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NATURAL DISTURBANCES AND BIODIVERSITY IN WILDERNESS LANDSCAPES

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At least three levels of biodiversity can be described, including diversity of species, genetic diversity within species, and the diversity of biotic communities and ecosystems across a landscape. This paper focuses mainly on the third level of biodiversity. It is concerned with the natural processes that interact to create and maintain a diverse mix of plant and animal communities in wilderness areas, and with the ways in which the designation and management of wilderness areas may influence these processes and thus may alter the natural patterns of biodiversity of the landscape level.

The word "wilderness" is used here in a generic sense to refer to any landscape in which natural ecological and geological processes predominate. The general concepts developed below apply to Wilderness Areas officially designated under the Wilderness Act of 1964, and also to undesignated roadless areas in National Forests, to the ecosystems within many large National Parks, and other wildland areas (Houston 1971).

NATURAL PROCESSES THAT CREATE BIODIVERSITY

Nearly all wildland areas contain a diverse mix of biotic communities. This diversity results from the interplay of two fundamental processes that operate in all landscapes. The first process is the response of organisms to underlying variation in the physical environment. This variation is

very striking in mountainous areas, where we can readily identify gradients or progressive changes in elevation, geologic substrate, and topographic position. Higher elevations and north-facing slopes typically provide cooler and wetter conditions, and thus support different plant species than the warmer, drier habitats at lower elevations and on south-facing slopes. Even in landscapes with little physical relief. e.g., prairies, there usually are gradients in soil structure, nutrient availability, and other ecologically important characteristics. In general, landscapes containing a greater variety of habitats, as a result of these environmental gradients, tend to support a greater diversity of biotic communities.

The second natural process that creates and maintains biodiversity at the landscape level periodic disturbance of involves biotic communities and the ecological succession that takes place after disturbance (Pickett and White 1985). The kinds of natural disturbances vary from region to region. In the Rocky Mountains, for example, fire, insect outbreaks, avalanches, and landslides are some of the important forms of natural disturbance; in deserts, flash floods may be more important disturbances; fires and hurricanes are important in the Everglades. Regardless of the nature of the disturbance, the results are similar: established plants are killed or injured, and the space that they formerly occupied becomes available for colonization by other plants. Many plant species can only survive in places where they have little competition from

other plants; they become established only after disturbances and persist for a time but are gradually crowded out by other species that are more tolerant of crowding and competition.

The importance of this second process in creating and maintaining biodiversity is well illustrated by the succession of plants and animals after fire in Yellowstone National Park (Despain, in press; Romme and Despain 1989a,b,c). Lightning has ignited fires for centuries on the forested high plateaus of the Yellowstone region, and extensive fires have occurred many times in the past, even before Europeans came into the region. Many of these past fires were high-intensity fires that killed the forest canopy over hundreds or thousands of acres, as occurred again in 1988. The dominant plant species during the first 25 or so years after such a fire are herbs and shrubs, such as fireweed (Epilobium angustifolium), many of which that were uncommon in the forests that species, like dragonhead burned. Some apparently (Dracocephalon parviflorum) germinate and flower only after a fire, then persist as buried seeds until the next fire (Stickney 1986). Eventually, however, trees become re-established, and after some 200-400 years of succession, the forest again resembles the forest that burned.

In addition to the succession of plant species after fire, there is a succession of animal species. For example, three-toed woodpeckers (Picoides arcticus and P. tridactylus) are common in recently burned forests, where they drill into the fire-killed snags for beetles and other insects, but they are rarely seen in older forests. Mountain bluebirds (Sialia currucoides) and tree swallows (Iridoprocne bicolor) also prefer recently burned forests, where they use the fire-killed snags for nesting and perching. These species would decline in numbers if fire were excluded from Yellowstone's forests for a very long time (Taylor 1973, Romme and Knight 1982). However, there also is another group of animals, including the pine marten (Martes americana) and the goshawk (Accipiter gentilis), that is

largely restricted to old growth forests. These species would disappear if the entire landscape burned or was clearcut.

Thus, the maximum diversity of species is likely to exist in a landscape containing a variety of habitats; and habitat variety results not only from the effects of environmental gradients, e.g., elevation and topography, but also from natural disturbances and the successional sequences that follow.

MAINTAINING BIODIVERSITY IN WILDERNESS AREAS

It is important to recognize that these natural processes of biodiversity are dynamic, and that wilderness landscapes are ever changing. This recognition bears on a fundamental question in wilderness management, namely what it is that we are trying to manage for. Some people think of a wilderness area as a place that does not change except as humans alter it. It follows from such a conception that the goal in wilderness management should be to preserve, or, if necessary, to re-create the scene that was witnessed by the first explorers to reach the area before modern human activities changed things. This concept seems to be fundamentally wrong. Reconstructions of the mosaic of communities that existed in the Yellowstone landscape during the last 250 years indicated that the mix of plant communities was continually shifting; fires burned some areas every decade, creating early successional communities dominated by herbs and shrubs, while succession in other previously burned areas re-established forest communities (Romme and Despain 1989a,b,c). This was occurring even in the 1700's and early 1800's, when there were no Europeans in the Yellowstone region to modify natural ecological processes.

