

# Landscape Diversity: The Concept Applied to Yellowstone Park

William H. Romme and Dennis H. Knight

Changes in landscape patterns may influence a variety of natural features including wildlife abundance, nutrient flow, and lake productivity. Data suggest that cyclic changes in landscape diversity occur on areas of 100 km<sup>2</sup> in Yellowstone National Park. When properly managed, large wilderness areas provide the best and probably the only locale for studying the kind of landscape changes that occurred for millennia in presettlement times. (Accepted for publication 12 May 1982)

Each successive level of biological organization has properties that cannot be predicted from those of less complex levels (Odum 1971). Thus, populations have certain attributes distinct from the characteristics of the individuals of which they are composed, and communities have unique properties beyond the attributes of their component populations. An important level of organization that is now receiving more attention is the landscape, or mosaic of communities that covers a large land unit such as a watershed or a physiographic region (Forman and Godron 1981).

The importance of large-scale landscape patterns has been widely recognized (e.g., Bormann and Likens 1979, Forman 1979, 1982, Forman and Boerner 1981, Forman and Godron 1981, Habeck 1976, Habeck and Mutch 1973, Hansson 1977, Heinselman 1973, Loucks 1970, Luder 1981, Pickett 1976, Reiners and Lang 1979, Rowe 1961, Shugart and West 1981, Sprugel 1976, Sprugel and Bormann 1981, Swain 1980, White 1979, Wright 1974, Zachrisson 1977, and others). A few studies have quantitatively treated changes in landscape patterns (e.g., Hett 1971, Johnson 1977, Johnson and Sharpe 1976, Shugart et al. 1973). We recently made a detailed analysis of landscape composition and diversity in a pristine watershed in Yellowstone National Park in relation to fire and forest regrowth following fire (Romme 1982). In this paper we describe the natural changes that have occurred in landscape

pattern over a period of 240 years and the possible consequences of these changes for certain aspects of ecosystem structure and function. Although we focus on Yellowstone in this analysis, the concepts are applicable to other ecosystems as well.

The term *landscape diversity* refers to the diversity of plant communities making up the vegetational mosaic of a land unit. Landscape diversity results from two superimposed vegetation patterns: the distribution of species along gradients of limiting factors, and patterns of disturbance and recovery within the communities at each point along the environmental gradients (Forman and Godron 1981, Reiners and Lang 1979). Both of these patterns contribute to the vegetational diversity of the Yellowstone landscape.

Over the park's 9000 km<sup>2</sup>, elevation ranges from about 1800 m along the Yellowstone River in the northern portion to over 3000 m on the high peaks of the east and northwest. As a result, there are pronounced gradients of temperature and moisture, with related patterns in species distribution. The areas at lower elevations in the north support open sagebrush (*Artemisia tridentata*) parks on drier sites and aspen (*Populus tremuloides*) woodlands and Douglas fir (*Pseudotsuga menziesii*) forests in more mesic locations (Despain 1973). On the cooler subalpine plateaus one finds extensive upland coniferous forests of lodgepole pine (*Pinus contorta* var. *latifolia*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and whitebark pine (*P. albicaulis*), broken by occasional meadows and sagebrush parks on alluvial and lacustrine soils. The high peaks are covered by forests of spruce,

fir, and whitebark pine on sheltered slopes, with alpine or subalpine meadows and boulder fields on the more exposed sites. Pollen analysis of pond sediments indicates that these basic patterns of species distribution have been relatively stable during the last 5000 years (Baker 1970).

However, vegetational patterns related to the second source of landscape diversity—perturbation—have undergone changes during this time. Most of the changes have been natural, as described below, but some aspen and sagebrush communities in northern Yellowstone appear to have been altered somewhat by fire suppression during the last century. Comparisons of 100-year-old photographs with recent photographs of the same sites show that forests today are generally more dense, with an increase in conifers and a decrease in aspen, and that many sagebrush parks now contain more shrubs and fewer grasses and forbs. Streamside thickets of willow (*Salix* spp.) and alder (*Alnus* spp.) also appear less extensive and robust than formerly (Houston 1973).<sup>1</sup> Some have attributed these changes to excessive browsing by elk (*Cervus elaphus*) (Beetle 1974, Peek et al. 1967).

