

3 Nature Reserves and Land Use: Implications of the “Place” Principle

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Many nature reserves are undergoing human-induced change despite our best attempts to keep them natural. Some of this change is due to the fact that the boundaries of nature reserves do not include all of the “places” in the landscape that are needed for ecosystem function and that are used by native species. The ecological principle of place emphasizes that ecological processes and organisms reflect the biophysical stage on which they occur. Abiotic factors, such as topography, climate, soil, and hydrology influence rates of processes, such as ecological productivity and disturbance regimes. The population status of organisms reflects this milieu of physical and biological interactions. Nature reserves whose boundaries exclude key biophysical settings are most apt to lose native species and change from their pre-EuroAmerican settlement condition. We offer four points of view for judging whether reserves include the “right” biophysical settings—those that will allow the reserve to function well. These involve disturbance initiation and run-out zones, life-history requirements of organisms, population source and sink areas, and climate change. A case study of the Greater Yellowstone Ecosystem illustrates that management conflicts can arise when administrative boundaries conflict with ecological boundaries. The place principle offers a basis for managing nature reserves and surrounding lands to maintain adequate function. We explore guidelines for selecting new reserves and managing existing reserves. Consideration of these guidelines should help managers maintain well-functioning nature reserves in the upcoming century of global change.

National parks, wilderness areas, and other nature reserves are a cornerstone of conservation in many nations. As the term nature reserve implies, these tracts are reserved primarily for natural ecosystems and native organisms. They are often managed with relatively little human intervention to let natural factors regulate ecological processes and organisms (Boyce 1998). Beyond serving as primary habitats for species that cannot tolerate more intense human land use, nature reserves are considered as benchmarks or

reference systems that can be used to better understand human impacts on areas outside of reserves (Sinclair 1998).

Despite our attempts to protect these areas from human impacts, however, many nature reserves are undergoing human-induced change (U.S. General Accounting Office 1994; Murray 1996; Landres et al. 1998a). Key natural disturbances are changing in intensity, size, and frequency, bringing about novel vegetation dynamics. Exotic weeds and diseases are invading nature reserves and exerting negative effects on native species. Air and water pollutants are entering reserves from exogenous sources. Some native species are suffering population reductions and extinctions in nature reserves (Newmark 1987, 1995). These changes are likely due to several factors, among which are land-use practices on surrounding ownerships (Wilcove and May 1986; Knight and Landres 1998; Woodroffe and Ginsberg 1998).

Many reserves are surrounded by gradients in land use, including public lands used for resource extraction, private lands dedicated to agriculture and rural residential development, and suburban and urban areas (Knight and Landres 1998). In recent decades, many people have relocated to the lands surrounding nature reserves (Propst et al. 1998). Consequently, land use has become more extensive (expanding into natural habitats) and more intensive (exerting greater human impact) on these surrounding lands (Hansen and Rotella 2000). What might be the connections between this development on adjacent private lands and the changes observed in nature reserves?

In this chapter, we suggest that the ecological principle of “place” (Dale et al. Chapter 1; Hansen and Rotella 1999) can help us understand some of the interactions between nature reserves and use of private lands. We first explore the implications of the place principle for understanding change in nature reserves. We then provide a case study from the Greater Yellowstone Ecosystem. Finally, implications for conservation and management are discussed.

3.1 The “Place” Principle and Nature Reserves

3.1.1 *Biophysical Factors and Ecosystems*

Environmental conditions such as temperature, soil nutrients, and proximity to water vary from place to place. Biological activities are promoted by some levels of these abiotic factors and constrained at other levels. Consequently, spatial variation in abiotic factors causes ecosystem processes and organisms to vary in space (Hansen and Rotella 1999; Dale et al., Chapter 1). Ecological productivity is high in some landscape settings and low in others. Viable populations of a species may be able to persist in some places but not others. Human communities may have the benefit of high levels of ecological services in particular locations but have to pay to import these services in other locations. The ecological principle of place emphasizes that

the potential for natural ecosystems and human communities varies in space. Knowledge of this spatial variation can improve our ability to manage landscapes sustainably (Harris et al. 1996).

This variation in abiotic factors is often not randomly distributed. Rather, heterogeneity in abiotic factors varies predictably with topography, latitude, distance from coastlines, and other factors (Whittaker 1960). For example, temperature often decreases and precipitation increases at increasing elevations. Similarly, soils often grade from coarse texture with low water-holding capacity on ridge tops to fine textured with higher water-holding capacity in valley bottoms. These predictable patterns of abiotic factors lead to corresponding patterns in ecological processes.

This interplay of abiotic factors, ecological processes, and organisms can be described by drawing analogy to the theater (Hutchinson 1965; Harris et al. 1996). If organisms represent actors that interact to produce the drama of ecological dynamics, then the landscape represents the stage on which the drama unfolds. The distribution of biophysical conditions across the landscape influences the behavior of the organisms and the nature of ecological processes, much as the theater and stage sets influence the integrity of a play. Each theater and stage set offers particular constraints and opportunities to the performers. Similarly, the distribution of environmental conditions across landscapes shapes the behaviors of organisms and ecosystems. Much of the challenge of conservation and landscape management is to maintain, restore, or create the suite of biophysical patterns that will support the ecological dynamics that will best achieve management objectives.

3.1.2 "Right" Places for Nature Reserves

The place principle has important implications for nature reserves. Specifically, the principle implies that reserves can function properly only if they contain the right places. By "right places" we mean the locations that contain the range of abiotic conditions and habitats that are required to maintain natural ecological processes and native organisms and communities. If some of these places are omitted from inclusion in the reserve, natural disturbance regimes, ecological productivity, and species dynamics all may change to levels outside of the pre-EuroAmerican Settlement range of variation. In some cases, the boundaries of nature reserves were drawn in ways that omitted key landscape settings. This is akin to performing a play on only a portion of the stage. Just as the play would change as portions of the stage were removed, ecosystem dynamics change as portions of the landscape are made unavailable.

