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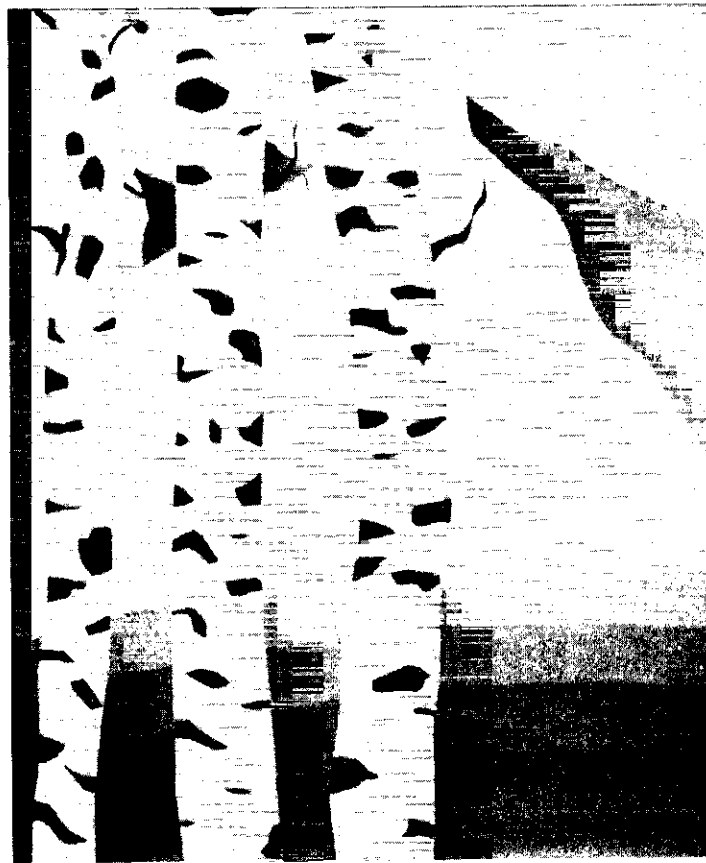
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Biodiversity on Rangelands



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Joseph A. Chapman, Dean
College of Natural Resources

Biodiversity on Rangelands

Edited by
Neil E. West

College of Natural Resources
Utah State University
Logan, Utah

Proceedings of the Symposium
Biodiversity on Rangelands

February 16, 1993
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Biodiversity on Rangelands: Definitions and Values

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Abstract

Biodiversity is not just one phenomenon but is a concept cluster that involves many facets of biological variety. These facets include taxonomic richness; genetic differences within each taxon; the communities, ecosystems, and landscapes organisms occupy; and the knowledge of nature local people living on the land possess. Biodiversity is prized for a variety of intertwined moral, aesthetic, and practical reasons. The role of biodiversity in the globe's life-support systems is poorly understood but probably pivotal. The world's rangelands possess biodiversity out of proportion to their area or productivity. Livestock grazing may influence biodiversity either positively or negatively depending on what is being valued. It is impossible to maximize simultaneously all features of biodiversity. Therefore, management of rangelands to favor certain aspects of biodiversity will require compromise.

INTRODUCTION

I predict that the biodiversity issue will heavily influence rangeland management during the coming decades (West 1993). If the profession is not to be totally reactionary in its stance, it needs to become better versed in how others view biodiversity. Action is best preceded by education. I have organized this volume to help educate the profession about this issue.

In this brief first paper, I have only two objectives: first, to outline the different definitions of biodiversity and, second, to explain why biodiversity has become so topical. Subsequent papers will then take up subsets of the broad topic and will present rangeland examples.

DEFINING BIODIVERSITY

In simplest terms, diversity is synonymous with variety. In the natural world, variety can exist both in the environment and in the biota. I am here interested primarily in biological diversity, which I refer to in the shortened form as *biodiversity*.

Biodiversity has been defined as the variety of living organisms; the genetic differences among them; and the communities, ecosystems, and landscapes in which they occur (Noss 1990, West 1993). There is also gathering momentum to include the local people engaged in sustainable lifestyles. Their culture and indigenous knowledge could be considered as part of total biodiversity (Figure 1). The interactions among these components should not be overlooked.

Biodiversity is not one phenomenon but is what Peters (1991) calls a *concept cluster*. Viewing biodiversity from different perspectives leads to different perceptions of what is involved and of what is important.

Because of natural human tendencies to prefer different perspectives, I see no hope for ever tightening the definition of biodiversity. Thus, in order for us to have a respectful and productive discussion of biodiversity, we need to understand where each of us prefers to stand and on what temporal and spatial scales we are focusing. There is no single position that is best for all problems or questions addressed. One should choose his approaches based on the level or levels at which the problem or question lies (Allen and Hoekstra 1992). If one has trouble expressing what his focus is, ask his choice of methods for inventory and monitoring tools (Noss 1990). The answer will be very telling about which levels of integration and spatial and temporal scales are favored. Furthermore, without a tightly stated purpose for estimating biodiversity, one cannot easily decide on the most relevant measure(s) of biodiversity. Failure to make objectives explicit ensures continued frustration because what constitutes ecological good remains as much a matter of human opinion and value systems as it is a subject of science.

Patterns and processes at one spatial or temporal scale affect those at other scales. For instance, diminishment of small neotropical migratory birds, which could be largely due to loss of winter habitat in the tropics, may eventually influence ecosystem structure and function at higher latitudes. Possible mechanisms of change are (1) altered predation on insects and seeds, (2) propagule dissemination, and (3) pollination.

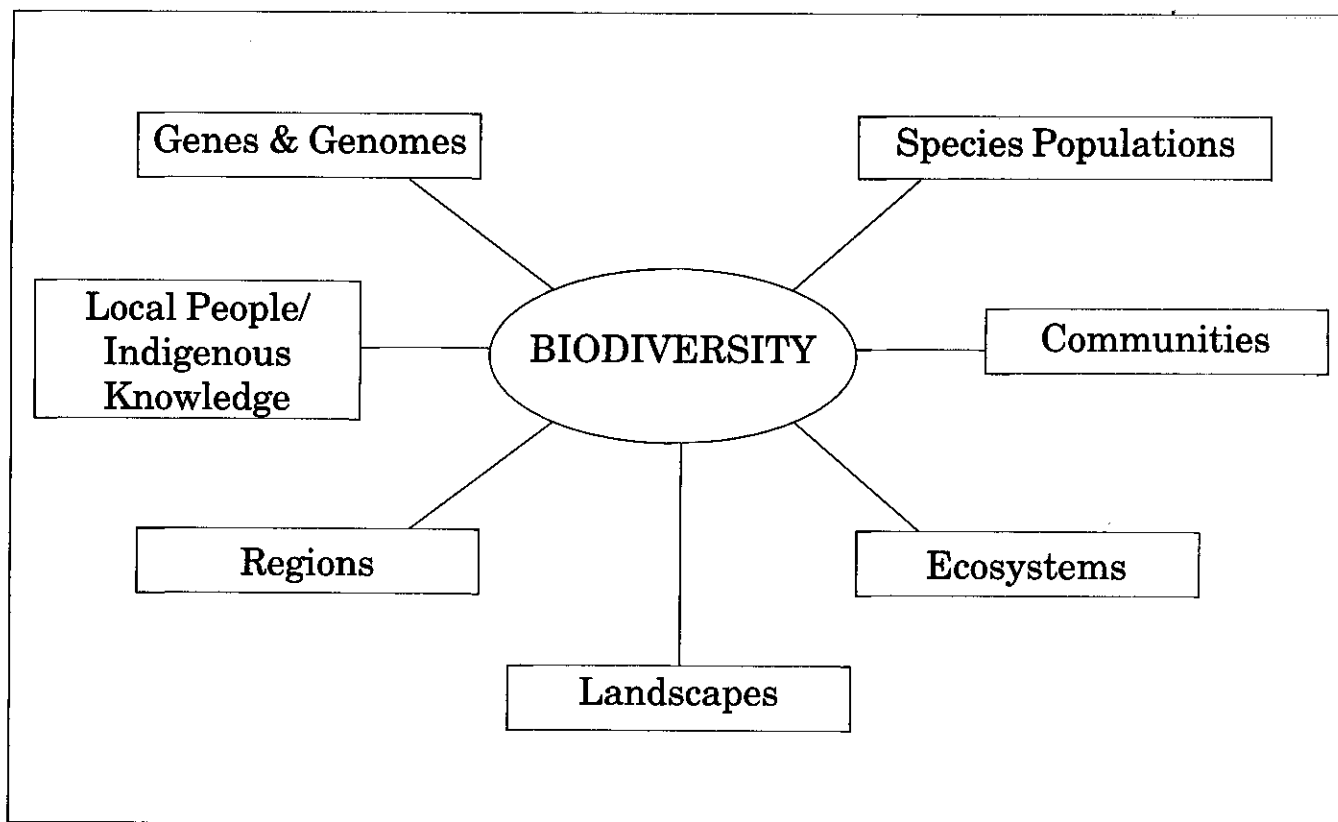


Figure 1. Components of biodiversity

Another example of interactions among levels involves the low relative values of plant community richness (alpha diversity based on taxonomic species) in the Great Basin and in the Great Plains. This impression is gained from using only conventional taxonomic-based descriptors, e.g., vegetation is dominated by a few very widespread species. These species (e.g., *Artemisia tridentata*, *Bouteloua gracilis*), however, have enormous genetic variation within them. They have survived many swings in past environments, largely because of the huge genetic bases of variation invisible to the unaided human eye. Thus, greater or lesser diversity at one scale does not automatically translate to greater or lesser diversity at other scales. Biodiversity will, therefore, have to be considered at all levels relevant to the questions being asked. The choice of questions is driven by human values as well as by curiosity.

VALUES OF BIODIVERSITY

Why has biodiversity become such a "hot" topic of late? I think three major forces are involved: global environmental change, accelerated species extinctions, and changing societal values. These forces are linked, of course, resulting in political activity that leads to legislation, regulation, and changed human behavior. Political action has "leapfrogged" science on this topic, but science is only one contributor to the debate.

The first basic reason to be concerned about biodiversity involves morality (Table 1). Many people believe that humans have a moral obligation to protect fellow creatures on earth, whether any intrinsic value is placed on them or not. The strength of this feeling depends on one's own philosophical and religious orientation, namely, mankind's place in nature (terrified, central, coequal, exterminator, or outside nature).

Some primitive cultures are terrified of nature and develop behavior to appease its demons. This behavior may involve everything from avoiding, to worshipping, to exterminating certain organisms, depending on their place in the culture's mythology.

Under the Judeo/Christian/Muslim heritage, man has been the center of nature; and other forms of life are manipulated to meet the needs and wants of humans. While the older literature portrays Western man as an exterminator, a recent random sampling of public attitudes toward management of forests in the United States in general and in Oregon in particular (Shindler et al. 1993) showed that twice as many people now feel that management actions should consider rather than ignore the needs of rare and endangered species.

A growing subculture within Western society considers other organisms as coequals. These "deep ecologists" were, however, preceded in this view by the Jains and by some Native-Americans. Animal rightists are concerned only with sentient animals similar to humans. Thus, their view remains anthropocentric.

Most Western scientists have considered themselves as outside natural systems. The idealism of the leading ecologists, e.g., Frederic Clements, had little room for incorporation of man's influence on ecological processes like succession. Economists also externalized biodiversity as outside the economic system. Fortunately, both ecologists and economists are now realizing these errors and are beginning to be more inclusive in the systems with which they deal (Constanza and Wainger 1991).

Equity among human generations, nations, and classes is beginning to play a more important role in policy formulation about biodiversity. The tension between the nations of the "North" and "South" became very evident at the Conference on Global Environment at Rio de Janeiro in 1992. The developing nations of the Southern Hemisphere are willing to trade access to genetic material if the nations of the Northern Hemisphere will not deny them economic reward for doing so. The equity among generations is at the core of the sustainability issue (Meadows et al. 1992). Which view of man in relation to nature becomes dominant will be settled in the political more than in the scientific arena. We have to face the fact that the morality issue makes biodiversity problems "wicked" (Allen and Gould 1986), and only more or less useful and temporary solutions can be reached.

The second major reason biodiversity is important involves aesthetics and amenities (Table 1). Most humans want to see and appreciate the living fraction of nature. Some are willing to part with some of their material wealth to support ecotourism, zoos, wildlife films, etc. Thus, there is a mix of philosophy and economics in this facet of biodiversity.