A more common explanation appears to be the virtual elimination of fire in this area from 1886 to 1975. Houston (1973) found that fires formerly recurred at average intervals of 20–25 years in northern Yellowstone, a disturbance frequency that probably was essential for the persistence of plant species and communities representing early stages of secondary succession (notably aspen and herbaceous plants). In the absence of fire, succession has proceeded unchecked and other species such as Douglas fir and sagebrush have become increasingly predominant. Thus fire

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<sup>1</sup>Houston, D. B. 1976. The Northern Yellowstone Elk. Parts III and IV. Vegetation and habitat relations. Unpublished report, Yellowstone National Park, Wyoming.

prevention appears to have modified the overall composition of the northern Yellowstone landscape, reducing landscape diversity by increasing the area covered by late successional plant communities at the expense of early successional communities. The magnitude of this change is relatively small in the context of the entire northern Yellowstone landscape, however, since aspen and herbaceous communities comprised a small fraction of the landscape even in presettlement times (Despain 1973). Similar changes have also been described in several other western parks and wilderness areas following effective fire control (Habeck 1976, Habeck and Mutch 1973, Kilgore and Taylor 1979, Loope and Gruell 1973, Lunan and Habeck 1973). Because a major management goal in the large national parks is to preserve ecosystems in their primeval state (Houston 1971), Yellowstone recently instituted a new fire management policy that allows lightning-caused fires to burn without interference if they do not threaten human life, property, or other values (US National Park Service 1975).

The situation seems to be different on the high subalpine plateaus that dominate most of the central, western, and southern areas of the park. Because of inaccessibility, effective fire control was not accomplished here until about 1950 when fire-fighting equipment and techniques were greatly improved (US National Park Service 1975). Moreover, our research indicated that fire occurs naturally at very long intervals because of very slow forest regrowth and fuel accumulation after fire (Romme 1982). On an average site, 200 years or more are required for a fuel complex to develop that is capable of supporting another destructive fire. On dry or infertile sites, 300–400 years may be necessary. Fires ignited prior to that time are likely to burn a very small area and have a minimal impact on the vegetation (Despain and Sellers 1977, Romme 1982). Recent uncontrolled fires in the park that burned intensely in 300-year-old forests have been observed to stop when they reached a 100-year-old stand, even though weather conditions remained favorable for fire (Despain<sup>2</sup>, Despain and Sellers 1977). Thus, in an ecosystem where fire historically occurred at intervals of 200+ years on any particular site, suppression during the last 20–30 years probably has had very little effect on overall landscape pattern. Any major

changes that have occurred are largely the result of natural processes that would have taken place even in man's absence.

Although the subalpine landscape apparently has not been substantially altered by man's activities (excluding, of course, those areas of intensive development for visitor use), it has by no means been static during the last 100 years. We found evidence that major fires occur cyclically, i.e., thousands of hectares may burn at intervals of 300–400 years with relatively few major fires in the same area during the intervening periods (Romme 1982). Such a fire cycle can occur because: geologic substrate, soils, and vegetation are very similar over much of the plateau region; forests over large contiguous areas grow and develop a fuel complex at approximately the same rates; and the plateau topography has low relief and few natural barriers to fire spread. Thus one extensive fire tends to be followed by another fire in the same area some 300–400 years later. In other parts of the Rocky Mountains where topographic barriers are more numerous, where succession occurs more rapidly, or where fuel characteristics are different, this particular type of fire cycle may not occur.