What are the "right places" to include in nature reserves? The simple answer is that nature reserves should include a variety of biophysical settings. The importance of particular combinations of biophysical settings needs to be judged relative to which landscape attributes exert strong influence over ecosystem function and organism performance. Here we judge the right

places, or suites of biophysical factors, from four points of view: organism life histories, disturbance regimes, population source and sink dynamics, and climate change.

3.1.2.1 Life Histories of Organisms

Most species occur in particular biophysical settings. The suite of biophysical conditions within a nature reserve sets constraints on the types of species the reserve can support. If abiotic conditions are outside the tolerances of an organism, survival, growth, and reproduction may be reduced (Hansen and Rotella 1999). Abiotic factors may also influence organisms by altering rates of processes. Disturbance rates alter habitat quality for organisms, and primary productivity influences food availability at higher trophic levels.

Some species have a narrow range of requirements and occupy throughout their lifetimes a particular landscape setting with specific environmental conditions. Studies by Whittaker (1960), for example, elegantly demonstrated that tree species are found in particular locations along elevational gradients due to the effects of climate and soils. Other organisms actively move across abiotic gradients on a daily, seasonal, or life-stage basis. If resources and conditions vary in time and space, such organisms can maintain access to a particular set of conditions by moving across the varying environmental gradient. Examples are migratory birds that move seasonally to maintain access to food supplies. Other species move along abiotic gradients to gain access to two or more different habitat types (e.g., amphibians that use aquatic and terrestrial habitats in different life stages).

Nature reserves that do not include the range of habitats and conditions required by species often require more intensive management. Serengeti National Park, Tanzania, for example, contains both wet-season and dry-season habitats, allowing several species of ungulates to use natural migration routes (Sinclair 1998). Kruger Park, South Africa, in contrast, is situated only in wet-season habitats. Traditional ungulate migration routes were cut off by the park fences. Consequently, considerable human intervention has been needed to maintain these species and their habitats. Wells were drilled to provide adequate water for these herds. These animals are now largely resident near water sources and substantially impact the vegetation. Culling is now used to control herd sizes and reduce negative impacts on the vegetation.

3.1.2.2 Disturbance

Disturbances tend to be initiated in particular landscape settings and move to other locations in the landscape. Interactions between the location where disturbance gets started (initiation zones) and locations where disturbances move to (run-out zones) influence the nature of the disturbance regime in an area (Baker 1992). In southwest Montana, for example, lightning strikes

occur across the landscape but more frequently ignite fires in dry valley-bottom grasslands than in moister conifer forests in the uplands (Arno and Gruell 1983). These fires then spread up slope to the conifer forests. Thus, the juxtapositioning of grasslands and conifer forests strongly influences the regional fire regime. Local disturbance regimes can best be maintained in nature reserves that include the disturbance initiation zones within their boundaries (Baker 1992). In the case of the example above, a reserve placed only in the upland conifers may suffer more or less frequent fire, depending on the management of the valley-bottom grasslands outside of the reserve.

It is also important to include disturbance run-out zones within reserve boundaries. Run-out zones may contain unique abiotic conditions and habitat patterns important to ecological processes and organisms. For example, flood severity often increases from headwaters to large floodplains. The large scour area and bare gravel bars that form on flood plains support vegetation communities not found in other landscape settings. A reserve that does not contain this disturbance run-out zone will not include these unique riparian vegetation communities. In reserves that omit either the initiation or run-out zones, human manipulation of disturbance may be required to maintain landscape patterns and organisms (Baker 1992; Sinclair 1998).

3.1.2.3 Population Sources and Sinks

New discoveries in population dynamics suggest a less visible, but still important, way that reserve location may influence organisms. Within the range where a species is found, some locations may be population source areas and other locations population sinks (Pulliam 1988). Source areas are characterized by having birth rates that exceed death rates, while sinks are the opposite: Death rates are higher than birth rates. These differences in demographics are sometimes due to biophysical factors. Individuals may suffer less physiological stress and have higher energy availability in more equitable biophysical settings (Hansen et al. 1999). Source and sink areas may be difficult to detect because population densities can be similar in both sources and sinks (Pulliam and Danielson 1991). Surplus individuals produced in source areas may immigrate to the sink areas and maintain relatively high densities there. In this case, individuals may persist in the sink areas only if population source areas are maintained. Thus, populations in nature reserves that include only sink habitats depend on source populations in other areas for their continued existence. Such sink populations may suffer extinction if population sources outside the reserve are degraded. Sinclair (1998) suggested that most of Serengeti National Park is a sink for the lion population and that the species is maintained there because of connectivity with the Ngorongoro Conservation Area, which is a population source area for lion.

3.1.2.4 Climate Change

The location of nature reserves is also relevant to how well reserves will fair under potential future climate change. Halpin (1997) predicted that 47–77% of biosphere reserves globally will undergo a change in ecoclimatic zone under a doubling of atmospheric CO₂. The magnitude of predicted changes varies among reserves. Those at higher latitudes are more likely to change than those in equatorial locations. The ability of organisms to cope with climate change is also likely to vary with reserve. Organisms have a greater ability to relocate to suitable habitats in reserves that include a wide range of biophysical conditions. Also, reserves that are connected to other reserves by seminatural habitats, such as along mountain chains, are more likely to exchange organisms with other reserves under climate change. Local analyses are needed to determine how much change a given nature reserve is likely to experience and what management strategies might be used to cope with these changes (Halpin 1997).