The third, major, and so far most recognized value of biodiversity results from the goods humans desire, such as food, medicine, fuel, building material, and industrial products (Table 1). Crops and domestic animals can be viewed as "borrowed" from the "genetic library" of nature (Ehrlich and Wilson 1991). The potential of the "library" has scarcely been tapped. Transgenic (between phyla) gene splicing provides enormous possibilities. Despite the novel and movie *Jurassic Park*, we still cannot resurrect whole organisms. Thus, extinction should still be regarded as a final, irreversible loss of options.

The fourth, least understood, but most important value of biodiversity (in my opinion) is the array of "services" provided by natural ecosystems as life-support systems (Table 1). Essential ecosystem services include maintenance of the gaseous composition of the atmosphere, amelioration of climates, genesis, fertility, and stability of soils, disposal of wastes, cycling of nutrients, and natural control of pathogenic and parasitic organisms. Loss of biodiversity can be assumed to negatively influence both the quality and quantity of ecosystem services and ultimately has unfavorable economic consequences. Although it is logical to expect that reducing the taxonomically based biological variability of a system will lead to a reduction in its resilience and an increase in the probability that rare, extreme events cannot be absorbed, the quality of science so far brought to bear on this topic has not been strong. Dr. Whitford and I will have more to say about these issues in this volume.¹

¹See West and Whitford, this volume.

TABLE 1. REASONS TO BE CONCERNED ABOUT BIODIVERSITY

Morality	<ul style="list-style-type: none"> mankind's place in nature terrified, central, coequal, exterminator, outside equity intergenerational, geographical socio-economic class
Aesthetics and Amenities	<ul style="list-style-type: none"> ecotourism zoos, botanical gardens, films, etc.
Goods	<ul style="list-style-type: none"> foods medicine fuel building material industrial products
Services (Life Support Systems)	<ul style="list-style-type: none"> cleaning up air and water ameliorating climates soils—genesis, fertility, stability energy flow + waste disposal nutrient cycling + waste disposal natural control of parasites and pathogens

Rangelands are untilled lands with self-sown vegetation that have been extensively managed on ecological rather than on agronomic bases. Because the changes on these lands have been largely due to livestock grazing rather than to tillage and tree harvest, most of their biodiversity remains. Accordingly, we may expect increasing focus on preservation and management of that biodiversity (Huston 1993). How to accommodate both biodiversity and human needs will be our challenge.

I hope to have now made it easier for the reader to move to succeeding papers and to take up various facets of the very broad concept cluster that characterizes biodiversity. As you will see, livestock grazing is but one traditional value of rangelands and one influence on the various facets of biodiversity. Grazing management may either positively or negatively influence biodiversity, depending on what is being valued. It is impossible for all features of biodiversity to be simultaneously maximized (West 1993). Therefore, we need some understanding to aid us in reaching compromises. It is in this spirit that this volume was written.

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Genetic Aspects of the Biodiversity of Rangeland Plants

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Abstract

Biodiversity is the variety of life and its processes. Diversity cannot be described unless the differences between organisms can be detected and measured. The concept of genetic diversity is usually confined to individual organisms, populations, and species and may be considered as heritable differences among taxa capable of gene exchange. New macromolecular methods together with traditional morphological, cytogenetic, hybridization, and breeding-system analytical methods are providing greater detail that allows a finer resolution of genetic diversity. Rangeland plant biodiversity studies of shrub, forb, grass, and tree taxa are demonstrating genetic diversity at several levels. Case studies of several taxa illustrate that there is an unevenness of genetic diversity data available from rangelands and, in general, rangeland plant genetic diversity studies are in the beginning stages. The influences of past climatic changes on plant genetic diversity are also only just beginning to be understood. Both conservation and use of rangeland plant resources have genetic bases. Genetic diversity studies are important for discovering and documenting the sources and patterns of variation. That information is vital if genetic diversity is to be protected and preserved so that rangeland plant resources can be effectively used and sustained to maintain future options.

INTRODUCTION

West (1993) defined biological diversity (biodiversity) as the variety of life and its processes, including the variety of living organisms, the genetic differences among them, the communities, ecosystems, and the landscapes in which they occur, plus the interactions of these components.

Chambers and Bayless (1983) made a telling point that we believe needs emphasis: The diversity of any group, whether it is a local population or a multispecies community, cannot be described unless the differences between individuals or species can be detected and measured.

Our treatment addresses plant genetic diversity on rangelands. Stubbendieck et al. (1986) list 200 important North American range plants. The Range Plant Handbook (USDA Forest Service 1937) treats 339 species (mostly) or genera of rangeland plants with some reference to an additional 500 species and states that western rangelands are naturally inhabited by over 1,200 genera and 10,000 species of flowering plants. However, this represents only a small portion of plant biodiversity and an even smaller portion of overall biodiversity. To illustrate these points, the number of described species (a measure of biodiversity) of organisms (Wilson 1988, Cook 1991) found over the world has been estimated as follows:

Virus	1,000
Monera	5,000
Protista	50,000
Fungi	45,000
Plantae	280,000
Animalia	1,100,000
Total	1,481,000

Wilson (1988) believed the absolute number, including undescribed species, might exceed 5,000,000; Pimentel et al. (1992) placed that number at 10,000,000. Considering only plants, the levels of taxonomic biodiversity, in a hierarchical descending order, are as follows:

Kingdom
 Division
 Class*
 Order
 Family*
 Tribe**
 Genus*
 Section**
 Species*
 Variety**
 Form**
 Population

*Many of these categories (taxa) have subordinate subdivisions, e.g., subclass, subfamily, subgenus, and subspecies, when the lineage is complex.

**In simpler lineages, not all categories are used, e.g., tribe, section, variety, and form may or may not be included.

GENETIC DIVERSITY AND WORKING GENETIC DEFINITIONS

Genetic diversity has been recognized as meaning (Schonewald-Cox et al. 1983) (1) species diversity, (2) allele diversity, (3) allele frequency differences (between individuals within populations and between populations), or (4) the combination of species diversity with allelic variations. An allele (allelomorph) is one of a pair, or series, of alternative forms of a gene that can occur at a given locus in homologous chromosomes. A shorter definition of genetic diversity is the heritable differences among individuals of species or other taxa capable of gene exchange (McArthur 1984). Genetic diversity is at the base levels of biodiversity, as viewed above, but is manifest with decreasing impact from population to species to genus because gene exchange becomes rarer as the scale of taxonomic units broadens.

Measuring genetic diversity began with the science of genetics when Gregor Mendel discovered the principles of gene segregation and independent assortment in garden pea (*Pisum sativum*) hybrids by examining the nature of inheritance of such traits as plant height and seed color and shape (Gardner 1968, Monaghan and Corcos 1985, Corcos and Monaghan 1993) in the mid-nineteenth century. Measures of genetic diversity are becoming more and more sophisticated as new techniques are developed (Table 1).

Morphological traits continue to be important in assaying genetic diversity, but these traits are not always simply

inherited. As it turns out, Mendel was fortunate to select simply inherited traits because many genetic traits are quantitatively inherited through many genes and are consequently more difficult to analyze. Elegant numerical and statistical procedures are currently available as analytical tools, often in the form of software packages, e.g., parsimony analysis, principal components analysis, canonical analysis, discriminant analysis, cluster analysis, etc. These techniques are especially useful in understanding more complex inheritance patterns such as quantitative inheritance and continuous variation (Falconer 1960).

Traditional genetic traits, including the more analytically difficult quantitative ones, are coded for by deoxyribonucleic acid (DNA) for most organisms, including higher plants. DNA is the replicating hereditary material that is organized into the genes of the nuclear chromosomes of Mendelian inheritance (genes that segregate and independently assort). It should be noted, however, that chromosomes also have noncoding or genetically inert regions and some areas of highly redundant or surplus DNA for which function is poorly understood. There are also genes in cell organelles such as chloroplasts and mitochondria that are non-nuclear, i.e., cytoplasmic. A complete set of nuclear chromosomes is known as a genome (x). A diploid ($2n$) individual has two sets of chromosomes, one set from the maternal parent and one from the paternal parent. The reproductive cells of the plant undergo reduction division (meiosis) and are consequently n or haploid. Production of a new plant through sexual reproduction restores the $2n$ chromosome number.

Many plant groups have a high frequency of polyploidy. Polyploidy is the condition of multiple genomes being present in an organism. For example, a plant that has four sets of chromosomes is tetraploid ($4x$). However, most polyploids behave genetically as sexual diploids, so that if, for example, the base chromosome number (genome) is 9 then the genetic formula would be $2n = 4x = 36$. The terms *haploid* and *diploid* have two meanings: x and $2x$ as the first two entries in a polyploid series (haploid, diploid, triploid, tetraploid, etc.—referring to multiples of the base chromosome number), but also n and $2n$ at any level of x to signify the gametes (gametophytes or sex cells) and parental plants (sporophytes). Polyploids may be autopolyploids where the constituent genomes are identical or allopolyploids where constituent genomes are different though similar enough to function together in the same organism. In reality most polyploids are something in between these extremes. Aneuploidy is the loss or gain of one or a few (less than a genome) chromosomes. Other genetic materials are cytoplasmically inherited, i.e., hereditary transmission is dependent on the cytoplasm or structures in the cytoplasm rather than on nuclear genes. Some genetic material is maternally effected, i.e., inheritance from the mother to offspring is unaffected by inheritance from the father as, for example, the cytoplasmic genes mentioned above. Paternal inheritance (such as chloroplast DNA in pinyon pine) also occurs, but is rarer.

In addition to morphological and chromosomal traits, molecular, including macromolecular, traits can serve as genetic markers (Table 1). Some of these are direct proteinaceous products of chromosomal DNA, e.g., isozymes are

TABLE 1. MEASURES OF GENETIC DIVERSITY¹

Morphometrics	Serology (Immunology)
Alpha Taxonomy	Chemotaxonomy
Numerical Taxonomy	Nucleic Acids
Chromosomes	DNA
Genomes	DNA/DNA Hybridization
Ploidy	nuclear DNA
Mapping	cpDNA
Protein Sequencing	mDNA
Protein Electrophoresis	rDNA
Seed Storage Proteins	RFLP
Rubisco	RAPD
Isozymes	Physiological Ecology
Allozymes	Breeding Studies

¹For definitions see the texts, Vickery and Wullstein (1987), Crawford (1990), and Cook (1991).

functional enzymes that can be identified by electrophoresis and used to analyze genetic variation within and among plant populations and taxa. Current use of the term *isozyme* is restricted to enzymes encoded by different loci, thus separating isozymes from a special class of functional enzymes that are encoded at a particular locus, in which case they are referred to as allozymes or enzyme alleles (Gottlieb 1982). Protein- and nucleic-acid sequencing techniques are powerful tools that are useful in quantifying genetic variation at all levels from individuals in a population to all forms of life. Genetic and evolutionary distances can be mapped using these techniques (Crawford 1990). Currently in the forefront are the DNA analyses, RFLPs and RAPDs. Both techniques involve the generation of multiple identical copies of DNA strands produced by the polymerase chain reaction (PCR) that uses the DNA polymerase ("production machinery") of a thermal alga to amplify template DNA in vitro (Mullis 1990). RFLPs (restriction fragment length polymorphisms) are the products of enzymatic "scissors" that excise portions of DNA from specific starting and ending points from nuclear chromosomes or from organelle genomes. RFLPs are used to map fragment positions to make comparisons in the DNA strands of the organisms being studied. RAPDs (random amplified polymorphic DNA) analysis is the comparison of many short DNA strands of similar length that can allow quick, powerful analyses. Other molecular techniques and appropriate references are listed in Table 1. The PCR technique is useful for looking at genetic diversity in the past as well as in currently living organisms. For example, DNA from fossil material as old as Miocene (ca. 20,000,000 years BP) can be multiplied and analyzed (Golenberg et al. 1990).

Whole syndromes, e.g., breeding systems, photosynthetic pathways, germination characteristics, and a whole array of macromolecules are useful in establishing patterns of genetic diversity and phylogenetic relationships (Ford 1964, Harborne 1973, Brussard 1978, Gates 1980, Willson 1983, Richards 1986, Nei 1987, Lovett Doust and Lovett Doust 1988, Crawford 1990).