#### LITTLE FIREHOLE RIVER WATERSHED

We conducted our study in the Little Firehole River watershed, which covers 73 km<sup>2</sup> on the Madison Plateau, a large rhyolite lava flow in west-central Yellowstone. Coniferous forests predominate, with lodgepole pine occurring throughout and subalpine fir, Engelmann spruce, and whitebark pine being found on more mesic sites. Alluvial deposits in the central and northern parts of the watershed support subalpine meadows or open coniferous forests with rich shrub and herbaceous understories. The topography is generally flat or gently sloping, with an average elevation of about 2450 m.

Fire history during the last 350 years was determined using the fire-scar methods developed by Heinselman (1973) and Arno and Sneek (1977). Major fires occurred in 1739, 1755, and 1795 ( $\pm$  5 years), collectively burning over half of the upland area. Of the forested areas that did not burn at that time, nearly all were located either on topographically protected sites (ravines, lower northeast-facing slopes) that burn rarely (Romme and Knight 1981, Zachrisson 1977), or in places that had been burned by a moder-

ately large fire in 1630, less than 200 years earlier, and were covered by young forests. Since 1795 only three fires >4 ha have occurred, and all three were relatively small (<100 ha). The absence of recent large fires is almost certainly due to a lack of suitable fuel conditions over most of the watershed, not to fire suppression by man. In fact, park records show that only one fire has been controlled in this area, a 90-ha burn in 1949. The fire probably would not have covered a much larger area even without suppression, since it was surrounded by young forests and topographically sheltered sites. Today the areas burned in the 1700s support lodgepole pine forests that are all developing more-or-less synchronously; in another 100–150 years extensive portions of the watershed will again have fuel conditions suitable for a large destructive fire.

Three stages of forest regrowth following fire (early, middle, and late successional) can be recognized on upland sites. Early successional stages are usually present for about the first 40 years and are characterized by an abundant growth of herbs and small shrubs. The large dead stems of the former forest remain standing throughout most of this period, and an even-aged cohort of lodgepole pine becomes established. Middle successional stages are marked by the maturation and dominance of the even-aged pine cohort, beginning with canopy closure around 40 years and lasting until senescence around 250–300 years. Herbaceous biomass and species diversity are lowest during this period (Taylor 1973). During late successional stages (250–300+ years) the even-aged pine canopy deteriorates with heavy mortality and is replaced by trees from the developing understory to produce an all-aged, usually mixed-species stand, which then persists until the next destructive fire.

We used our data on fire history and on the rates and patterns of forest succession after fire to reconstruct the sequence of vegetation mosaics that must have existed in the Little Firehole River watershed during the last 240 years. Past landscape patterns were reproduced by first making a map showing the age (time since the last destructive fire) of all homogeneous forest units in 1978, based on extensive field sampling and aerial photography. Then, to reconstruct the landscape of 1738, for example, we subtracted 240 years from the age of each stand in 1978 and determined in which successional stage a stand of that age would

<sup>2</sup>D. G. Despain, personal communication.

have been. Where a fire had occurred more recently than the date of interest (e.g., areas that burned in 1739 in the reconstruction for 1738) we assumed that the stand was in a fire-susceptible late successional stage (Romme 1982).

Figure 1 shows the proportions of the Little Firehole River watershed covered by early, middle, and late successional stages at different times since 1738. In 1738 most of the area was covered by late successional forests, but fires in 1739, 1755, and 1795 greatly reduced the old-growth forests and replaced them with early successional stages. Middle successional stages became most abundant around 1800 and have dominated the watershed since. The early successional stages that were common in the late 1700s and early 1800s have been very uncommon since the mid-1800s. A decrease in middle successional stages after 1938 and an associated increase in late successional stages reflect forest maturation on areas burned in 1739.