3.1.3 Historic Criteria for Reserve Selection

Given the importance of reserve location for conservation, we might expect that nature reserves were carefully placed relative to biophysical gradients. This was not the case for many national parks and wilderness areas in the United States. Knowledge of the interactions between biodiversity, biophysical gradients, and natural disturbance was underdeveloped when most reserves were established (Craighead 1991). Moreover, conservation of biodiversity was often not a key criterion for reserve selection. Many national parks were selected because of their scenic grandeur, geologic or biological uniqueness, potential for tourism, and public ownership (Newmark 1987). In the case of Wilderness Areas, a key criterion was lack of human impact, as evidenced, for example, by an absence of roads.

Such selection criteria likely biased the location of nature reserves toward relatively harsh sites. Lands with high potential for agriculture and other intense human land uses were often claimed for private ownership and lands that remained public were relatively harsh in climate and were lower in soil fertility (Huston 1993). Even on public lands, resource extraction was often first concentrated on the most productive sites. Hence, the areas that remained roadless at the time of the Wilderness Act in 1964 were often high in elevation and extreme in climate.

This history of reserve selection suggests that more equitable biophysical settings are underrepresented in our nature reserves (Scott et al., in review). In mountainous areas, valley bottoms, and lowlands with warmer temperatures, longer growing seasons, more fertile soils, and high ecological productivity are often outside reserve boundaries. In arid systems, reserves often omit areas of higher precipitation and soil water-holding capacity.

3.1.4 Land Allocation and Biodiversity

What might be the consequences of nature reserves being placed in harsher landscape settings? As mentioned above, these more equitable settings are apt to represent important habitats, population source areas, and possible disturbance initiation or run-out areas. In reserves in more extreme biophysical settings, organisms that migrate seasonally across elevational or precipitation gradients are apt to cross administrative boundaries. Species that exhibit source-sink population dynamics may be dependent on source areas that are on private lands. Thus, nature reserves that omit equitable biophysical settings may experience changes in ecosystem function and biodiversity as lands outside of the reserve undergo human development.

The rate at which seminatural private lands outside of nature reserves have developed appears to be accelerating in recent years. Human population density is growing rapidly in rural landscapes in the United States. Some of this growth may be a function of expansion around the periphery of urban areas. Such is the case around Denver and Phoenix. Another factor is that people are increasingly attracted to live near nature reserves because opportunities for recreation and high-quality lifestyles abound in such locales (Johnson and Rasker 1995).

An ironic consequence of this rural residential development can be an erosion of the ecosystem qualities that originally attracted the new residents. One effect of this development is a reduction of the functional size of a reserve. The number of species an ecosystem can support is strongly related to its area (Huston 1994; Rosenzweig 1995). Population sizes of species with large home ranges such as grizzly bear (*Ursus arctos horribilis*) have been associated with the size of the wildlands they inhabit (Picton 1994; Woodroffe and Ginsberg 1998). Evidence of the relationship between habitat area and species viability comes from Newmark (1987), who found that extinction rates of mammals in National Parks in the western United States were correlated with park size. As semi-wildlands are developed around reserves, the area of habitat available to organisms is decreased and likelihood of extinction is increased. This rate of extinction is likely to be even greater than predicted based on species-area relationships if humans are developing the more equitable biophysical settings that are especially important habitats for many species.

Beyond converting natural habitats to human land uses, humans can have more subtle effects on ecosystem function and biodiversity. Human activities often favor invasive organisms and facilitate the spread of these weedy species from private lands into nature reserves (Landres et al. 1998b). Suppression of disturbance on private lands can alter the flow of natural disturbance regimes into nature reserves (Baker 1992). Land uses such as agriculture and livestock grazing can favor predators that then exert strong negative effects on prey species in adjacent wildlands (Terborgh 1989; Hansen et al. 1999).

A key implication of the ecological principle of place is that many nature reserves cannot function adequately as islands in a human-dominated matrix because they do not include key places for ecological processes and native species. The dynamics of ecosystems within reserve boundaries can be heavily influenced by the state of the ecosystem outside the boundaries. As these surrounding lands are increasingly developed by humans, ecosystem processes and organisms within the reserves will change. Fortunately, a variety of strategies can be used to minimize or cope with these boundary effects (see below).

3.2 Case Study: Biodiversity and Land Use in Greater Yellowstone

3.2.1 Biophysical Gradients and Land Allocation

The Greater Yellowstone Ecosystem (GYE) (Fig. 3.1; see color plate) represents an interesting example where nature reserve boundaries bisect key biophysical gradients. Yellowstone National Park was established in 1872, largely to protect unique hydrothermal and geological features and remnant wildlife populations (Mackintosh 1991). The original boundaries included a largely rectangular area and centered on the key geological and thermal features. Soon after its establishment, there were calls to expand the size of the park to better include key wildlife habitats (Craighead 1991). Eventually, a small area of ungulate winter range was added to the northern boundary of the park and national forests were designated on surrounding lands.

The concern over Yellowstone National Park's boundaries largely stemmed from its location on the Yellowstone Plateau. The plateau and the surrounding mountains are relatively high in elevation. The severe winters, short growing season, and relatively infertile volcanic soils greatly constrain primary productivity (Despain 1990). The length of growing season increases at lower elevations and soil fertility is relatively high in some midslope and valley-bottom settings in the area. Consequently, primary productivity is highest in the lowlands (Hansen et al. 2000). Natural disturbances like wildfire vary across this elevational gradient (Barrett 1994), and many wildlife species migrate seasonally between lowland and upland habitats (Frank 1998).