In general, the techniques of measuring genetic diversity are complementary. Vickery and Wullstein (1987) compared six approaches to the classification of the six species includ-

ing nine experimental populations of *Mimulus*, section *Erythranthe*. This species complex is a closely related group occupying riparian areas of western North America. Vickery and Wullstein used alpha taxonomy (phenetic classification of herbarium, field, and greenhouse specimens), numerical taxonomy (100 morphological or sensory traits of greenhouse-grown plants), experimental hybridization (in all combinations), chemotaxonomy (floral flavonoid pigments), allozyme-isozyme (11 enzymes), and DNA/DNA hybridization (between the experimental populations). They concluded that the six methods are only partially congruent, but definitely complementary. The numerical taxonomic and experimental hybridization methods produced the clearest distinctions and groupings, but all methods added clarity and detail. This set of experiments did not include DNA or protein sequencing, which may have been even more definitive. More, rather than fewer, measures of genetic diversity contribute to establishing relationships and quantifying variation.

INDIVIDUAL AND POPULATION GENETIC DIVERSITY

Natural evolutionary processes and human-directed selection work at the individual (intrapopulation) and population (interpopulation) levels. It is at these levels that gradual, adaptive changes occur (Charlesworth 1990). This viewpoint is the consensus for how evolution occurs (Mayr 1991). Other views suggesting more relative importance of larger-scale mutation and random genetic drift also would operate at these levels more effectively than at levels above the population, although such views are not as generally acceptable to modern population biologists as the gradual, adaptive model originally suggested by Charles Darwin (Charlesworth 1990, Mayr 1991). Unfortunately, most of the studies on rangeland plant species are at higher levels, e.g., subspecies, species, and genera (see next section).

Some examples of intrapopulation and interpopulation variation that is of prime importance on rangelands whether the focus of attention is evolutionary processes or human-directed selection and management deal with grazing resistance or tolerance, drought resistance, and pest (insects and

disease) resistance. It is well known that some forage plants are better adapted to grazing than others at various levels of consideration, e.g., perennials versus annuals, species versus species, population versus population, individual versus individual (Hanks et al. 1973, Rickard et al. 1975, Caldwell et al. 1981, Hodgkinson and Williams 1983, Delucia and Schlesinger 1991, Halls et al. 1994, Jaindl et al. 1994). This differential adaptation is essentially genetic and has important management implications. Likewise, drought (Wilson and Sarles 1978, Ehleringer and Cooper 1988, Hardegree and Emmerich 1990, Johnson et al. 1990) and pest (Asay et al. 1983, Nelson et al. 1989, Haws et al. 1993) resistance have genetic components. When genetic gain through selection is an objective, other characteristics such as nutritive quality and biomass production become important. Gain in quality traits like these is accomplished by identifying individuals (or clones) with those traits and increasing by selective means the frequency of those traits or individuals in the next generation (Carlson and McArthur 1985, McArthur 1988, Karn and Tober 1990, Vogel et al. 1993). Sometimes it is desirable to merge traits from different populations rather than individuals within the same population. Besides the traditional breeding techniques just described, a small amount of pioneering work has been accomplished incorporating the area of biotechnological or genetic engineering into plant improvement research on rangeland plants (McArthur 1988). Genetically engineered plants and microbes show promise for increasing productivity and shortening selection time, but they also pose potential risks for altering the environment in unknown ways (Olson 1986).

Observable characteristics are not always heritable. Traits may be variably expressed in genetically identical individuals. This phenomenon is known as phenotypic plasticity (Wayne and Bazzaz 1991). The relationship between genotype and phenotype is not one to one but one to many. This relationship must be discovered to select for traits in a breeding program or to understand and manage population dynamics. Discovering the relationship between genotype and phenotype may be difficult. The use of clonal materials in multiple environments (reciprocal transplant gardens) and temporal observation of trait expression are some of the methods used to elucidate this relationship (Pendleton et al. 1988, McArthur et al. 1992a).

CASE STUDIES OF GENETIC DIVERSITY

As in many other aspects of science, research on rangelands lags behind other areas in respect to genetic diversity. Genetic diversity of commercial tree species, agronomic crops, and other areas has received much more attention than rangeland plant species (Miksche 1976, Simmonds 1976, Hamrick et al. 1979, Hamrick 1982). Studies of genetic diversity, implementing principally the measures of Table 1, are found in many recent books, e.g., Harper 1977, Futuyma 1979, Nei and Koehn 1983, Scandalios 1984, Hartl and Clark 1989, Falk and Holsinger 1991, Adams and Adams 1992, and current research periodicals, e.g., *Agronomy Journal*, *American Journal of Botany*, *American Naturalist*, *Crop Science*,

Ecology, *Evolution*, *Forest Science*, *Genetics*, *Genome*, *Heredity*, *Journal of Ecology*, *Journal of Evolutionary Biology*, *Journal of Heredity*, *Nature*, *Science*, *Oecologia*, *Silvae Genetica*, *Systematic Botany*, *Theoretical and Applied Genetics*.

A particularly elegant case study of genetic diversity is that of the Hawaiian silversword alliance (Asteraceae-Madiinae). These descendants of long-range dispersed North American tarweeds have been characterized by hybridization, chromosome pairing, and cpDNA studies among the three extant Hawaiian genera (28 species) and their mainland relatives (Carr and Kyhos 1986, Kyhos et al. 1990, Baldwin et al. 1991). For the balance of this section, we discuss some examples of genetic diversity for rangeland species of shrubs, forbs, grasses, and trees.

SHRUBS

Shrub dominance often defines rangelands, i.e., lands not intensively managed by agronomic or forestry principles, so it is appropriate that we begin our case studies of genetic diversity with shrubs. Shrubs, however, do not constitute any cohesive phylogenetic unit (McArthur 1989). Shrubs are widely distributed in plant communities dominated by other life forms (Küchler 1964), but are dominants, usually, only in habitats that place plants under considerable stress such as drought or aridity, nutrient-poor soils, fire, shade, poor soil aeration, winter cold, short growing seasons, and wind (McArthur 1984, 1988, West 1992). Most of these conditions are best met in arid or semiarid continental climates that also characterize most of the world's rangelands (Walter 1973). Küchler's (1964) data base provides some additional insight on shrub diversity and speciation (Table 2). Fifteen plant families were identified as having dominant shrubs on Küchler's (1964) map, Potential Natural Vegetation of the Conterminous United States. Shrub values include extending the grazing season and increasing community diversity and ecosystem stability (McArthur 1988).

Hall and Clements (1923) produced a classical work some 70 years ago, entitled *The Phylogenetic Method in Taxonomy, The North American Species of Artemisia, Chrysothamnus, and Atriplex*. They chose the three genera for their pioneering monograph because they were set up to study in western North America and because these shrub genera had "taxonomic and ecologic interest. They have been objects of the most active evolution, with which has gone the widest distribution, both as to climate and soil. Ecologically, they are unsurpassed in the number of dominants and subdominants they furnish to the vegetation."

Hall and Clements (1923) used morphological and distributional information in their treatment and made substantive contributions in regard to plant relationships. We here review some more current genetic diversity work on these genera.

The genus *Artemisia*, with up to 400 species worldwide, includes the plant that most nearly epitomizes the American West, sagebrush. McArthur et al. (1981) limited the term sagebrush to the endemic American subgenus *Tridentatae*, which includes some 25 taxa (species, subspecies, varieties,

forms) centered around big sagebrush (*A. tridentata*), with its five subspecies: basin big sagebrush (*A. t. ssp. tridentata*), mountain big sagebrush (*A. t. ssp. vaseyana*), Wyoming big sagebrush (*A. t. ssp. wyomingensis*), subalpine big sagebrush (*A. t. ssp. spiciformis*), and xeric big sagebrush (*A. t. ssp. xericensis*). Sagebrush forms a polyploid complex, $x = 9$, to $8x$ (McArthur et al. 1981, McArthur and Sanderson, unpublished) of mostly autopolyploid, interfertile taxa and populations. Genetic diversity and gene exchange have been documented in continuing studies through artificial hybrid seed set data and morphological, seed germination ecology, browsing preference, coumarin, flavonoid, monoterpene, and RAPDs DNA profiles, of parental populations and artificial and natural hybrids (Hanks et al. 1973, McArthur et al. 1979a, 1981, 1988, 1992b, McArthur and Welch 1981, Welch and McArthur 1981, 1986, Welch et al. 1987, 1991, Meyer et al. 1990, Stevenson et al. 1990, Bray et al. 1991, Meyer and Monsen 1991, Wilt et al. 1992, Weber et al. 1994). With genic modifications of a single autopolyploid genome, sagebrushes (*Tridentatae*) vary widely in many characteristics, including size. Pygmy sagebrush (*A. pygmaea*) is prostrate; basin big sagebrush may be up to 4.5 m tall. Natural hybrid zones among big sagebrush subspecies are providing insights into the nature and stability of hybrid zones (McArthur et al. 1988, Freeman et al. 1991). Hybridization has apparently been important in the origin of several sagebrush taxa (Ward 1953, Beetle 1960, Goodrich et al. 1985, McArthur and Goodrich 1986, Winward et al. 1986, McArthur et al. 1988, Rosentreter and Kelsey 1991, Winward and McArthur 1995).

The genus *Chrysothamnus* (rabbitbrush) consists of 16 species and some 50 recognized taxa, including subspecies. The genus is wholly shrubby and is endemic to western North

America (Anderson 1986a, McArthur and Meyer 1987). Its five sections are distinguished by characteristic floral, stem, and achene differences. Three species complexes, each with several subspecies, dominate the genus: rubber rabbitbrush (*C. nauseosus*), Parry rabbitbrush (*C. parryi*), low rabbitbrush (*C. viscidiflorus*). The genus is essentially diploid, $2x = 18$ with a limited amount of tetraploidy known only from the low rabbitbrush complex (Anderson 1986b). Some taxa are good colonizers of disturbed sites; some are broadly adapted and others are more specific. Gang and Weber (1995) have recently shown gene diversity by RAPDs DNA markers in a single population and a tight geographic cluster of ten populations of rubber rabbitbrush (*C. nauseosus* ssp. *hololeucus*). Earlier work on rubber, resin, phenolic compounds, volatile compounds, nutritive quality, seed germination syndromes, and host specificity of gall-forming tephritid flies has documented genetic diversity in rabbitbrush (Hanks et al. 1975, McArthur et al. 1978, 1979b, Dodson and George 1986, Hegerhorst et al. 1987a, 1987b, Meyer et al. 1989, Bhat et al. 1990, Halls et al. 1994, Floate et al. in review).

The genus *Atriplex* (shrubby forms = saltbush) is a large genus consisting of some 250 species worldwide (Osmond et al. 1980, McArthur and Sanderson 1984). Western North American forms include both herbs and shrubs. The approximately 20 North American shrubby saltbushes include several large genetically diverse species (Blauer et al. 1976, Stutz 1978, McArthur and Sanderson 1984), e.g., fourwing saltbush (*A. canescens*), shadscale saltbush (*A. confertifolia*), Gardner saltbush and allies (*A. gardneri* complex). Shrubby saltbushes rampantly naturally hybridize; many species have high polyploid forms, $x = 9$ (Stutz et al. 1979). We discuss here only fourwing and shadscale saltbushes.

TABLE 2. NUMBERS OF GENERA AND SPECIES AND GROWTH FORMS OF SELECTED FAMILIES.¹

Family	Shrub genera Number	Species western U.S., all growth forms	World total, all growth forms	Growth habits ²
Anacardiaceae	1	9	150	S, T
Asteraceae	17	126	2546	H, S
Caprifoliaceae	5	28	317	S
Chenopodiaceae	8	29	441	H, S
Ericaceae	1	82	1211	S, T
Ephedraceae	1	10	40	S
Fabaceae	19	70	3276	H, S, T
Fagaceae	3	20	700	S, T
Fouquieriaceae	1	1	9	S, T
Lamiaceae	5	24	1175	H, S
Polygonaceae	1	20	250	H, S
Rhamnaceae	6	68	295	S
Rosaceae	23	81	760	H, S, T
Scrophulariaceae	4	22	454	H, S
Zygophyllaceae	2	2	22	S

¹Adapted from McArthur (1984).

²Growth habits of congeneric relatives: H = herbs, S = shrubs, T = trees.