To further describe historic patterns in landscape diversity, we calculated three diversity indices (similar to those used for measuring species diversity) and applied them to our landscape reconstructions for 1778–1978. We computed a richness index, based on the number of community types present; an evenness index, reflecting the relative amount of the landscape occupied by each commu-

nity type; and a patchiness index, indicating the size and interspersion of individual community units as well as the structural contrast between adjacent communities (Romme 1982). Figure 2 shows the results of plotting a weighted average of all three indices, as a measure of overall landscape diversity, and the Shannon index (Pielou 1975), which we calculated by using the proportion of the watershed covered by a community type as a measure of abundance. Both indices reveal a similar pattern: Landscape diversity was high in the late 1700s and early 1800s following the extensive fires of 1739, 1755, and 1795; it fell to a low point in the late 1800s during a 70-year period with no major fires; and it increased again during this century as a result of two small fires plus some variation in the rate of forest maturation in areas burned in 1739 and 1795. This variation in rates of succession is attributable to several factors including localized high densities of the mountain pine beetle (*Dendroctonus ponderosae*) (Romme 1982).

The dramatic changes in landscape composition and diversity in the Little Firehole River watershed during the last 240 years (Figures 1 and 2) must have been associated with significant changes in ecosystem structure and function, including net primary productivity, nutrient cycling, total biomass, species diver-

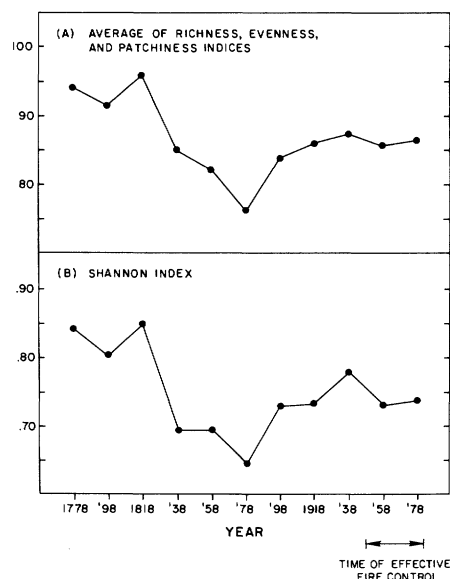


Figure 2. Changes in two measures of landscape diversity in the Little Firehole River watershed from 1778–1978.

sity, and population dynamics of individual species. These relationships cannot be fully quantified at this time, but speculation based on existing knowledge is useful.

#### IMPLICATIONS FOR WILDLIFE

Taylor and Barmore (1980) censused breeding birds in a series of lodgepole pine stands representing a gradient from the earliest successional stages after fire through late successional stages in the park. Their data show the pattern of avifaunal succession in a single homogeneous stand. In attempting to answer the question of how breeding bird species and populations change with time in an entire subalpine watershed, we used Taylor and Barmore's (1980) census data to estimate the number of breeding pairs in each stand within our reconstructed vegetation mosaics, summing the estimates for all to arrive at an estimate of breeding pairs in the entire watershed.

Figure 3 shows the results for three representative species and for the total number of breeding pairs of all species. Mountain bluebirds (*Sialia currucoides*) require open habitats with dead trees for nesting. Such habitat was most abundant in the Little Firehole River watershed during the late 1700s and early 1800s when 25–50% of the area was covered by early forest successional stages following the large fires of the 1700s (Figure 1). Consequently, bluebirds may have been very numerous at that time. However, as forests matured bluebird populations