Rather than trying to preserve a static scene that we think is the way a wilderness area "should" look, a more effective strategy is to preserve the natural processes that maintain biodiversity (Graber 1983, Christensen et al. 1989). For example, because lightning-caused fires have long been a primary source of diversity in the Yellowstone landscape, the National Park Service in 1972 changed its former policy of suppressing all fires and began allowing some lightning fires to burn without interference (Despain et al. 1982). Several other large National Parks and National Forest Wilderness Areas have similar fire management policies that emphasize maintaining the natural processes that create biodiversity instead of trying to "freeze" the appearance of the landscape at any particular point in time (Lotan et al. 1985).

Allowing natural disturbance processes to continue operating in wilderness areas seems to be a necessary part of maintaining natural biodiversity, but this is not always an easy task. With some kinds of disturbances, e.g., hurricanes, there presently is nothing we can do to alter their behavior and effects. But there are other kinds of disturbances that we can control, at least to some extent. A good example is fire; we can suppress most fires (though some in 1988 were uncontrollable even with modern technology), and we can intentionally ignite fires. In either case we alter the natural frequency and effects of fire, and we need to consider the potential effects on biodiversity of any proposed policy for managing fires and other natural disturbances in wilderness areas. The very act of establishing a wilderness area may subtly alter the area's biodiversity and the processes that maintain it. Let us then use fire as a specific example as we examine two major issues in the maintenance of biodiversity in wilderness areas: effects of boundaries and effects of different strategies for dealing with natural disturbances.

BOUNDARY EFFECTS ON NATURAL DISTURBANCE & WILDERNESS BIODIVERSITY

Designating an area as wilderness always entails drawing a boundary. The location of this

boundary, and the size and environmental heterogeneity of the area it encloses, have profound and long-lasting effects of biodiversity. Generally, the larger a wilderness is, the more species and kinds of biotic communities it will contain. However, a small, mountainous area may support more species and communities than a large, flat area because the pronounced environmental gradients in the former area create so many more kinds of habitats. On the other hand, if many of the species in the small mountainous wilderness are represented by very few individuals, then they may disappear within a short time if there is no longer any suitable habitat available for them outside the wilderness Small populations are vulnerable to area. extinction because of genetic and demographic changes that often take place, and because a local accident or disturbance can eliminate all or most of the population (MacArthur and Wilson 1967, Soule et al. 1979, Wilcox 1980).

The natural processes of disturbance and succession also are profoundly influenced by the size of the reserve. Consider, for example, the effects of the 1988 Yellowstone fires. Extensive, high-intensity fires of this kind have long been a natural part of the yellowstone environment. apparently occurring at intervals of 100-300 vears (Romme and Despain 1989a,b,c). Several lines of evidence suggest that the 1988 fires were a nearly natural event in the ecological history of the region. The large size of the fires was a result primarily of unusually dry and windy weather conditions, coupled with the fact that the landscape was covered by extensive forests that had developed since the last extensive fires in the early 1700's (Romme and Despain 1989a,b,c).

The fires in 1988 did not destroy the biodiversity of Yellowstone wilderness. On the contrary, they probably increased biodiversity. Fire history research indicates that the yellowstone landscape had been dominated by closed forests in middle and late successional stages since the mid 1700's and that early successional forests had become increasingly rare

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in the twentieth century (Romme and Despain 1989a,b,c). The 1988 fires burned nearly 800,000 acres, thus creating a large expanse of early successional forests that will persist for several decades before succession returns the burned areas to closed forest once again. Despite the enormous extent of the fires, however, there still remains hundreds of thousands of acres of unburned forest that continue to harbor pine marten, goshawk, and the other species that do not thrive in recently burned areas. Yellowstone now has a more even mix of forests in all stages of succession than it has in the last 200 years. It seems, then, that a wilderness area the size of Yellowstone National Park (2.2 million acres) is large enough to absorb fires of this magnitude, and the natural wilderness processes that have shaped the Yellowstone landscape for thousands of years are still operating pretty much as they always have. Yellowstone's biodiversity was maintained or even increased in 1988.

Let us imagine, however, what the effects of the 1988 fires might have been if Yellowstone Park were only 10,000 acres in size. All or nearly all of such a small wilderness area could have burned in 1988, and this one fire might have eliminated its old-growth forest and the associated plant and animal species. Such a disturbance would be a catastrophe, even if the disturbance were essentially natural, because the boundaries of the wilderness area did not encompass a large enough area to accomodate the effects of that disturbance.