Fourwing saltbush includes a remarkable polyploid series extending from $2x$ to $20x$ (Stutz and Sanderson 1979; Sanderson and Stutz 1994). The $20x$ populations are among the highest chromosome numbers known in flowering plants. Fourwing saltbush also has a remarkable breeding system. Polyploid forms, especially the widely studied tetraploids, are known to be trioecious with genetic males, genetic females, and a labile monoecious or hermaphroditic gender (McArthur 1977, McArthur and Freeman 1982, Barrow 1987, Pendleton et al. 1992) thought to be a gender fitness adaptation to environmentally heterogeneous, patchy environments (McArthur et al. 1992a, Freeman et al. 1993). Fourwing saltbush populations are also known to be variable in adaptation to soil salinity (Welch 1978, Richardson and McKell 1980) and winter hardiness (Van Epps 1975) and to vary in nutritive content (Welch 1978, Welch and Monsen 1981), stem rooting (Richardson et al. 1979), seed production, fill and germination (Springfield 1970), growth rate and form and site adaptation (Stutz et al. 1975, McArthur et al. 1983a, Stevenson et al. 1990, Watson 1990), and in genetic marker isozymes (McArthur et al. 1986), flavonoids (Sanderson and Stutz 1994), and RAPDs DNA (Stutz et al. unpublished).

Shadscale saltbush, like fourwing saltbush, has a remarkable polyploid series, going from $2x$ to $10x$ (Stutz and Sanderson 1983). Like several other western rangeland shrub species, the higher polyploids of shadscale tend to be smaller and adapted to more xeric environments than diploids (Sanderson et al. 1989). Shadscale populations are differentiated by ploidy level, morphology, and flavonoid chemistry into two major and ten smaller geographic races (Sanderson et al. 1990).

The shrub examples above come from just two of the families listed in Table 2 (sagebrush and rabbitbrush from Asteraceae and saltbush from Chenopodiaceae). These families, along with Ericaceae and Rosaceae, are perhaps the most important contributors to the shrub flora of western rangelands in terms of numbers of species, populations, and individuals. Some other examples of rangeland shrub genetic diversity are listed below, but we make the point that our knowledge base is not well developed, nor are the examples exhaustive. The number of shrub species of Table 2 are only those that belong to a genus that is listed by K uchler (1964) as having species that are important in the vegetation (McArthur 1984, 1993).

The genetic diversity of *Gutierrezia* (matchbrush and relatives) and *Parthenium* (guayule and relatives) (Asteraceae) and their respective congeners has been studied by chromosome number ($x = 4$ for *Gutierrezia*, $x = 18$ for *Parthenium*), with diploid ($2x$) and polyploid ($> 2x$) species and races and structure, plant morphology, and cpDNA (Solbrig 1971, Estilai et al. 1985, Lane 1985, Hashemi et al. 1986, 1987, 1988, Lane and Jansen 1990, Suh and Simpson 1990). *Grayia brandegei* (spineless hopsage) (Chenopodiaceae) populations differ in phenotype, geographic distribution, and chromosome number ($x = 9, 2x, 4x$ populations) and exhibit an unusual heterodichogamous breeding system (Stutz et al. 1987, Pendleton et al. 1988). The *Purshia/Cowania* (bitterbrush/cliffrose) complex (Rosaceae) has been characterized by plant morphology, chromosome number ($x = 9, 2x$),

hybridization and breeding system, seed germination syndromes, and DNA patterns (Stutz and Thomas 1964, Nord 1965, Koehler and Smith 1981, McArthur et al. 1983b, Baker et al. 1984, Meyer 1989, McArthur and Pendleton 1990, Pendleton and McArthur 1994, Jabbes and Brunsfeld unpublished). *Ceanothus* (Rhamnaceae) is a North American endemic with 51 of its 55 species found in western North America and most of them limited to that region. This group of plants is homoploid ($x = 12, 2x$) and divided into two large sections, each of which has considerable amounts of intrasectional gene exchange, but little intersectional gene exchange as determined by natural and artificial hybridizations and genomic analyses (Nobs 1963, Franklin et al. 1985). Taxonomic difficulties regarding the large genus *Salix* (Salicaceae) ($x = 19, 2x-8x$) are being resolved using isozyme and DNA patterns (Brunsfeld et al. 1991, unpublished).

We conclude these brief examples of rangeland shrub biodiversity with reference to three studies that compare ecogenetic patterns among suites of shrubs in communities. Slauson and Ward (1986) reported that antelope bitterbrush (*Purshia tridentata*), true mountain mahogany (*Cercocarpus montanus*), mountain snowberry (*Symphoricarpos oreophilus*), and Utah serviceberry (*Amelanchier utahensis*) had different patterns of intraspecific genetic variability in experimental garden plots. Chamise (*Adenostoma fasciculatum*), wedgeleaf ceanothus (*Ceanothus cuneatus*), and whiteleaf manzanita (*Arctostaphylos viscida*) exhibit intraspecific and interspecific genetic variability across natural environmental gradients (Baker et al. 1982). Criddle et al. (1994) report that big sagebrush (*Artemisia tridentata*), rubber rabbitbrush (*Chrysothamnus nauseosus*), and antelope bitterbrush (*Purshia tridentata*) populations grown in uniform gardens maintain genetically based metabolic heat (temperature coefficient of metabolism) relationships based upon their collection sites.

FORBS

Forbs are important components of rangeland plant communities. They provide much of the ecological and botanical diversity on rangeland sites, increase seasonal forage quality and site nutrient capital (especially legumes), and generally enhance aesthetics and buffer wildfire effects (Shaw and Monsen 1983, Rumbaugh and Townsend 1985, McArthur et al. 1987, McArthur 1988). Legumes (Fabaceae) are probably the most important rangeland forbs (some legumes are shrubs and trees as well—see Table 2). Legumes are valuable forage plants that have been consciously used as forage plants by pastoralists for over 11,000 years (Mathison 1983), but legumes also include some poisonous plants, notably some species of the large genus *Astragalus* (Williams and Barneby 1977). Adaptive and nutritive quality variation has been documented for a number of rangeland legumes, both native (*Hedysarum* spp. [sweetvetch], *Lupinus* spp. [lupine]) and more intensively for introduced (*Astragalus* spp. [milkvetch], *Hedysarum* spp. [sweetvetch], *Medicago falcata* and *M. sativa* [alfalfa]) materials (Rumbaugh and Townsend 1985, McArthur 1988).

There are many rangeland forbs in the large Asteraceae family (USDA Forest Service 1937). Some examples of genetic diversity in this family on rangelands include that of Pacific aster (*Aster ascendens*), pussytoes (*Antennaria* spp.), gumweeds (*Grindelia* spp.), balsamorhiza (*Balsamorhiza* spp.) and mulesears (*Wyethia* spp.), and the golden asters (*Chrysopsis* spp., *Heterotheca* spp., *Pityopsis* spp.). Pacific aster is one of some 500 aster species, many of them North American. It is $x = 13$ and occurs as $2x$ and $4x$ races. Genomic and morphological analyses demonstrate that Pacific aster is of hybrid origin from *A. falcatus* ($x = 5$) and *A. occidentalis* ($x = 8$), and that local populations include a rich array of genetic diversity (Allen 1985, 1986). The North American pussytoes ($x = 14, 2x-10x$) includes 20 sexually reproducing dioecious species and five morphologically variable, polyploid agamic complexes that harbor abundant genetic diversity, as documented by isozyme, morphological, hybridization analyses, and genomic studies (Bayer and Stebbins 1987, Bayer 1988). Genomic and hybridization analyses demonstrate population differences and genetic diversity in several species of gumweeds ($x = 6, 2x-4x$) (Dunford 1986). Populations of the related balsamorhizas (*Balsamorhiza* spp.) and mulesears (*Wyethia* spp. [$x = 19, 2x-5x$, some aneuploidy]) demonstrate within and between population differences in morphological and chromosomal characteristics (Helton et al. 1972, Robson et al. 1988). Morphological, anatomical, habit, habitat, and chromosome studies of the golden asters ($x = 5, 9, 2x-4x$, some aneuploidy) reveal genetic diversity at several taxonomic levels (Semple et al. 1980).

Other examples of rangeland forb genetic diversity include those of low larkspur (*Delphinium nelsonii*), flax (*Linum* spp.), Rocky Mountain beeplant (*Cleome serrulata*), Utah sweetvetch (*Hedysarum boreale*), and penstemon (*Penstemon* spp.). Populations of low larkspur have been shown to differ in isozyme patterns and fitness over a distance of 50 m (Waser and Price 1985, Waser 1987). Flax species, including the Eurasian (*L. perenne*) and North American (*L. lewisii*) perennial blue flax species ($x = 9, 2x$), have been characterized by cpDNA patterns, morphology, hybridization, and breeding systems (Ockendon 1968, Coates and Cullis 1987, Pendleton et al. 1993). The physiological and morphological characteristics of Rocky Mountain beeplant affect fitness components over moisture gradients within populations (Farris 1987, 1988). Seedling establishment characteristics, nitrogen fixation capability, and nutritive value among populations of Utah sweetvetch revealed sufficient genetic diversity to assure adaptation to a wide array of sites in a garden and greenhouse study (Johnson et al. 1989). Populations of several species of *Penstemon* have distinctive seed germination syndromes that are correlated in various degrees with habitat (Kitchen and Meyer 1991, Meyer and Kitchen 1992). The scope of this report precludes presentation of other examples of rangeland forb genetic diversity. Genetic studies of rangeland forbs are, however, woefully incomplete.

GRASSES

Grasses include not only the staff-of-life grains, but also the most important and extensive forages for livestock and

wild ungulates in virtually all habitats (Heath and Kaiser 1985). The grass family, Poaceae, is enormous, with about 10,000 species worldwide. About 40 species receive significant use as sown pasture plants (Knight 1983). These plants are not important on rangelands, except for particular genotypes of orchard grass (*Dactylis glomerata*), smooth brome (*Bromus inermis*), and fescue (*Festuca* spp.) that are adapted to drier climatic regimes than are ordinary for their respective taxa (Knight 1983, McArthur 1988). Those species are not native to North America nor are many other grass species that are used in rangeland improvement projects (McArthur 1988). However, there are many excellent native grasses as well. The importance of grasses on North American rangelands is illustrated by the inclusion of 94 grasses among the total of 200 important range plants by Stubbendieck et al. (1986).

For case study illustrations, we have chosen to review some rangeland grasses of the tribe Triticeae, Indian rice grass (*Oryzopsis hymenoides*) of the tribe Stipeae, and orchard grass (*Dactylis glomerata*) and cheatgrass (*Bromus tectorum*) of the tribe Poeae.

The tribe Triticeae is large, 325 species, and includes many forage grasses, as well as the familiar cereal crops wheat, barley, and rye (Dewey 1984). Forty-eight species (three annuals, 45 perennials) are native to North America, including wheatgrasses (*Pascopyrum smithii*, *Pseudoroegneria* spp.), ryegrasses (*Elymus canadensis*, *Leymus cinerius*) and bottlebrush squirreltail (*Elymus elmoides*) (Dewey 1982, McArthur 1988). The base chromosome number for Triticeae is $x = 7$, with a polyploid range of $2x-12x$ (Dewey 1984). Dewey and colleagues determined genomic formulas for many Triticeae taxa on a worldwide basis by chromosome pairing studies in synthetic hybrids, e.g., Dewey 1982, 1983, Asay et al. 1987, Wang 1988, Jensen and Bickford 1992, Jensen et al. 1992). These researchers have found that the genomes are sorted out in a wide array of combinations in various polyploid taxa with similar (identical?) genomic combinations sometimes being present in Eurasian and North American taxa. Genetic diversity within and among populations has allowed widespread natural and managed distribution and selection for a large array of plant materials for particular purposes in respect to growth rates, nutritive quality, site adaptation, insect resistance, etc. (Dewey 1980, Asay et al. 1983, 1985, McArthur 1988). Currently, efforts are under way to develop native bluebunch (*Pseudoroegneria spicata*) and Snake River (*Elymus wawawai*) wheatgrasses for seedling vigor and grazing tolerance from the abundant genetic diversity present in natural populations of these taxa (Jones et al. 1991, Kitchen and Monsen 1994). Additional noteworthy aspects of genetic diversity in ecotypic adaptation (phenological development and growth rate) for bottlebrush squirreltail (Clary 1975), and in isoenzymes in weedy rye (Sun and Corke 1992) have been documented. An entire issue of *Plant Systematics and Evolution* (vol. 160, no. 1-2, 1988) was devoted to molecular aspects of genetic diversity within the Triticeae, e.g., RNA, DNA, and isozymes (McIntyre 1988, McIntyre et al. 1988, West et al. 1988).