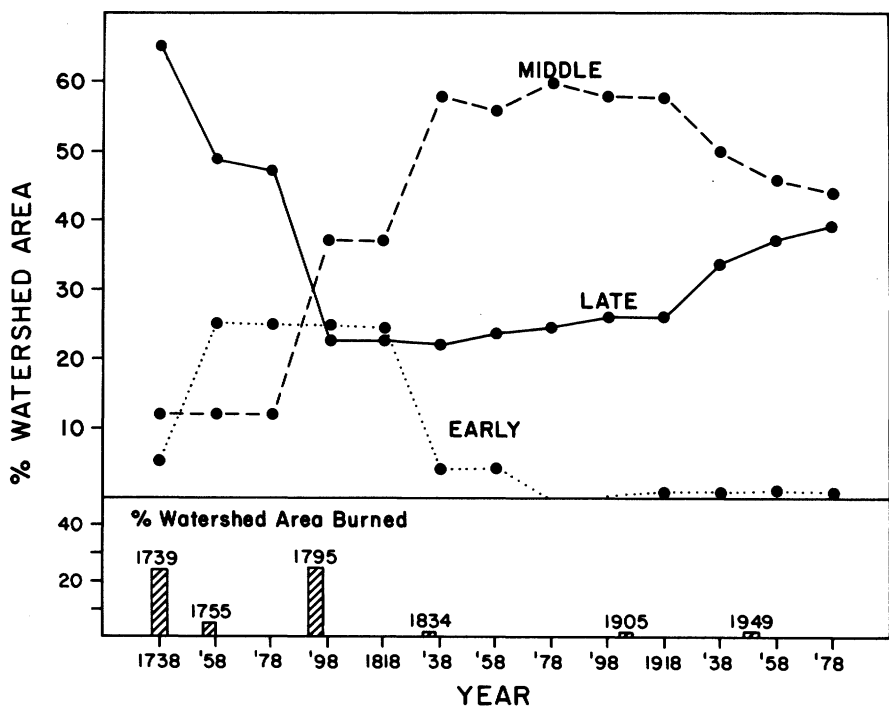
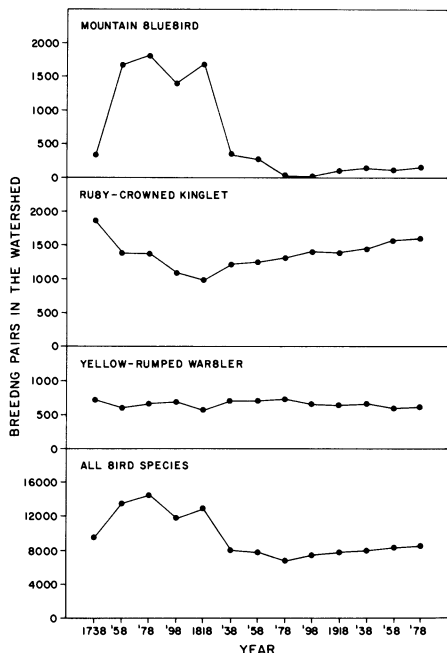


Figure 1. Percent of watershed area covered by early, middle, and late stages of forest succession from 1738–1978 in the 73-km<sup>2</sup> Little Firehole River watershed, Yellowstone National Park.

probably dropped dramatically (Figure 3). Today bluebirds are uncommon in the watershed except in the 90-ha area that burned in 1949. Note that this probable population decline was a perfectly natural event, occurring at a time when European man had not yet entered the area.

In contrast to the bluebird, ruby-crowned kinglets (*Regulus calendula*) prefer mature forests. Thus, kinglets were less common when bluebirds were most abundant (Figure 3). The yellow-rumped warbler (*Dendroica auduboni*) breeds successfully in a variety of habitats and as a result the population of this species probably has fluctuated little during the last 240 years despite the major landscape changes that have occurred (Figure 3). Figure 3 also shows that the total number of breeding pairs of all species has probably fluctuated greatly in the last few centuries. The highest numbers apparently were in the late 1700s and early 1800s when landscape diversity was also greatest (Figure 2).

The population estimates shown in Figure 3 can be challenged easily on the basis that they were derived solely from habitat availability, i.e., the number of hectares of forest present in each age class. Of necessity we have ignored other critical determinants of population



**Figure 3.** Estimated population sizes of breeding birds in upland forests of the Little Firehole River watershed, based on data from Taylor and Barmore (1980) and the trends shown in Figure 1. Populations in meadows and riparian forests, which cover approximately 16% of the watershed, are not included because appropriate population density data are not available for these habitats.