The boundaries of Yellowstone National Park cut across these gradients in climate, soils, primary productivity, and natural disturbances. Land allocation across the GYE was largely stratified by elevation. Yellowstone National Park and other nature reserves in the ecosystem are placed primarily at higher elevations (Fig. 3.2). Other public lands, such as the national forests, are at intermediate elevations. Private lands are mostly located at lower elevations. An important consequence of this pattern of land allocation is that the productive lowland habitats are mostly outside of

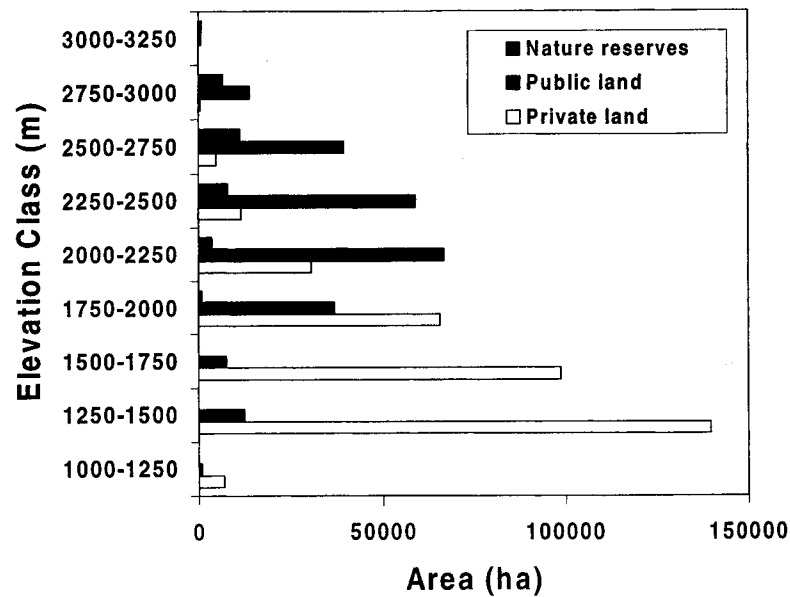


FIGURE 3.2. Distribution of land allocation across elevations for the Greater Yellowstone Ecosystem.

the nature reserves and on private lands. The term Greater Yellowstone Ecosystem was coined to emphasize that ecological processes and organisms are integrated across biophysical gradients from lowlands to the alpine zone and, consequently, coordinated management across the ownership jurisdictions is required to maintain these processes and organisms (Craighead 1991; Patten 1991).

3.2.2 Human Demography, Land Use, and Effects on Ecosystems

The northern Rocky Mountains are known for their wildness and low human-population densities. In recent decades, however, many people have moved to the private lands of the GYE. The population of the GYE has increased 55% since 1970. Of the 20 counties in the GYE, 13 were among the fastest-growing 25% of counties in the United States in the 1990s. Many of the new residents and businesses have been attracted to the GYE by outdoor recreation, scenery, and other environmental amenities (Johnson and Rasker 1995).

This population growth has had a large impact on rural private lands across the GYE. Many new residents have chosen to live outside of towns and cities. Consequently, rural residential development has been rapid in

recent decades. Gallatin County, Montana, in the northwest portion of the ecosystem, is typical in these trends. The number of rural residences increased by more than fourfold between 1970 and 1995 (Hansen and Langner, in preparation).

Scientists are just beginning to examine the impact of rural residential development on biodiversity and ecosystems. Initial studies indicate substantial negative impact on native wildlife due to fragmentation of natural habitats, invasion of nonnative weeds and predators, and harassment of wildlife by pets and recreationists (Whitcomb et al. 1981; Riesbame et al. 1996; Theobald et al. 1996; Hansen et al. 1999; Hobbs and Theobald, Chapter 2).

How much has the functional size of the natural habitats of the GYE been reduced by development on private lands? Hansen and Langner (in preparation) analyzed the rate of loss of seminatural lands in Gallatin County, Montana. They assumed that the zone of influence of a home has a radius of 2 km. The zone of influence of a home likely varies depending on the ecological process or species of interest. The radius of 2 km is conservative for some impacts; bird reproductive success here was found to be correlated with density of homes within 6 km of nests (Rotella and Hansen, unpublished data). Figure 3.3 shows the cumulative proportion of private land in

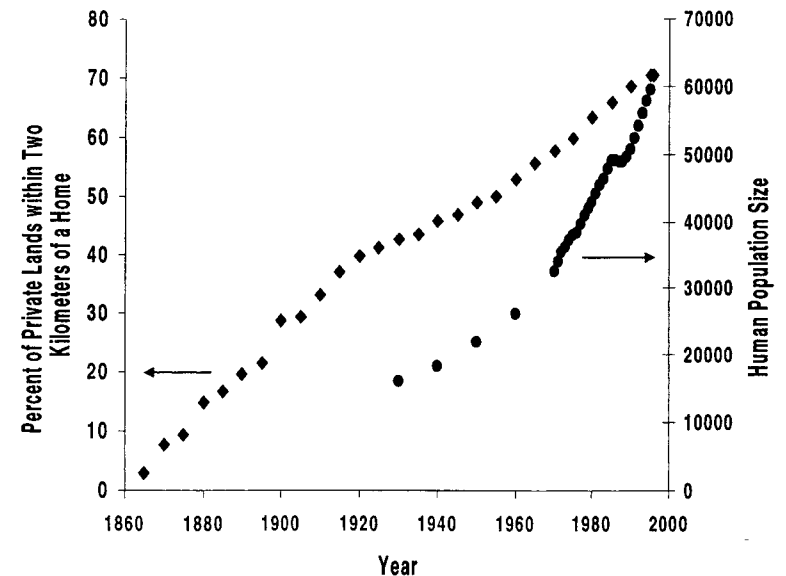


FIGURE 3.3. Land-use and human population trends in Gallatin County, MT. Cumulative proportion of private lands influenced by rural residential development from 1860 to 1995 is shown on the left axis. Human population size 1930-1995 is shown on the right axis. From Hansen and Langner (in preparation).