Indian ricegrass is $2x$ ($x = 24$, with some aneuploidy). Populations are widely distributed in the North American West on both clay and sandy soils. Use of Indian ricegrass as a reclamation plant is limited because of problems of seed dormancy and shattering before harvest. Population variability in physiological and ecological traits and hybridization with other Stipeae are evidences of genetic diversity (Jones 1990).

Orchardgrass occurs in mixed ploidy ($x = 7$, $2x-4x$) populations on the Iberian Peninsula where $2x$ and $4x$ plants partition the habitat based on physiological, metabolic, and phenological differentiation (Lumaret et al. 1987, 1989). Results from cpDNA studies suggest that $4x$ plants are autopolyploid.

Cheatgrass has expanded from its Eurasian and North African homeland to North America and become a serious westwide rangeland weed (Mack 1981). It is a cleistogamous annual ($x = 7$, $2x$) that through multiple introductions and a hundred annual cycles has differentiated into locally adaptive populations as measured by isozymes, plant biomass, and seed production, weight, and germination characteristics (Novak et al. 1991, 1993, Rice and Mack 1991a, Meyer unpublished). Populations are locally adapted, with some being more heterogeneous than others (Rice and Mack 1991a, 1991b, 1991c).

TREES

Trees are generally not characteristic of rangelands, except for upland sites, e.g., quaking aspen (*Populus tremuloides*), Gambel oak (*Quercus gambelii*); pygmy forests, e.g., pinyon-juniper woodland (*Pinus* spp.-*Juniperus* spp.); and riparian corridors, e.g., willows (*Salix* spp.), cottonwoods (*Populus* spp.) (USDA Forest Service 1937, Stubbendieck et al. 1986). Some of these taxa may be considered as trees or shrubs depending upon local habitat and growth conditions, e.g., oaks and willows. Morphological, breeding-system, and macromolecular studies are revealing interesting patterns of genetic diversity within and between populations of these rangeland tree species, e.g., juniper (Ernst 1989, Van Haverbeke and King 1990, Tausch, unpublished data), pinyon (Lanner 1974, Bailey and Hawksworth 1988, Keim, unpublished data), cottonwoods (Keim et al. 1989, Paige et al. 1991), willows (Brunsfield et al. 1991, unpublished).

GENETIC DIVERSITY-ENVIRONMENT INTERACTION

Many rangeland plants, as a group, are highly variable genetically and show various levels of hybrid introgression within and between taxa. Most rangelands represent the kinds of xeric and ecologically heterogeneous environments where genetic diversity generally increases (Nevo and Beiles 1989). These are also areas with a high susceptibility to the high level of climatic variation of the Quaternary (Tausch et al. 1993). The Quaternary, approximately the last 2 million years of the Pleistocene + Holocene, has had considerable and continuous climatic variation (Smiley et al. 1991) with up to

24 glacial events of 50,000 to 100,000 years in length (Van Donk 1976). The many genetically variable plant species present on rangelands and elsewhere (Kerr 1992) appear to be a product of adaptation to the past cycles of climatic variability (Tausch et al. 1993). Measuring that diversity can be a difficult task (Roberts 1992), but its incorporation into conservation policies can increase the options for decisions on the preservation of biological diversity (Brooks et al. 1992).

Vegetation response to climatic change can be described with three models of response: migration, orthoselective, and relic. Migration involves shifts in geographic position in response to climatic change. Orthoselective species are those that manage to remain in place over wide oscillation in climate. Relic species are found in areas where climatic change has been minimal. Many of the rangeland species described above best fit the orthoselective model of vegetation response to climate change (Nowak et al. 1994), indicating adaptation to changing, heterogeneous environments over long periods of time. Other species, particularly those from more mesic environments, generally fit the migration model (Bradshaw and McNeilly 1991). Relic taxa are rare on rangelands, e.g., the interpretations of Stutz et al. (1975) for gigas diploid *Atriplex canescens* and of Bowns and West (1976) for *Coleogyne ramosissima*.

Ogden (1989) has proposed the term *coenospecies* for persistent taxa that have varied in ecologic isolation and taxonomic distinction and more or less frequently hybridized in the past. Such genetic variability represents an adaptation to repeated cycles of changing climate in heterogeneous environments (Pease et al. 1989, Holt 1990). Such taxa are globally represented (Ogden 1989, Schoonmaker and Foster 1991). Most rangelands have sufficiently heterogeneous (patchy) environments and contain genetically variable species. The presence of interfertile species (coenospecies), such as the many found on rangelands that have been described above, increases the genetic diversity of those areas (Wayne and Bazzaz 1991). Their presence can substantially affect competitive dynamics and can potentially increase the rapidity with which a plant community can respond to environmental changes (Tausch et al. 1993). An understanding of the phylogenetic diversity within species or taxonomic groups can also substantially affect species conservation priorities (Faith 1992).

DIVERSITY AND DEVELOPMENT

The science of genetics is a discipline structured to measure, quantify, and track variation. Its principles form the basis of manipulation of plant materials toward a desired end through controlled breeding, selection, and aspects of biotechnology. So, on the one hand, the discipline lies at the heart of understanding and quantifying biodiversity and, on the other, its principles can be used to limit biodiversity by serving to provide plant materials that are not natural and that replace natural plant materials. Both of these aspects of genetics are valuable and important, depending on perspective (Namkoong 1991, McArthur 1993).

We have shown through case studies and literature citations that rangeland genetic diversity is an important, albeit largely underdeveloped, field of study. Only by knowing what the resource is and by understanding its dynamics can we know what resources we have to manage and subsequently manage those resources for the desired objectives; recognizing that an objective may be nonmanagement or wilderness. Humankind with a unique cognizance and control of living things and environments has a responsibility, we think, to share the planet with our fellow-traveling sister species. Furthermore, humankind has an ethical responsibility to future generations to keep the sister species and their genetic diversity around both for the joy of life of future generations and for keeping their options open. Humankind has had an impact on biodiversity since prehistory (Ledig 1992). That influence has greatly increased of late.

Another responsibility of humankind, we think, is to take care of itself. That is done, in part, by understanding the plant genetic resources and making them more productive in feeding ourselves and domestic and wild animals, and in culturing, and managing, to various intensities, parts of our landscape. Naturally occurring, genetically selected, and even biotechnologically produced plant materials can be used for these purposes. Application of the principles of the science of genetics allows us to do these seemingly disparate things. The choice is ours, options are open, discussions and actions will continue. These can come to a better end result as the understanding of the genetic diversity foundation is solidified.

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Population Diversity with Special Reference to Rangeland Plants

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Abstract

Population diversity is the second level in the diversity hierarchy immediately above genetic diversity and below species diversity. It is revealed through variation in characteristics among individuals that form the population. The modular structure of plants contrasts with the unitary structure of animals and leads to a need for a clear definition of the plant individuals. Developmental stages and age classes are common components of structural diversity that should vary in healthy plant populations. Data regarding these components are gathered with techniques that ensure that the fate and reproduction of each individual plant is maintained. Techniques such as population viability analysis use measures of the probability of individuals progressing from one stage or age to another stage or age. When these measures are obtained under differing management objectives they can be used to project the vulnerability of the population to management options. Examples are presented that demonstrate the risk of a population explosion of a cheatgrass population and the risk of extinction for bluebunch wheatgrass under two grazing systems.

INTRODUCTION

Population diversity is revealed through variation in characteristics among its individuals. We can subdivide or categorize individuals and determine the fates (alive or dead; reproductive or nonreproductive) of individuals by category. The categories may represent the changes in sizes, ages, or stages of development of the individuals or they may depict the heterogeneous environment in which the individuals must exist. By constructing these groups and by following fates, we can begin to predict long-term stability of a species on a site and to predict its susceptibility to changes in environmental factors or to changes in management.

Population diversity is the second level in the diversity hierarchy immediately above genetic diversity and below species diversity; therefore, one must recognize that genetic diversity is nested within population diversity and may contribute to the overall population diversity along with environmental components. Since genetic diversity has been treated in another paper,¹ I will limit my discussion of population diversity to the variation in traits, such as size,

age, and reproduction, that arises from interactions among individuals and from interactions between individuals and their environment.

I will formulate a basic framework about populations that is common to plants and animals. I will provide descriptions of common methods used to collect data pertaining to plant population diversity. I will discuss how species and environmental interactions affect population size classes, age distributions, and stages of development using rangeland plant examples.

Populations are often impacted by unpredictable risks such as abnormal environmental conditions, disease outbreaks, or devastating events such as fires and floods. These risks may be rare occurrences, but they can devastate local populations. The size of a population and its distribution across the landscape may dictate its success in sustaining the species within the community. As an aid in predicting this sustainability, I will discuss how population viability analysis can be used by managers to forecast the impact of risks (events or interactions), both predictable and unpredictable, on a population's stability.

¹See McArthur and Tausch, this volume.

WHAT IS A POPULATION?

The general public is acquainted with the term *population* as it is used to describe numbers of humans in specific locations. They are familiar with some of the basic descriptions of human demography, the study of births, deaths, and movements of people in and out of a given location. The beginnings of population biology as a science are largely unknown, but the description by John Graunt of age structure and mortality in English communities during the plague epidemics of the early 1600s (Petty et al. 1964) is one of the earliest examples of population descriptions. Many recognize Malthus's publication of *An Essay on the Principle of Population* as the first to recognize that populations are restricted by limited resources (Malthus et al. 1992).

A population, as it pertains to both plants and animals, is the number of individuals of a species in a definable location at a moment in time. Demography is the study of the dynamics of a population and of the conditions that regulate population change over time. A description of population diversity will require knowledge of the types and numbers of individuals that form the population and will require a description of variation among the individuals.

The determination of an individual is simple for most animals because they are *unitary organisms*; organisms that cannot be subdivided into parts forming additional individuals. The definition of an individual for plants and some animals (e.g., sponges and coral) becomes less clear. These groups are classified as *modular organisms* with the unit of organization being the module. In plants, some commonly recognized examples of modules include branches from shrubs or herbs, grass tillers, and "root suckers" in trees like aspen (*Populus tremuloides* Michx.). A modular individual is often constructed of many connected modules that are capable of surviving independently if provided the appropriate environmental conditions (White 1979).

When determining population sizes for plants it is critical to define the type of individual being counted. When possible, counts should be made of genetically distinct individuals (genets). Each genet is an individual that arises from a single zygote or seed. For clonal plants, counting genets may be impractical, if not impossible, without killing the individual or without describing the genotypes of all individuals; therefore, modules with a high probability of surviving independently (ramets) are generally counted. Ramet-producing plants are commonly referred to as plants that reproduce vegetatively. Many common rangeland grasses fall into this category, such as western wheatgrass (*Pascopyron smithii* [Rhydb.] A. Löve) and blue gramma (*Bouteloua gracilis* [H.B.K.] Lag. ex Steud.).

Managing areas for population diversity requires a knowledge of the dynamics of the individuals that compose the population over time. A simple mathematical equation relates the four basic components that influence changes in population sizes during a time interval from time t to time $t+1$:

$$N_{t+1} = N_t + B_t + I_t - D_t - E_t$$

In other words, the number of individuals at the end of the interval (N_{t+1}) equals the number of individuals in the population at the beginning of the interval (N_t), plus the number of births or new propagules (B_t), plus the number of individuals immigrating into the population (I_t), minus the number of deaths (D_t), minus the number of individuals emigrating out of the population (E_t) during the interval.

Just as the definition of an individual is easier to define for animals than for plants, so is the definition of births easier to define for animals than for plants. Birth for plants may refer to several different stages in development including viable seeds, germinated seeds, and clonal growth (vegetative reproduction). The preferred phase of a plant's life cycle that equates to births is the production of viable seeds because they are the product of genetic recombination producing a new genetic individual, a genet (cf. Harper 1977). Yet for many species, seed viability is difficult to determine without chemical tests such as a standard tetrazolium chloride test (see Bewley and Black 1982). Unfortunately, even these tests may provide overestimates of viability (Roberts 1972). An alternative is to use total seed number regardless of the viability status; however, total seed number is an overestimate of the potentially viable seeds since it is the upper limit if all seeds are viable. For taxa (e.g., the grasses) where visual inspection can determine many nonviable seeds (e.g., unfilled caryopses), such inspections should be completed before estimating seed numbers. Equating germination to birth should be done cautiously, recognizing that the seed phase of the life cycle is ignored, thus ignoring the impacts of seed predation, microbial pathogens, deep burial in the soil, and dormancy on the total number that germinate. Clonal growth produces a new individual, a ramet (cf. Harper 1977), in the population, but it does not increase the genetic diversity of the population since it is genetically identical to the parent plant.