**Table 1.** Relative values of plant communities and successional stages for elk habitat in the Little Firehole River watershed.\*

Plant community type	Potential forage value	DISTANCE COEFFICIENT			
		DISTANCE (m) TO COVER OR WATER			
		0-320	320-800	800-1500	1500+
Alluvial woodland adjacent to moist meadow	10	1.0	0.9	0.7	0.5
Meadow	9	1.0	0.9	0.7	0.5
Upland forest; early successional stages	7	1.0	0.9	0.7	0.5
Upland forest; late successional stages	3	1.0	0.9	0.7	0.5
Upland forest; middle successional stages	2	1.0	0.9	0.7	0.5

\*Based on models and discussions by Asherin 1973, Basile and Jensen 1971, Black et al. 1976, Hershey and Leege 1976, Lonner 1976, Lyon 1971, Marcum 1975, 1976, Pengelly 1963, Reynolds 1966, Stelfox et al. 1976, Thomas et al. 1976, and Winn 1976.

density. Nevertheless, the overall patterns are valid to the extent that they show the constraints of habitat on potential populations.

We were also able to consider the effect of landscape change on elk. Using a model much like that developed by Thomas et al. (1976), we examined changes in three critical habitat features during the last 200 years, namely, forage quantity and palatability, shelter (or cover), and water. The forage and shelter provided by an individual forest stand change greatly during postfire succession. Early successional stages usually have the best forage whereas middle and late successional stages provide the best shelter. However, because elk use several different kinds of habitat, the distribution and interspersed of plant communities and successional stages is critical. Thus the center of a large meadow or recently burned area may receive little elk use, despite abundant forage, if it is too distant from shelter or water, and the potential shelter of very extensive tracts of mature forest may be largely ignored if little forage is available (Black et al. 1976, Hershey and Leege 1976, Marcum 1975, Reynolds 1966, Stelfox et al. 1976, Thomas et al. 1976, Winn 1976).

We developed a relative ranking system by which every type of plant community and successional stage in the Little Firehole River watershed was assigned a value from 0-10 to indicate potential forage value (Table 1). These values were subjective, based on published literature and our own observations in the study area. We then divided the watershed into 1429 units of 5 ha each, identified the dominant vegetation type within each unit, and assigned appropriate values to each. Every value was multiplied by a distance coefficient

reflecting the distance to the nearest shelter or water if those features were not present within the unit itself (Table 1), the product being our elk habitat index. In this manner we analyzed our reconstructed vegetation mosaics for 1778, 1878, and 1978.

Figure 4 (a, b, and c) shows the results for three 5-ha units having different histories of fire and forest regrowth. As a result of changes in stand structure, the quality of elk habitat has varied greatly. However, when we averaged the values for all 1429 individual 5-ha units to obtain an estimate of elk habitat quality for the watershed as a whole, we found much less difference among the landscapes of 1778, 1878, and 1978 (Figure 4d). There are probably two main reasons for this result. First, temporary increases in habitat quality in one part of the watershed (due primarily to the great improvement in forage after fire) have been balanced by decreases resulting from forest maturation on other areas burned earlier. Second, and probably more important, the best habitat is in and around moist meadows where forage, shelter, and water all occur in close proximity. In fact, our model may underestimate the habitat quality of subalpine meadows in the park, since we reduced our elk habitat index in the centers of large meadows to reflect the distance to shelter. However, the shelter requirement apparently is much less critical for elk populations that are not hunted by man, and elk in the park are frequently observed feeding in the centers of large meadows.<sup>3</sup> We were unable to determine whether the large fires in the surrounding uplands had burned the meadows and adjacent allu-

<sup>3</sup>L. Irwin, personal communication.

vial woodlands. We assumed that the fires in these areas were of low intensity and produced little change in community structure or elk habitat. Although our results suggest that fires may not greatly influence the overall quality of elk summer range on the high plateaus of Yellowstone, elk are attracted to recently burned areas (Davis 1977), and over much of the subalpine zone, moist meadows are less common than in the Little Firehole River watershed. Where meadows are less common, summer elk populations may fluctuate in response to changes in the upland landscape.