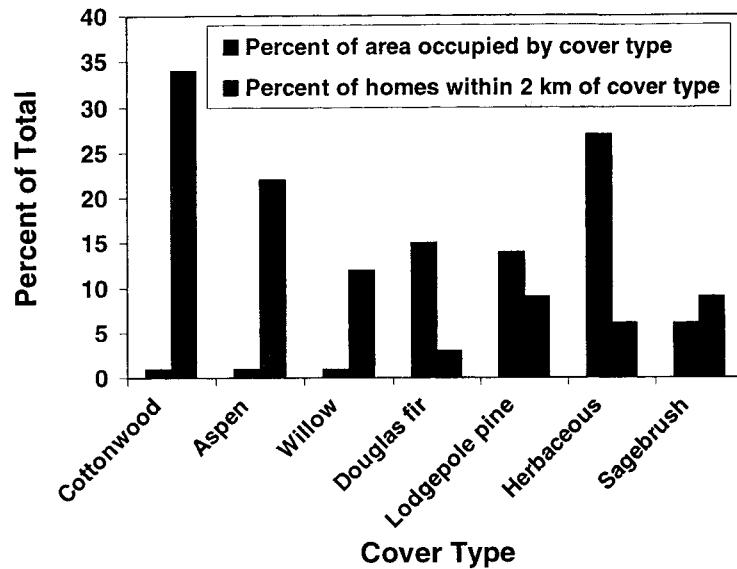


FIGURE 3.4. The distribution of rural residences relative to vegetation cover types in Gallatin County, MT. The percentage of the county occupied by each cover type is shown on the left axis. The proportion of the total rural residences with 2 km of each cover type is shown on the right axis. From Hansen and Langner (in preparation).

the county that is within 2 km of one or more houses from 1860 to 1995. Notice that the increase has been almost constant over this time period at a rate of about 5% per decade. We might expect that the rate of habitat impact would decrease in modern times as new homes are placed within 2 km of existing homes. However, this rate has not decreased, largely due to the rapid increase in human population size since 1970 (Fig. 3.3). Currently, only about 30% of the private lands in the county are more than 2 km from a home. This analysis illustrates how development on private lands can erode the area of natural lands around nature reserves.

The impact of humans on many native species in Gallatin County is likely even larger than expected based on species–area relationships because the rural residential development has not been located randomly relative to biophysical factors. Rural homes in the county are disproportionately dense near deciduous habitats (cottonwood, aspen, willow) (Hansen and Langner, in preparation) (Fig. 3.4). These deciduous habitats cover only about 3% of the county and are hot spots for primary productivity and biodiversity (see below). These data suggest that rural residential development may be having a particularly strong influence on native species because it is concentrated in the equitable biophysical settings. This process is likely to continue into the future, further eroding the size and quality of habitats across the GYE.

3.2.3 Conflicts at Reserve Boundaries

Many of the conservation controversies in the GYE ultimately stem from the location of Yellowstone National Park relative to biophysical gradients. We will briefly mention examples involving natural disturbance and wildlife habitats and then provide more detail on source–sink population dynamics from our studies on birds.

Wildfire is the dominant natural disturbance in the GYE. Fire frequency and size vary with biophysical setting, ranging from relatively small, frequent fires at lower elevations to very large fires at 200- to 300-year intervals at higher elevations (Romme 1982; Barrett 1994). Neither fire-initiation nor run-out zones are entirely included in Yellowstone National Park. Fires initiated in the productive lowlands on the windward side of the park likely spread into the park in presettlement times (Hansen et al. 2000). This area is now managed as the Targhee National Forest. Extensive clear-cutting across the Targhee has dramatically reduced fuel loads and likely reduced the potential for fire to spread of into the park. Thus, the nature of the disturbance regime in the park may be altered due to land-use practices in disturbance initiation zones outside of the park. The spread of fire from the park to surrounding private lands is also a difficult management question. Current policy allows wildfires to burn in the park. However, land managers and property owners on the leeward side of the park are concerned that this policy puts their lands at increased risk of fire.

Elk, bison, and other ungulates in the GYE historically migrated between summer habitats at high elevations and winter range at lower elevations (Frank 1998). Human development on private lands in lowlands has reduced the ungulates' access to traditional winter range. This loss of winter habitat on private lands may have led to higher densities of elk on the winter range within Yellowstone National Park and exacerbated the loss of woody plants there due to herbivory. Over the last two decades the area of winter range available to the Northern Range elk herd was expanded by land acquisition and conservation easements. A greater proportion of this elk herd now winters outside of Yellowstone National Park (Lemke et al. 1998). Densities of elk on the winter range inside of the park have decreased and may allow higher growth rates of woody plants (Singer et al. 1998).

Bison illustrate most visibly, perhaps, the difficulties of managing when administrative boundaries do not coincide with ecological boundaries. Bison have increasingly migrated out of Yellowstone National Park in recent years, possibly because of increased population size and/or ease of movement along snow-cleared roads (Meagher 1989). The herd carries the pathogenic bacterium *Brucella abortus*, and livestock growers are concerned that the disease brucellosis will spread from bison to cattle. The current management policy is to slaughter diseased bison as they leave the park. This policy has been highly controversial and has led to Congressionally mandated reviews, lawsuits, and public protests (Keiter 1997).