Plant death is normally defined as occurring when no photosynthetic portions of the plant are active during normal seasons of activity. Simply, green plant parts have turned brown. For seeds, death is more difficult to define without viability tests.

Immigration and emigration in animals is common due to their mobility, but most plants are immobile after germination; therefore only the seed phase is capable of dispersal into and out of a population. Most seeds disperse only short distances from their parents. Dispersal distance is enhanced by adaptations for seed transport such as barbs and hooks for external transport or such as the development of fleshy fruits for internal animal transport.

In stable populations, emigration and immigration tend to cancel each other since the probability of successfully leaving the population is likely equal to the probability of a seed from another population successfully dispersing to this population. In the simple model, E_t equals I_t , resulting in population changes being driven by changes in births and deaths.

An exception can be found where populations remain stable along the fringes of their range of existence due to harsh environmental conditions. These populations may rarely produce viable seeds; therefore they rely on immigra-

tion from nearby populations to periodically replenish their numbers. This may be the situation when managing rangelands for the maintenance of peripheral species that are rare within a location, yet more common elsewhere. Management to maintain these peripheral populations may require cooperation among managers in adjoining jurisdictions (i.e., states or landowners) so that dispersal is maintained.

STRUCTURAL DIVERSITY IN POPULATIONS

Diversity at the population level is largely a description of the variation in the structural composition of the population. Population structure can be divided several ways, for example: (1) sex ratios; (2) age classes; (3) developmental stages; or (4) size classes. Sex ratios are generally more important for animal than for plant populations since most plants contain both sexes on the same individual (monoecious, hermaphroditic). Some rangeland ecosystems, however, provide exceptions. In arid ecosystems such as the salt-desert shrub of the Great Basin, U.S.A., a large proportion of woody species are dioecious, including the dominant species shadscale (*Atriplex confertifolia* [Torr. and Frem.] Wat.) and four-winged saltbush (*A. canescens* [Pursh] Nutt.). In addition, some species are capable of changing their sex ratios under different environmental conditions (Freeman et al. 1981). Insights into changes in population diversity of these species might require knowledge of sex ratios and their changes through time.

Although age class is commonly used to describe animal populations, evidence suggests that for most animals and plants size may be a better predictor of survival and reproduction than age (see references in Caswell 1989, p. 31). Age class distributions are commonly used to describe the stability of tree populations in forested stands (Daubenmire 1968). Graphically, a stable age structure is represented by a reverse J-shaped age distribution (Figure 1a). In general, the population is growing or stable when the greatest number of individuals are in the youngest age classes and progressively fewer individuals are in older age classes. Distributions with similar numbers of individuals in all age classes typically indicate a reduction in population growth and if continued may lead to reductions in population after several generations (Figure 1b). Caution must be taken, however, when using age class distributions to predict the stability of species that reproduce or establish episodically since age distributions represent only a single moment in time.

In harsh environments, such as arid ecosystems, perennial plants have adapted their life-history strategies to cope with an unpredictable environment by relying on episodic establishment of new individuals. The production of adequate numbers of viable seeds may occur only in years with sufficient moisture during flower and seed production. For example, bluebunch wheatgrass (*Pseudoroegneria spicata*) seed production and flowering culm production vary widely from year to year (Mueggler 1975).

Age class distributions alone do not provide all the necessary information to forecast adequately population trends. Knowledge of the age-specific birth and death rates and of the

regularity of seed production and germination is required. If the reproduction occurs regularly and at nearly the same levels per individual each year and if survival is age dependent, then age class distributions may strongly reflect population trends. Otherwise populations are described better by classifying the individuals into size classes or developmental stages. Generally, size class or stage of development is a better predictor of an individual's fate than its age (e.g., Werner 1975, Sarukhán et al. 1984).

Some perennial plants with plastic growth can switch from being reproductive in one year to nonreproductive in the next. Thus, stages like seed, seedling, sapling, clonally reproducing, sexually reproducing, and both clonally and

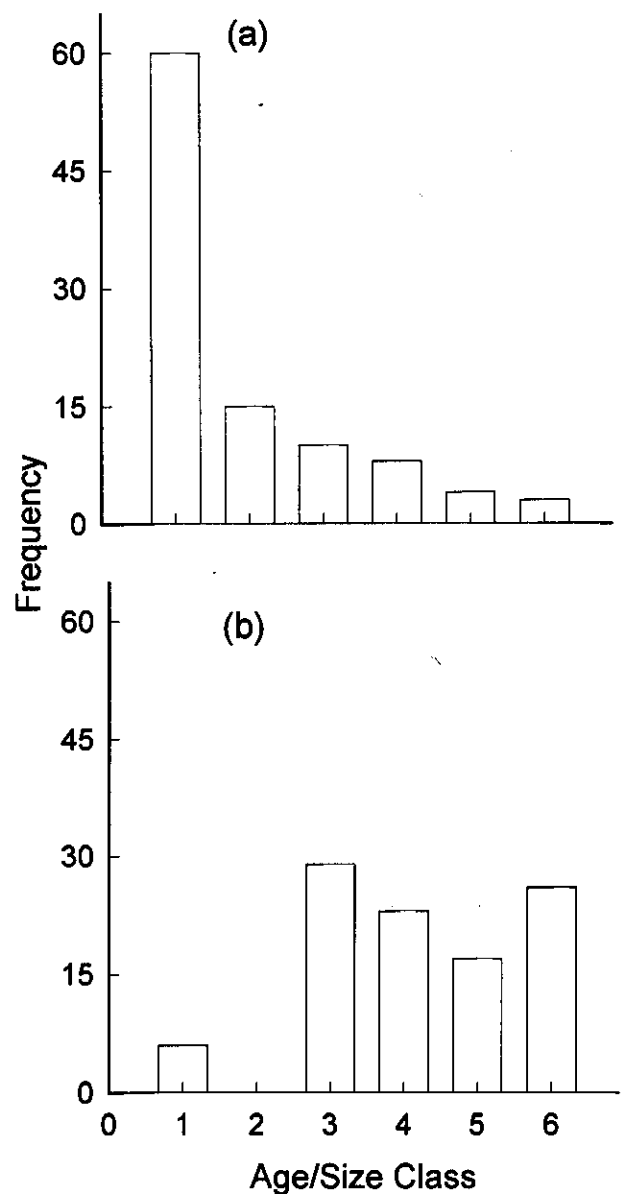


Figure 1. A hypothetical age or size class distribution demonstrating (a) a stable or growing population and (b) a slowing or declining population.

sexually reproducing individuals, provide several structural classes among which individuals may shift in either direction, in contrast to age classes that by definition are unidirectional.

Annual censuses of populations allow counts of individuals in each structural class. If fates of the same individuals are monitored each year, then probabilities of an individual successfully making a transition from one structural class to the next can be estimated. These transitional probabilities (P) are calculated as a ratio of the number of individuals in a class that change to another class. For example, the proportion ($P_{n \rightarrow r}$) of nonreproductive adults at time t ($N_{n,t}$) that become reproductive adults at time $t+1$ ($N_{r,t+1}$) is calculated as follows:

$$P_{n \rightarrow r} = \frac{N_{n \rightarrow r, t+1}}{N_{n, t}}$$

One method of describing the structural diversity of a population is to develop a diagrammatic life table (Figure 2) that combines the relative numbers of individuals in each

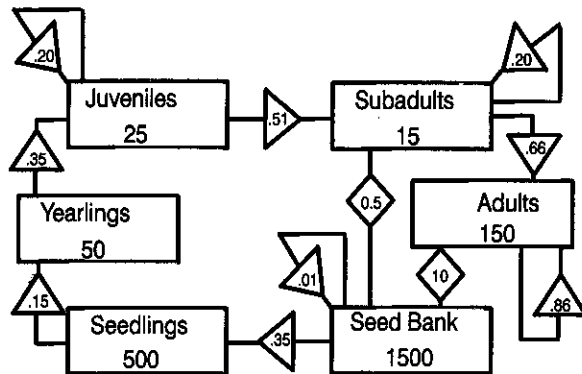


Figure 2. Diagrammatic life table for bluebunch wheatgrass. Rectangles represent the numbers of individuals in that stage of development, triangles represent the transitional probabilities between each stage, and diamonds represent the number of viable seeds per individual.

category with their transitional probabilities. Simple diagrams can convey the potential for dynamism in age- or size-dependent populations. Complex diagrams demonstrate the multiple paths available to individuals in some classes in the next generation.

Transitional probabilities in life tables are often viewed as static values, but the displayed probabilities normally represent the mean or median of several proportions. When data for multiple years are available, both the mean probability and the variation around that mean should be presented. The variation is used in developing models that project the likelihood that populations will increase, decrease, or remain constant.

TECHNIQUES FOR SAMPLING POPULATION DIVERSITY

Techniques used to collect estimates of demographic parameters vary depending on the plant and on its stage of development. In all cases, density (numbers of individuals

per unit area) must be accurately determined at different times (t_i and t_{i+1}) and there must be a method to identify that the same individuals are being tracked through time. Methods for tracking individuals include using markers such as toothpicks, colored wire collars, and numbered tags. However, markers associated with the plants are vulnerable to removal or destruction; therefore censuses using data collected with markers may be biased.

Alternative methods that do not rely on the presence of markers use coordinate systems to map the position of individuals and to verify their continued existence. Many types of coordinate systems have been used to monitor rangeland plant populations. Pantographs aid in drawing scaled maps of plant locations and plant basal area in permanent plots (Wright and Van Dyne 1976, West et al. 1979). Mapping tables use a sighting scope to mark the plant position on an acetate map placed on a table directly above the plot (Chambers and Brown 1988, Pyke 1990). Mapping tables are more accurate than pantographs for relocating individuals in dense populations. Photographs may provide maps of plant positions in sparse communities where canopies do not overlap (Owens et al. 1985). Using scanners and digital processing, large mature and juvenile plants may be detected and analyzed over multiple censuses within a geographic information system. Measured coordinates can use an angle-distance technique (Muir and McCune 1992, Hutchings 1986) or an x,y-coordinate technique (Cullen et al. 1978) to measure the position of the plant within the plot.

Methods for monitoring seed fates are more difficult. Mark and recapture techniques have been used successfully for several species in differing habitats. The marking method is normally a paint or dye applied to the seed surface (Watkinson 1978). Recapture of the seeds is dependent on the seed being seen by the observer. Techniques using radionuclide markers on seeds allow the observer to detect the seed even if it is hidden from view (Primack and Levy 1988). The fates of individual seeds have been followed by gluing thin nylon fishing line to seeds and connecting the line to a stake, thus allowing secondary dispersal of the seed once it comes into contact with the soil (Schupp 1990).

Analysis of mark and recapture data for plants or seeds requires techniques similar to those used to analyze animal mark and recapture data. Recapture and survival probabilities may independently depend on time. Only when the probability of recapture is 100 percent is it possible to directly measure the survival probability. When recapture probability is less than 100 percent, researchers must estimate both the survival and recapture probabilities; otherwise survival estimates will underestimate actual survival probabilities. For example, a survival probability for an organism may increase over time while recapture probability decreases over time. Techniques are available to treat independently survival and recapture probabilities (Lebreton et al. 1992), although these techniques are not commonly used for plant populations.

In lieu of marking individual seeds, a common technique identifies a known quantity of seeds and introduces those seeds in a location so that the surviving seeds can be collected at some later time. For seed bank longevity experiments, seeds are placed in bags that allow moisture and microorgan-

isms to move through the fabric (e.g., Hopkins and Graham 1987). Alternatively, seeds can be mixed with soil and buried with an inert material, such as sand or glass beads, placed above and below the soil-seed mixture, reducing some of the bias associated with a container holding the seeds (Vázquez-Yanes and Smith 1982). The layers of inert material mark the location of the seeds so remaining seeds can be extracted later. Tests of the germinability and viability at varying times can provide estimates of dormancy, seed survival, and seed bank persistence. Dormancy estimates based only on germinability will require germination tests under differing environmental conditions. Techniques using ranges of temperature treatments have been widely applied to rangeland plants (Palmquist et al. 1987).