### IMPLICATIONS FOR AQUATIC ECOSYSTEMS

One of the most interesting and attractive features of the park is Yellowstone Lake. This virtually unpolluted subalpine lake covers 354 km<sup>2</sup> and contains populations of the native cutthroat trout (*Salmo clarkii*). The trout support a complex food chain including pelicans, ospreys, otters, and bears. Some evidence indicates that the lake's net primary productivity has declined during the last century, as has its carrying capacity for trout and associated top predators (Shero 1977, US National Park Service 1975). Because the period of apparent decline coincides with attempts at fire control, some have suggested that the cause is reduced nutrient input to the lake due to biotic immobilization by forests. As noted earlier, however, our research indicates that the natural fire regime has not been greatly altered by

man's activities in the Yellowstone subalpine zone, particularly in the very remote areas that drain into Yellowstone Lake.

Rather than attribute the cause to fire suppression, we favor the hypothesis that lake productivity is to some extent synchronized with the long-term fire cycle that seems to prevail in the watershed of Yellowstone Lake. A variety of evidence supports this hypothesis. For example, experiments in the Rocky Mountains have shown that removal of mature forest from 40% of a subalpine watershed results in an increase in total water discharge of 25% or more (Leaf 1975). The increase is due to several factors related to the distribution and melting of the winter snowpack. Albin (1979) compared two small tributary streams of Yellowstone Lake; about 20% of one watershed was burned by fires 36 and 45 years previously, whereas the other watershed was unburned. The burned watershed had greater seasonal variation in streamflow and greater total water discharge per hectare. If a large portion of a subalpine watershed burns at intervals of approximately 300 years, as seems to occur in the Little Firehole River watershed, then streamflow also may exhibit a long-term cycle over and above yearly and seasonal fluctuations. During the high-discharge portion of the cycle, especially in years of high snowfall, debris is washed out of stream channels, new channels are cut, and new alluvial deposits are created. Such events influence habitat for fish as well as for floodplain species like willow and alder, which in

turn are important browse species for elk and other terrestrial animals (Houston 1973).

But more important to the question of Yellowstone Lake is the nutrient content of stream water. Immediately after deforestation by fire or cutting there often is an increase in dissolved minerals due to erosion, reduced plant uptake, increased microbial activity, increased leaching, and the release of elements from organic matter by fire (Bormann and Likens 1979, McColl and Grigal 1975, Wright 1976). The increase is usually short-lived, lasting several years at most (Albin 1979, Bormann and Likens 1979), but it may be important as a periodic nutrient subsidy (Odum et al. 1979) to oligotrophic aquatic ecosystems. As young forests become established, biotic immobilization is so effective that nutrient concentrations in stream water fall to very low levels (Bormann and Likens 1979, Marks and Bormann 1972, Vitousek and Reiners 1975). Thus a watershed dominated by early and middle forest successional stages (e.g., the Little Firehole River watershed during the 1800s) would produce relatively nutrient-poor water. As forests reach late successional stages, tree growth and net primary productivity decrease, nutrient uptake is less, and consequently the leachate is richer in dissolved minerals (Bormann and Likens 1979, Vitousek and Reiners 1975).<sup>4</sup>

Thus, although the possible connection between fire suppression and reduced productivity in Yellowstone Lake is plausible, an equally attractive alternative hypothesis is that extensive fires in the watershed about 100 years ago replaced many late successional forests with early successional stages. As young forests over much of the watershed began utilizing soil nutrients more efficiently, the total amount leached into stream water feeding the lake was reduced accordingly. If this is true, any recent decline in lake productivity may be a natural phenomenon that has occurred many times in the past and will be alleviated as forests in the watershed mature. Of course, the Yellowstone Lake watershed is very large (ca. 2600 km<sup>2</sup>), and landscape patterns over this large area may be in a state of dynamic equilibrium, or what Bormann and Likens (1979) have referred to as a shifting mosaic steady