Just as ungulates move down in elevation and leave the park, exotic species have invaded the park from the surrounding lowlands. Weedy nonnative plants are now common in the park, possibly due to dispersal from reservoirs on surrounding private lands (Kurtz 1999). These invasive plants may reduce forage quality for elk and other native herbivores and may outcompete native plant species. Similar invasions have occurred in stream systems. Human activities have favored nonnative trout in larger streams in the lowlands and these exotic fishes have displaced native cutthroat trout. The remaining cutthroat populations in headwater streams are highly fragmented and under threat of extinction (Shepard et al. 1997). Nonnative lake trout were recently discovered in Yellowstone Lake in the heart of the park and threaten the native trout population and the suite of carnivores that feed on the cutthroat. This population of cutthroat is also jeopardized by the exotic whirling disease that has been expanding in warmer waters in lowland habitats (D. Gustafson, personal communication). These introductions raise question as to whether invasions would be less likely if the lowland habitats were included in the nature reserve rather than subjected to intense land use.

Our own studies of birds in the GYE suggest that lowland habitats are especially important for the maintenance of regional populations (Hansen et al. 1999; Hansen and Rotella 1999). We sampled bird abundance and community richness across cover types and elevation zones in the northwest portion of the GYE. We found that birds were not randomly distributed among our samples. Rather, bird richness and abundance were high in sites with wet alluvial soils, equitable climate, and deciduous forest cover types—likely because these sites offer relatively high levels of food production and habitat structural complexity. We then extrapolated bird species over the study area based on these biophysical factors. Predicted bird species richness and total abundance were relatively low over most of the study area and high only in localized settings. Hot spots for bird richness were rare (2.7% of the study area), primarily at lower elevations, and the majority were on or near private lands. Only 3.0% of the total area in hot-spot habitats was in Yellowstone National Park.

We used these data as the basis for a risk assessment (Hansen et al. 1999) and found that the majority of the species most at risk of extinction were dependent on these hot-spot habitats. Reproductive success varied among the hot spots, however. Reproduction was relatively high in hot spots surrounded by seminatural lands, and simulation modeling indicated that these are population source areas. Hot-spot habitats surrounded by rural residential and agricultural land uses, however, had low reproduction and appear to be population sinks for this guild of at-risk species. These intense land uses favor higher densities of nest predators and brood parasites that enter the hot-spot habitats and reduce bird reproduction. These results suggest that the population source areas in the lowlands maintain the viability of many bird species across the region. Human development

appears to have converted some of these source areas to population sinks. Further intensification of land use near hot-spot habitats could lead to extinctions of some of these species across the region, including within nature reserves.

3.2.4 Management of the GYE

Many of the conflicts described above can be resolved only through coordinated management across the many ownership jurisdictions of the GYE. While this has been a considerable challenge, there have been some successes (Glick and Clark 1998). Some important lowland habitats outside of Yellowstone National Park have been placed in a conservation status through purchase or trade of the lands or purchase of conservation easements by both governmental and private organizations. Cooperative efforts to manipulate animal populations are in place for some species. The hunting of elk that migrate outside of the park is used to manage the size of the herd to prevent an overpopulation within the park (Lemke et al. 1998). Similarly, the endangered grizzly bear is managed to minimize bear mortality on public and private lands outside the park. Reintroduction programs are being used to restore native trout populations in lowland streams. Some local governments have begun to manage rural residential development to reduce impacts on ecosystems. These initial efforts at cooperative management will have to be strengthened, however, to maintain the quality of the GYE in the face of expected future intensification of use of private lands and increases in recreation on public lands.

3.3 Guidelines for Conservation and Management

The ecological principle of place not only helps us to better understand patterns in and around nature reserves, it also provides a context for managing existing reserves and for establishing new reserves. Here, we highlight some guidelines for conservation and management of nature reserves.

The designers of new reserves have the luxury of taking advantage of the best current knowledge on ecology, socioeconomics, and other factors. Halpin (1997) summarized and evaluated considerations for reserve selection that relate to climate change. We modify the list slightly with reference to the ecological principle of place.

- *Biophysical setting.* The major conclusion of this chapter is that reserves are most likely to function well when they contain the right configuration of biophysical settings. Hence, reserve boundaries should be set with consideration of disturbance initiation and run-out zones, habitat requirements of organisms, the spatial distribution of population source and sink

areas, and gradients in biophysical factors that allow organisms to relocate under changing climate.

- *Buffer-zone flexibility.* Land allocation and management of lands surrounding the reserve should maintain options for readjusting for future change. The biosphere reserve concept offers a sociopolitical construct for achieving this flexibility.
- *Landscape connectivity.* The degree of upheaval wrought by climate change will be partially influenced by the success of organisms in dispersing to newly created suitable habitats. Maintaining connectivity among reserves will aid this dispersal. However, the effectiveness of positioning reserves along latitudinal or elevational gradients, corridors between reserves, and management of the intervening human-dominated matrix remains poorly understood (Halpin 1997).
- *Redundant reserves.* In some cases, placing two or more reserves in a particular ecosystem type may be desirable as a hedge against unforeseen change within a reserve.