For measurements of sexual reproduction, the number of viable seeds must be estimated independently for each individual in a defined area so that estimates of both the central tendency for seed production and of variation in seed production can be made for the population of individuals. Combinations of bulk harvests of seeds from all plants (S) and of counts of individuals (N) in the same area can provide only estimates of the mean seed production per individual (S/N). These estimates assume a normal distribution of seed production among individuals, but distributions are typically skewed to the right; few individuals produce large numbers of seeds while most individuals produce few or none (Levin and Wilson 1978, Mack and Pyke 1983). The skewed distribution of seed production per individual generally makes the median a preferred measure of central tendency over the mean.

Competition among plants can differentially influence the vital rates of plants in different size or developmental stages. Density-dependent effects normally reduce the survival of the younger age classes or smaller stages of development. These effects can be roughly measured using experiments where competitors are removed. These experiments may overestimate the effect of competition because of confounding effects of the decomposition of the roots of the removed plants increasing nutrient availability for the remaining plants.

An alternative method is to grow plants under varying densities of competitors to develop the relationship between the density of competitors and the vital rates of the target species. For perennial plants, these experiments need to be conducted over several years to determine the effect of density on plants of different ages, sizes, and structural stages. Additive-series experiments provide an excellent method for developing these relationships (Silvertown 1987) since they incorporate changes in plant densities and in proportions of the competing species. Francis (1993) has demonstrated this approach for determining the density-dependent effect of cheatgrass on the seedling biomass of crested wheatgrasses (Figures 3a,b). Similar experiments need to be conducted for multiple years to explore the range of density-dependent effects on seed production and survival for rangeland plants.

PROJECTING FUTURE POPULATIONS

Land managers and conservation biologists over the last ten years have recognized a need for quantitative methods to

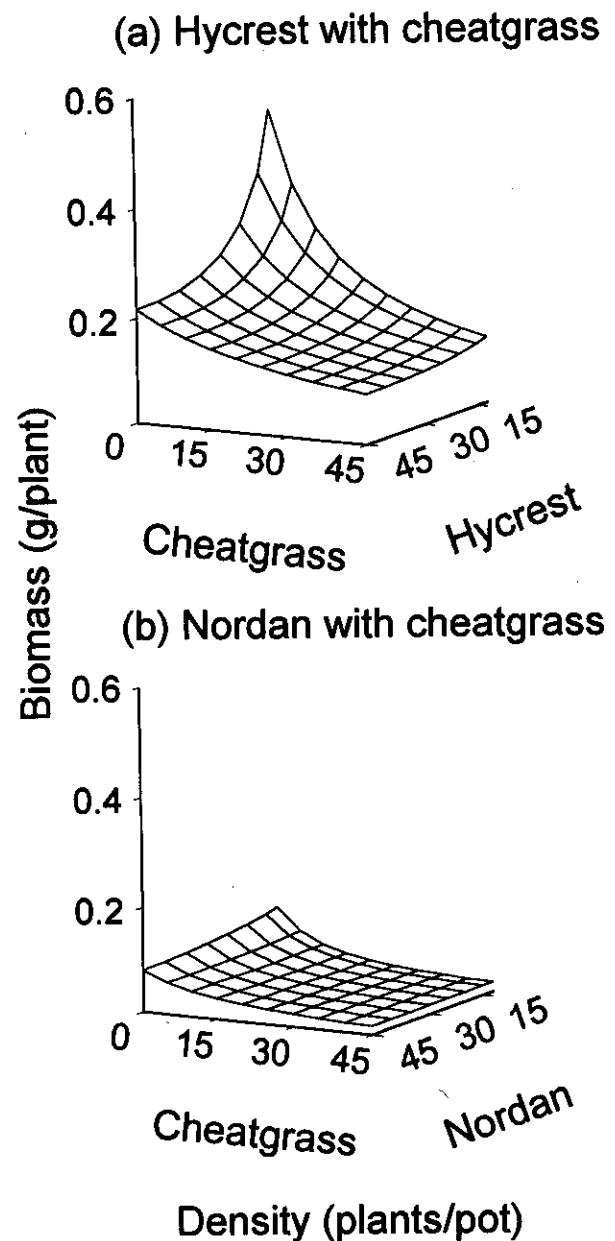


Figure 3. Median biomass per individual for seedlings of (a) "Hycrest" and (b) "Nordan" crested wheatgrass when competing with cheatgrass in two-species mixtures of varying densities in pots with dimensions of 33 cm upper diameter, 30 cm lower diameter, and 36 cm deep (from Francis 1993).

predict the risks of extinction for species existing in small populations. On the opposite end of the spectrum, managers and biologists are concerned with the potential for population explosions of recently introduced exotic species. Both of these concerns can be addressed using a population modeling technique known as Population Viability (Vulnerability) Analysis (PVA). PVA is similar to techniques that determine Minimum Viable Populations (MVP), a population level that a population must remain above to sustain itself. Defining a single MVP level is difficult and has become controversial (Soulé 1987). For the purpose of this paper, PVA will be presented since it incorporates the processes and the variabil-

ity that influence the level of the MVP as well as estimates of the risk to the population of management alternatives.

Two types of quantitative measures are possible in a PVA: (1) deterministic measures are those based on single values that predict the fate of a population; and (2) stochastic measures are those based on a probability of a fate for a population. These two types of measures have resulted in two schools of thought concerning population projections. The deterministic school relies heavily on the estimate of the population's finite rate of increase known as λ . Populations with $\lambda=1$ are stable whereas values above 1 and below 1 indicate a trend for a population to increase or decrease, respectively, over time. The usefulness of λ as a predictor of population stability for small populations has come under scrutiny. Values of λ are estimated when populations are assumed to have a stable age or stage distribution; however, small populations may never satisfy this assumption and thus invalidate the estimate of λ .

Stochastic measures incorporate estimates of the natural variability under which each population exists. Instead of providing a single measure for comparison against a goal (MVP), stochastic measures recognize that extinction, stability, or explosions for any given population are probabilistic expressions. They measure the chance of extinction or the chance of the population exceeding some upper or lower level during a time period.

The three major types of PVA are distinguished by the underlying models used to project future populations. The simplest forms are unstructured models that treat all individuals equally; that is, survival and reproduction rates do not differ among age or stage classes. These models use difference equations, such as exponential growth, logistic growth, or Ricker equations to predict population size at the next census as a function of the population size at the current census. An example of a series of unstructured models for PVA is found in the program DRAMA (Crow et al. 1992).

The complexity of models increases when internally structured population models are used to predict the numbers of individuals in each age or stage of development. Internally structured models are matrix models that allow stage-specific fates. These fates equal the transitional probabilities between stages discussed earlier in this paper. The simplest forms are the Leslie matrix for an age-classified population (Leslie 1945) and the Lefkovich matrix for a stage-classified population (Lefkovich 1965). Examples of three internally structured PVA programs are RAMAS/AGE (Ferson and Akçakaya 1990), RAMAS/STAGE (Ferson 1990), and RAMAS/SPACE (Akçakaya and Ferson 1992) for analyzing age-structured, stage-structured, and spatially structured populations, respectively.

The most complex forms of PVA are the individual-based models. These models examine the reproduction and survival of different genotypes in the population. Individual-based models predict the genetic structure of the population and predict changes in allele frequencies in a population. Three individual-based programs for PVA are VORTEX (Lacy and Kreeger 1992), ALEX (Possingham et al. 1992), and GAPPS II (Downer et al. 1992).

An effective PVA involves three steps. First is a combination of field demography and statistical analyses to estimate reproduction, germination, and survival probabilities for a population under different growing conditions (e.g., grazed vs. ungrazed or with and without competitors). If field data are available for multiple years, then estimates of the annual variability in these vital rates can be calculated. Second is a risk analysis to predict the impact of alternative actions upon the species persistence. Third is the implementation of the chosen management action followed by additional long-term monitoring of demographic data. At this stage, the manager cycles back to step one where the process begins again, making this process an integral part of adaptive resource management (Holling 1978, Walters 1986).

In the risk analysis phase, demographic data are run through a series of computer simulations (e.g., 1,000 simulations consisting of 50 generations per simulation) based on the initial numbers of individuals in each age or stage and based on the probabilities of individuals shifting to various stages. The process of shifting from one stage to another is often variable and unpredictable; thus some transition probabilities may have a degree of uncertainty associated with them that needs to be included in the model (Shaffer 1987). Four classes of uncertainty are generally recognized (Shaffer 1981). *Demographic uncertainty* is the unpredictable survival or reproduction not related to environmental conditions. *Environmental uncertainty* is the unpredictable survival or reproduction due to weather or changes in resource availability. *Natural catastrophes* are events like fire, floods, wind storms, etc., that rarely occur but have major impacts on the population. *Genetic uncertainty* is random change in the genetic composition of the population that has a range of beneficial to detrimental effects on the vital rates of the population.

Once the analysis is initialized with the population sizes for each stage, and their associated vital rates, then simulations can begin to evaluate the risk of extinction for rare species or of explosion for invasive species. The model estimates the risk of extinction by first determining when a simulated population became extinct, if ever. The model then repeats the process for the fixed number of simulations with the same initial data. A frequency distribution of extinction times or of probabilities of extinction can be developed (Figure 4a). However, a histogram of extinction times does not provide a useful picture of the probability of extinction since the probability of extinction at time t_x is not represented by the frequency of extinction in that single year, but is the summation of the probabilities in year x and all previous years. An improved method of displaying the probability of extinction is with a cumulative probability of extinction (Figure 4b).

Managers may find it more useful to know the probability of a population dropping below some specified threshold size rather than the probability of extinction. This threshold level is known as the quasi-extinction abundance (Ginzburg et al. 1982). Choosing a reasonable threshold level may eliminate criticisms of inherent difficulties in modeling low population sizes, such as the potential for finding a mate, the probability

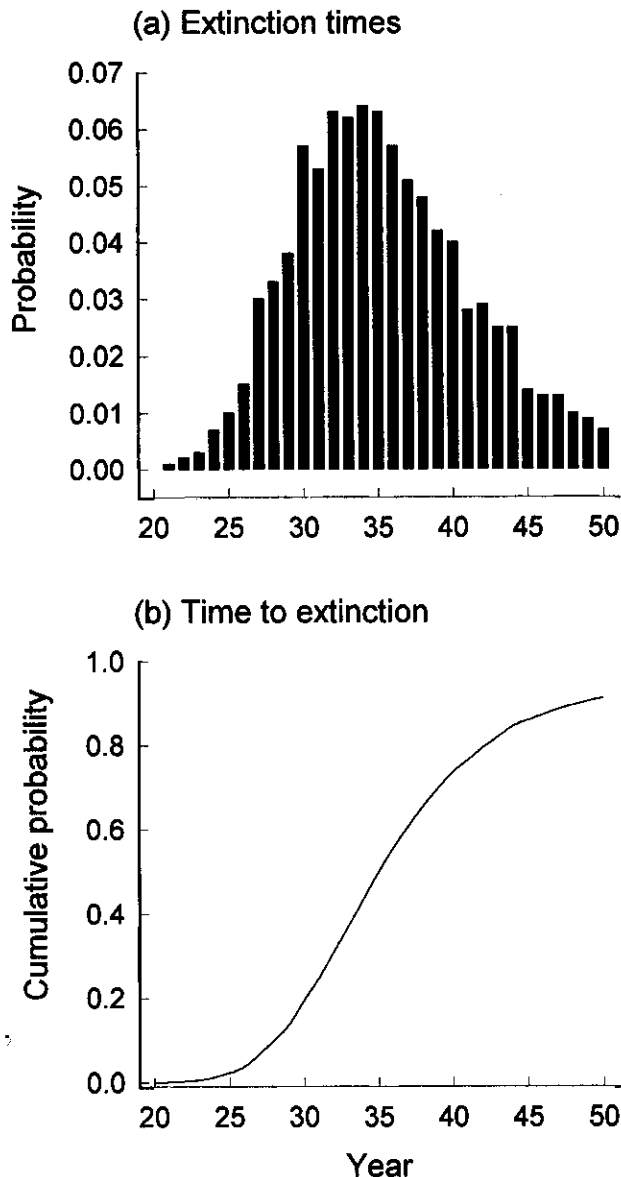


Figure 4. (a) A hypothetical distribution of the frequency of different time to extinction from 1,000 simulations and (b) a cumulative probability of extinction developed from the same data.

of successful pollination, or the consequences of inbreeding depression that may influence the population more at low population sizes (Gilpin and Soulé 1986). The calculation of the quasi-extinction risk is the same as the extinction risk, but the frequency distributions are based on the time when populations dropped below the threshold, rather than to zero.