One should not conclude from this discussion that every wilderness area must be as large as Yellowstone National Park to be ecologically viable. Natural disturbance in Yellowstone is probably on the extreme end of the spectrum for landscapes within the continental United States (though it probably is fairly typical of many boreal landscapes in Alaska and Canada). In deciduous forests of the eastern United States, for example, a major form of natural disturbance is the falling large, old trees which create openings in the forest canopy in which several species of shade-intolerant trees and shrubs can become established (Pickett and White 1985). This kind of disturbance occurs frequently, but affects only small areas (usually an acre or less); thus all stages of succession can be maintained within a wilderness preserve of several hundred or a few thousand acres. Similarly, ponderosa pine forests, which occur throughout much of the west, historically burned at intervals of decades or years and were far less severe than the fires in Yellowstone's lodgepole pine forests (Arno 1980). It is possible, then, to maintain a natural, fire-created mosaic of forest successional stages within a much smaller wilderness tract of ponderosa pine forest. We need to conduct research in our wilderness areas to discover the kinds of natural disturbances that are important in each particular area and to ascertain the spatial and temporal scales over which those disturbances operate.

MANAGING NATURAL DISTURBANCES IN WILDERNESS AREAS

Recent ecological research has demonstrated the importance of natural disturbance and succession in maintaining biodiversity of wilderness areas. However, it often is difficult to manage specific areas in such a way that these processes can continue to operate naturally. For many years, nearly all federal land management agencies in the United States attempted to eliminate all fires, both natural and human caused, on commodity-producing lands and in wilderness areas. Such a policy, if effective, would ultimately lead to impoverished biodiversity because early successional stages and their associated species would eventually disappear from the landscape (Taylor 1973). As a result of our better understanding of the role of natural fire in maintaining biodiversity, some wilderness areas in the United States now have implemented fire management policies that permit at least some lightning-caused fires to burn (Lotan et al. 1985). However, all fires still are routinely suppressed in many other officially designated wilderness areas.

There are some powerful reasons why many wilderness managers still attempt to prevent natural disturbances like fires. Fires are dangerous. They can easily burn out of a wilderness area and threaten human life, property, and other non-wilderness resources. In very small reserves, it may not even be feasible to allow lightning-caused fires to burn without interference, because they may burn the entire reserve. Managers of many small nature reserves therefore have chosen to suppress all wildfires, but to simulate the effects of natural fires with a program of prescribed burning. Fires are intentionally ignited by managers at carefully selected times when the fires can produce desired ecological effects, yet can be controlled if they threaten to burn a larger area than is wanted.

Some people have proposed that this kind of prescribed burning should be implemented in all wilderness areas, even the very large ones. They argue that uncontrolled lightning-caused fires are too dangerous and unpredictable even in an area as large as Yellowstone, and that the beneficial effects of fire on biodiversity can be obtained by periodically burning small areas under controlled conditions.

This kind of approach is probably our only option in small nature reserves, but for large areas it seems antithetical to the wilderness idea. Fires are admittedly dangerous and unpredictable, but those are both quintessential qualities of wilderness. Moreover, at least some of our large wilderness areas, e.g., Yellowstone, appear to be capable of supporting even large natural disturbances, as described above.

Another reason for not trying to replace natural disturbances with simulated ones is that we do not yet understand natural disturbances and their effects on the biota well enough to really reproduce them. For example, one of the most striking features of the 1988 Yellowstone fires was their heterogeneity. The fires created a complex mosaic of severely burned, moderately burned, lightly burned, and unburned patches (see the photographs in **BioScience**, November

1989, and in Western Wildlands, summer, 1989). The makeup of this mosaic has numerous implications for organisms and ecological processes. The spatial distribution of burned forests in relation to stream channels and watersheds will profoundly influence streamflow and the response of aquatic organisms (Minshall et al. 1989); the edge created in previously continuous forest will influence behavior of elk, bears, and other animals (Wallace and Knight 1989); and plant establishment and succession will be different on lightly burned and severely burned patches and in the centers and around the margins of large burned patches (Turner and Romme, in press). The point here is that our understanding of natural fire behavior prior to 1988 was not sufficient to have predicted the kind of heterogeneity that was actually produced by the fires. Had we been trying to simulate natural fires with prescribed burning in Yellowstone, we would not have incorporated the heterogeneity that was so important in the areas that burned naturally in 1988.

Wilderness areas are valuable for many reasons: aesthetic, recreational, scientific, and pragmatic. One value of wilderness that is sometimes overlooked is its value as a source of information. The earth was wilderness for most of its history, and nearly all of its creatures evolved in a wilderness setting. We are only beginning to understand the workings of the natural world. Ecologically intact and functional wilderness areas, where natural ecological and geological processes still predominate, provide unique glimpses into our roots.

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