Managers of existing reserves must cope with the legacy that they inherited from those that originally allocated lands in and around a reserve. The challenge is to understand current patterns of biophysical factors, organism dynamics, land use, and management approaches and to use this knowledge as a basis for achieving/maintaining the objectives of the reserve and surrounding lands. Possible steps to this end are as follows:

- *Assessment.* Quantify biophysical gradients, ecological processes, organisms, and land use to understand how well the reserve is functioning relative to its objectives. Approaches for assessment can be found in Hansen et al. (1999) and Bourgeron et al. (Chapter 13).
- *Habitat acquisition.* If key biophysical settings were not included in reserve boundaries, opportunities may exist to restore them. Means include land acquisition, conservation easements, tax incentives, education for private landowners, and local government planning and/or regulation.
- *Human intervention in reserves.* If surrounding lands necessary for reserve function cannot be conserved, human intervention within reserves may be required (Sinclair 1998). Intervention strategies may include manipulation of disturbance regimes and nutrient flows, control of overabundant native species or of nondesirable exotic species, and management of recreationists.
- *Coordinated management.* Neighboring agencies and landowners often have very different objectives and cultures. Nonetheless, coordination of management approaches across jurisdictions can greatly reduce boundary conflicts. Community conservation forums, regional management committees, or entirely new administrative structures may be needed to achieve this coordination (see also Botteron, Chapter 7, and Haufler and Kernohan, Chapter 4).

- *Monitoring.* As in any management endeavor, ongoing monitoring is needed to gauge the effectiveness of management implementations.

3.4 Conclusions

The value of nature reserves for conservation has become overwhelmingly apparent over the last century as land use has intensified on public and private lands. Many scientists and conservationists consider nature reserves to be “vignettes” of primitive times (Boyce 1998). However, we suggest that nature reserves are better seen as islands that feel the winds blowing from the sea of human-dominated landscapes around them. These winds have brought change to many nature reserves. Those changes will undoubtedly accelerate under the two vectors of global change—climate change and land-use intensification. The ecological principle of place offers a basis for better understanding interactions between reserves and their surroundings and better coping with global change. Place is the biophysical stage that determines the nature of the ecological drama in and around nature reserves. By managing the biophysical stage well, we have the best hope of maintaining well-functioning nature reserves. This management will require a new generation of approaches for cooperation among reserve managers and their neighbors.

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References

- Arno, S.F., and G.E. Gruell. 1983. Fire history at the forest-grassland ecotone in southwestern Montana. *Journal of Range Management* 39:332–336.
- Baker, W. 1992. The landscape ecology of large disturbances in the design and management of nature reserves. *Landscape Ecology* 7:181–194.
- Barrett, S. 1994. Fire regimes on andesitic mountain terrain in northeastern Yellowstone National Park, Wyoming. *International Journal of Wildland Fire* 4:65–76.
- Boyce, M.S. 1998. Ecological-process management and ungulates: Yellowstone's conservation paradigm. *Wildlife Society Bulletin* 26:391–398.
- Craighead, J.J. 1991. Yellowstone in transition. Pages 27–40 in R.B. Keiter and M.S. Boyce, editors. *The greater Yellowstone ecosystem: redefining America's wilderness heritage*. Yale University Press, New Haven, Connecticut, USA.
- Despain, D. 1990. *Yellowstone vegetation*. Roberts Rinehart, Boulder, Colorado, USA.
- Frank, D.A. 1998. Ungulate regulation of ecosystem processes in Yellowstone National Park: direct and feedback effects. *Wildlife Society Bulletin* 26:410–418.