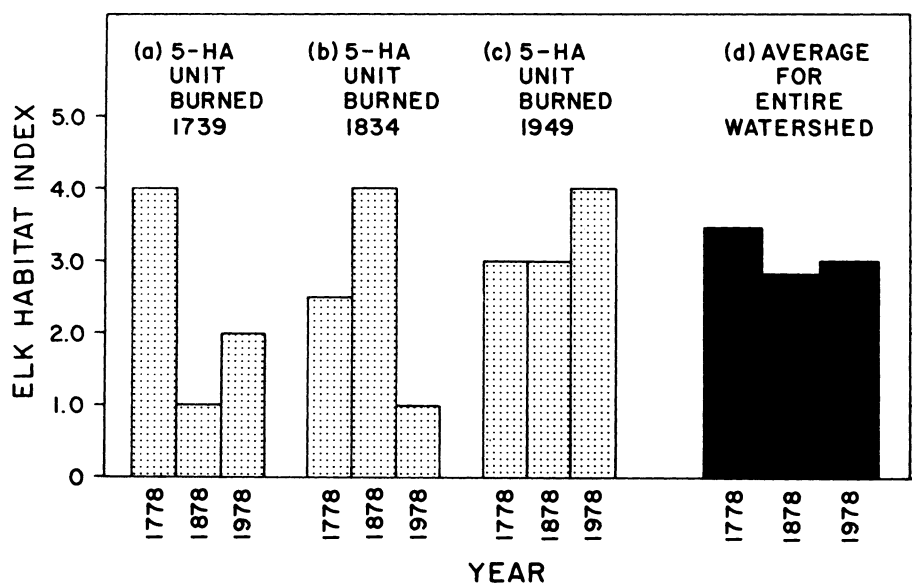


Figure 4. Elk habitat index (see text) for three representative 5-ha units and for the entire Little Firehole River watershed (d) in 1778, 1878, and 1978.

<sup>4</sup>Pearson, J. A., D. H. Knight, and T. J. Fahey. Unpublished ms. Net ecosystem production and nutrient accumulation during stand development in lodgepole pine forest, Wyoming.

state. If this is found to be true for the Yellowstone Lake watershed, then total nutrient input to the lake should be about the same from year to year (though the source would vary), and some other explanation for the decline in lake productivity will be required.

## CONCLUSIONS

After a century of ecological research that focused largely on species or individual communities or ecosystems, there now is a growing interest in still higher levels of organization such as the landscape and biosphere. Changes in landscape patterns influence a variety of natural features including wildlife, water and nutrient flow, and the probability of different kinds of natural disturbances. Given a sufficiently large area and a natural disturbance regime, various measures of landscape pattern may remain fairly constant over time despite dramatic cyclic changes in localized areas such as a small watershed. Such "steady states" have been demonstrated or hypothesized for a Swedish boreal forest (Zachrisson 1977), high-elevation fir forests in New England and elsewhere (Sprugel 1976, Sprugel and Bormann 1981), primeval northern hardwood forests of North America (Bormann and Likens 1979), and mesic deciduous forests of the southern Appalachians (Shugart and West 1981). Our results suggest that strong cyclic changes occur on areas of at least 100 km<sup>2</sup> in Yellowstone National Park, but more research is needed to determine if the landscape patterns in the park as a whole are in a state of equilibrium. Large wilderness areas, when protected from pollutants and managed so that natural perturbations can continue, provide the best and probably the only locale for studying the kind of landscape changes that occurred for millennia in presettlement times.

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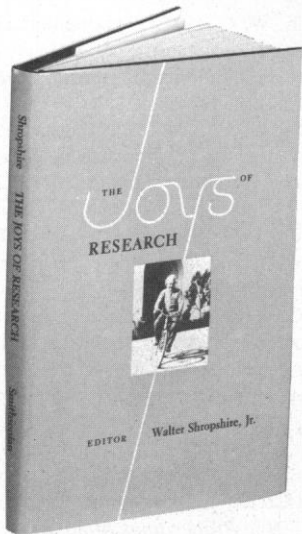
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