journal of Hydrology **190**:214-251.
Uses a simulation model to interpolate climate from meterological stations to the US on a 1-km grid.

Turner, M.G., D.B. Tinker, W.H. Romme, D.M. Kashian, C. M. Litton. 2004. Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). Ecosystems 7:751-775.
Used field surveys and allometric equations to quantify attributes of 90 11-year old post fire stands.

Whitlock, C. 1993 Postglacial vegetation and climate of Grand Teton and southern Yellowstone National Parks. Ecological Monographs 63: 173-198.
Describes the two climate regimes within GYE and uses this as a basis for understanding Holocene climate and vegetation.