- Glick, D.A., and T.W. Clark. 1998. Overcoming boundaries: the greater Yellowstone ecosystem. Pages 237–256 in R.L. Knight and P.B. Landres, editors, *Stewardship across boundaries*. Island Press, Washington, D.C., USA.
- Halpin, P.N. 1997. Global climate change and natural-area protection: management responses and research directions. *Ecological Applications* 7:828–843.
- Hansen, A.J., and J.J. Rotella. 1999. Abiotic factors. Pages 161–909 in M. Hunter, editor. *Managing forests for biodiversity*. Cambridge University Press, London, England.
- Hansen, A.J., and J.J. Rotella. 2000. Bird response to forest fragmentation. In R.L. Knight, F.W. Smith, S.W. Buskirk, W.H. Romme, and W.L. Baker, editors. *Forest fragmentation in the Southern Rocky Mountains*. Island Press, Washington, D.C., USA.
- 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* 9:1459–1476.
- 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.
- Harris, L.D., T.S. Hoctor, and S.E. Gergel. 1996. Landscape processes and their significance to biodiversity conservation. Pages 319–347 in O.E. Rhodes, R.K. Chesser, and M.H. Smith, editors. *Population dynamics in ecological space and time*. University of Chicago Press, Chicago, Illinois, USA.
- Huston, M. 1993. Biological diversity, soils, and economics. *Science* 262:1676–1680.
- Huston, M.A. 1994. *Biological diversity*. Cambridge University Press, Cambridge, England.
- Hutchinson, G.E. 1965. *The ecological theater and the evolutionary play*. Yale University Press, New Haven, Connecticut, USA.
- Johnson, J.D., and R. Rasker. 1995. The role of economic and quality of life values in rural business location. *Journal of Rural Studies* 11:405–416.
- Keiter, R.B. 1997. Greater Yellowstone's bison: Unraveling of an early American wildlife conservation achievement. *Journal of Wildlife Management* 61:1–11.
- Knight, R.L., and P.B. Landres, editors. 1998. *Stewardship across boundaries*. Island Press, Washington, D.C., USA.
- Kurtz, D. 1999. *Geographic characterization of exotic plant species in Grand Teton National Park Thesis*, Montana State University, Bozeman, Montana, USA.
- Landres, P.B., R.L. Knight, S.T.A. Pickett, and M.L. Cadenasso. 1998a. Ecological effects of administrative boundaries. Pages 39–64 in R.L. Knight and P.B. Landres, editors. *Stewardship across boundaries*. Island Press, Washington, D.C., USA.
- Landres, P.B., S. Marsh, L. Merigliano, D. Ritter, and A. Norman. 1998b. Boundary effects on wilderness and other natural areas. Pages 117–139 in R.L. Knight and P.B. Landres, eds., *Stewardship across boundaries*. Island Press, Washington, D.C., USA.
- Lemke, T.O., J.A. Mack, and D.B. Houston. 1998. Winter range expansion by the northern Yellowstone elk herd. *Intermountain Journal of Sciences* 4:1–9.
- Macintosh, B. 1991. *The national parks: shaping the system*. Division of Publications, National Park Service, Washington, D.C., USA.
- Meagher, M.M. 1989. Evaluation of boundary control for bison of Yellowstone National Park. *Wildlife Society Bulletin* 17:15–19.
- Murray, M.P. 1996. Natural processes: wilderness management unrealized. *Natural Areas Journal* 16:55–61.
- Newmark, W.D. 1987. Mammalian extinctions in western North American parks: a land-bridge island perspective. *Nature* 325:430–432.
- Newmark, W.D. 1995. Extinction of mammal populations in western North American national parks. *Cons. Biol.* 9:512–526.
- Patten, D.T. 1991. Defining the Greater Yellowstone Ecosystem. Pages 19–26 in R.B. Keiter and M.S. Boyce, editors. *The Greater Yellowstone Ecosystem: redefining America's wilderness heritage*. Yale University Press, New Haven, Connecticut, USA.
- Picton, H.D. 1994. A possible link between Yellowstone and Glacier grizzly bear populations. *International Conference on Bear Research and Management* 6:7–10.
- Propst, L., W.F. Paleck, and L. Rosan. 1998. Partnerships across park boundaries: the Rincon Institute and Saguaro National Park. Pages 257–278 in R.L. Knight and P.B. Landres, editors. *Stewardship across boundaries*. Island Press, Washington, D.C., USA.
- Pulliam, H.R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652–661.
- Pulliam, H.R., and B.J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American Naturalist* 137:S50–S66.
- Riebsame, W.E., H. Gosnell, and D. Theobald. 1996. Land use and landscape change in the Colorado Mountains, I: theory, scale and pattern. *Mountain Research and Development* 16:395–405.
- Romme, W.H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. *Ecological Monographs* 52:199–221.
- Rosenzweig, M.L. 1995. *Species diversity in space and time*. Cambridge University Press, Cambridge, England.
- Scott, J.M., F.W. Davis, G. McGhie, and C. Groves. In review. Biological reserves: do they capture the full range of America's biological diversity?
- Shepard, B.B., B. Sanborn, L. Ulmer, and D.C. Lee. 1997. Status and risk of extinction for westslope cutthroat trout in the upper Missouri River Basin, Montana. *N.A.J. Fish. Mgt.* 17:1158–1172.
- Sinclair, A.R.E. 1998. Natural regulation of ecosystems in protected areas as ecological baselines. *Wildlife Society Bulletin* 26:399–409.
- Singer, F.J., L.C. Seigenfuss, R.G. Cates, and D.T. Barnett. 1998. Elk, multiple factors, and persistence of willows in national parks. *Wildlife Society Bulletin* 26:419–428.
- Terborgh, J. 1989. *Where have all the birds gone?* Princeton University Press, Princeton, New Jersey, USA.
- Theobald, D.M., H. Hosnell, and W.E. Riebsame. 1996. Land use and landscape change in the Colorado Mountains, II: a case study of the East River Valley. *Mountain Research and Development*. 16:407–418.
- U.S. General Accounting Office. 1994. *Activities outside park borders have caused damage to resources and will likely cause more*. U.S. General Accounting Office GAO/RCED-94-59, Washington, D.C., USA.
- Whitcomb, R.F., C.S. Robbins, J.F. Lynch, B.L. Whitcomb, K. Klimkiewicz, and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern

- deciduous forest. Pages 125–205 in R.L. Burgess and D.M. Sharpe, editors. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York, New York, USA.
- Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* **30**:279–338.
- Wilcove, D.S., and R.M. May. 1986. National park boundaries and ecological realities. *Nature* **324**:206–207.
- Woodroffe, R., and J.R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. *Science* **280**:2126–2128.

4 Ecological Principles for Land Management Across Mixed Ownerships: Private Land Considerations

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Ecological objectives relating to sustainability and land management typically focus on maintaining and enhancing biological diversity and ecosystem integrity, objectives that require planning at landscape levels. Nearly all landscapes of sufficient size to address these objectives contain a diversity of landowners, including many private lands. For conservation planning to be effective in these mixed-ownership landscapes, a number of ecological principles and management considerations should be recognized. Ecological objectives need to be addressed in an ecosystem-management context in which social and economic objectives are integrated with ecological objectives. To accomplish this integration, the most effective approach focuses on a coarse filter; an approach that strives to meet ecological objectives through the identification of an appropriate mix of ecological communities correctly configured within the landscape. One effective coarse-filter approach has identified ecological site complexity as well as an understanding of historical disturbance regimes that shaped the inherent diversity and function of the ecological communities. Monitoring effectiveness of coarse-filter planning will need to be hierarchical to address all levels of biological diversity.

Private lands are critical elements in land-management planning for conservation objectives. In the Northeast and South, approximately 90% of the land is privately owned. Even in the West where Federal lands comprise higher percentages, private lands control much of the lower elevation and terrestrial/riparian interface zones (Hansen and Rotella, Chapter 3), thus representing a majority of area for many types of ecological communities. Further, private lands encompass a high percentage of habitat for many species listed as threatened or endangered under the Endangered Species Act. The Natural Heritage Data Network (1993) estimated that more than 50% of the federally listed threatened and endangered species occur only on private lands. In addition, most riverine systems pass through private land where land-management practices can influence many downstream characteristics. For all of these reasons, incorporating private lands into conservation planning efforts is essential if effective results are to be obtained.