These same techniques determine probabilities of population explosion for weedy species or of population recovery for rare species. These approaches could be useful when deciding on which species to concentrate limited labor and money. Those weedy species that are likely to explode in the shortest period of time need immediate action. For rare species, information on the impact of different management options can provide insight into the likelihood of recovery.

The reliability of any PVA, however, is dependent on the accuracy of the empirical data (mean and variance) and on the

assumptions used for unknown attributes. For matrix models, additional analyses can be performed to detect which portions of the species' life stages are likely to affect the population. These are called sensitivity and elasticity analyses (de Kroon et al. 1986, Caswell 1989). If critical stages of the life cycle are dependent on assumptions or scientific guesses, then the results of the PVA are strongly suspect. This does not mean that the PVA is useless, because it has identified areas of study for future data collection that will strengthen the PVA.

TWO EXAMPLES OF POPULATION VIABILITY ANALYSIS

The following PVA examples provide two different techniques for addressing management decisions on rangelands. The first projects the impacts of autumn vs. spring grazing regimes on a bluebunch wheatgrass population. The factor of interest is the probability of bluebunch wheatgrass becoming extinct in the next 50 years. The second example evaluates the potential for cheatgrass populations to explode on a site. Both examples are largely based on data from the literature with some parameters estimated when data were not available. An appendix provides the equations used to calculate these projections.

BLUEBUNCH WHEATGRASS

Bluebunch wheatgrass is a dominant native perennial bunchgrass in many communities in the Intermountain West, U.S.A. The population is divided into six age-stage classes (Figure 2): (1) a small persistent seed bank; (2) germinated seeds remain as seedlings for one year; (3) yearlings have survived one summer dormant season, but are too small to reproduce; (4) juveniles are older and larger plants than yearlings, but have not reached reproductive size; (5) subadults are small reproductive plants, but contribute very little seed to the seed bank; and (6) adults are large enough to reproduce consistently. Germination and survival rates for seeds in the seed bank, seedlings, and yearlings are based on data from Pyke (1990), while rates for juveniles, subadults, and adults are estimated from West et al. (1979). Reproduction per individual is not available, but is estimated from the seed production per unit area in Pyke (1990). The only difference between the two grazing treatments is that the fall treatment is given the full reproductive rate (10 and 0.5 seeds per adult and subadult), whereas the late-spring treatment produces half the number of seeds per stage. The estimates of reproduction rate were based on a 50 percent proper-use value for bluebunch wheatgrass. Grazing during the growing season in late spring will reduce the number of reproductive culms produced by each plant. Fall grazing maintains the level of grazing above the level of the apical meristems, thus ensuring that reproduction will not be affected by grazing. This is an area where further empirical data is necessary to improve the model.

Precipitation can significantly affect the survival of seedlings and affect the reproduction of this species. The amount of precipitation in a year is randomly selected from a normal distribution with a mean of 30 cm and a variance of

11.4 square cm. Seed production and seedling survival are assumed not to occur in years when precipitation is less than 20 cm, whereas they double when precipitation is above 36 cm. Precipitation between 20 and 36 cm is assumed to yield multiplicative survival and seed production factors between zero and two in a linear relationship with the precipitation (Appendix).

Autumn grazing of bluebunch wheatgrass led to a slight but continuous decline in the population over the projected 50 years, whereas late-spring grazing caused a more precipitous decline (Figure 5a). A manager can use this output to determine the probability of a population dropping below a minimal density. By selecting the threshold density to be 0.5 plants m^{-2} , the fall-grazed population has a 40 percent probability of dropping below the threshold in 50 years, whereas the late-spring-grazed population always drops below the threshold during the same time (Figure 5b).

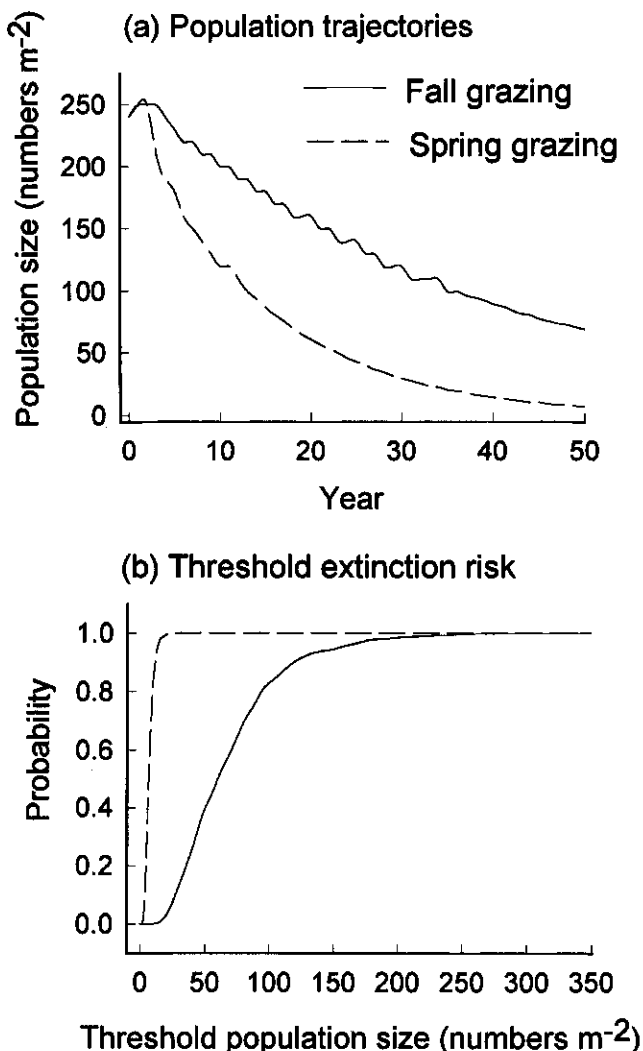


Figure 5. A comparison of fall and late-spring grazing on populations of bluebunch wheatgrass where (a) is the mean population size for 1,000 simulations over 50 years and where (b) is the probability of the population becoming extinct for each of 50 years based on the number of simulations where the population reached zero.

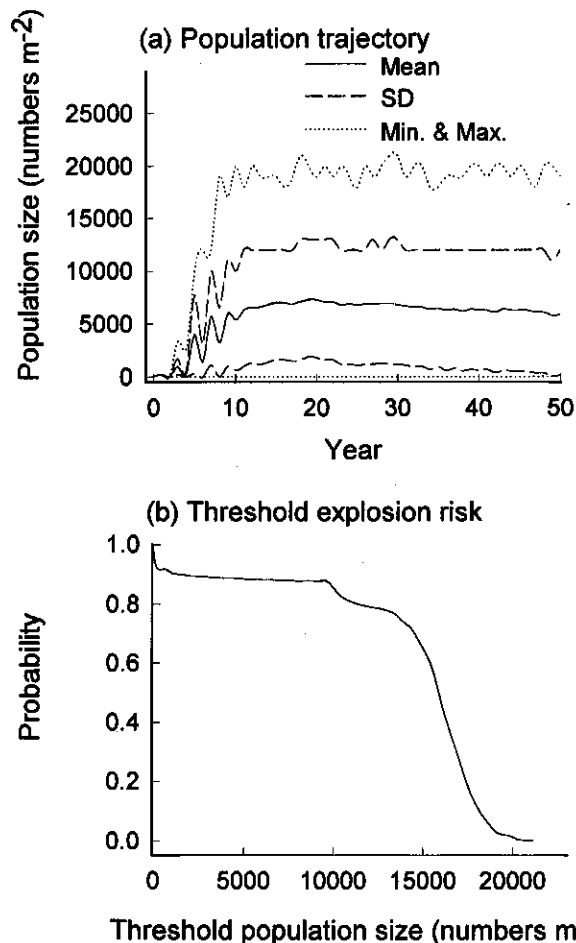


Figure 6. Beginning with an initial population of 10 reproductive cheatgrass individuals, (a) represents the mean, standard deviation (SD), minimum (Min.), and maximum (Max.) population size simulated 1,000 times over 50 years and (b) represents the probability of the population achieving or exceeding a population threshold sometime during 50 years.

CHEATGRASS

The same principles used to determine the chance of a population dropping below a critical density can also be used to determine the chance of a population increasing above a certain level. This is particularly important for highly competitive weedy species. Cheatgrass is a highly competitive annual plant that was introduced into the Intermountain West from Eurasia in the late 1800s and expanded to its current range in about 30 years. The demographic parameters that describe cheatgrass population dynamics are highly plastic both annually and over several locations (Mack and Pyke 1983).

The cheatgrass model incorporates the variability in all stages of a simple annual life cycle. The data used to estimate survival and reproductive rates were compiled from several studies (Mack and Pyke 1983, 1984, Pyke 1986, Reichenberger and Pyke 1990). Seed production in the model is regulated by a nonlinear density-dependent function (see Appendix). Random variation in seed-bank persistence, seed germination,

and plant survival was calculated using means and variances extracted from the above studies and was assumed to be normally distributed. The model was initiated with 10 reproductive plants m^{-2} and was run for 50 years.

Within 10 years the population stabilizes with a mean population size near 6,000 plants m^{-2} (Figure 6a), a realistic density in areas dominated by cheatgrass (Young et al. 1969, Upadhyaya et al. 1986). The plasticity in cheatgrass is seen in the high standard deviation. The potential for cheatgrass populations to explode is demonstrated by the high probability (0.88 to 0.92) of populations achieving sizes between 1,000 and 10,000 individuals m^{-2} at least sometime during a 50-year period (Figure 6b).

CONCLUSION

Managers have many tools available to them to monitor diversity at many levels. At the level of the population, population viability analysis is one tool for assisting managers in projecting the sustainability of species in an area. The accuracy of the projection will depend critically on a thorough understanding of the diversity and importance of life stages of the species and on accurate estimates of the rates of transition between these stages. Annual variation in these rates requires repeated measurements on the same individuals over a series of years. Knowing the effect that changes in management may have on each stage of a species will provide an additional tool in the decision-making process.

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APPENDIX

The following equations and distributions (Tables 1 and 2) were used in the simulations presented for bluebunch wheatgrass and for cheatgrass. Variables (x) selected at random from a normal distribution (N) with a mean of \bar{x} and a variance of s^2 will be represented by the equation $x = N[\bar{x}, s^2]$.

$$\bar{x}$$

$$N[\bar{x}, s^2]$$

TABLE 1. EQUATIONS USED TO DETERMINE SIMULATED POPULATION LEVELS OF BLUEBUNCH WHEATGRASS UNDER FALL AND LATE-SPRING GRAZING PRESENTED IN FIGURE 5.

Description	Grazing Time	Equation
Randomly selected rainfall	Both	$x = N[12, 4.5]$
Linear relationship between rainfall and plant growth	Both	$f1 = -2 + 0.25x$
Seedling survival and reproduction driver	Both	$f2 = \begin{cases} \text{if } f1 < 8, \text{ then } f2 = 0, \\ \text{if } f1 > 14, \text{ then } f2 = 2, \\ \text{otherwise } f2 = f1 \end{cases}$
Number of seeds contributed to the seed bank at time i+1	Fall	$B_{i+1} = (f1 * 10 * A_i) + (f1 * 0.5 * S_i) + (0.01 * B_i)$
	Spring	$B_{i+1} = (f1 * 5 * A_i) + (f1 * 0.25 * S_i) + (0.01 * B_i)$
Number of seedlings at time i+1	Both	$D_{i+1} = f1 * 0.35 * B_i$
Number of yearlings at time i+1	Both	$Y_{i+1} = 0.15 * D_i$
Number of juveniles at time i+1	Both	$J_{i+1} = (0.35 * Y_i) + (0.20 * J_i)$
Number of subadults at time i+1	Both	$S_{i+1} = (0.51 * J_i) + (0.20 * S_i)$
Number of adults at time i+1	Both	$A_{i+1} = (0.66 * S_i) + (0.86 * A_i)$

TABLE 2. EQUATIONS USED TO DETERMINE SIMULATED POPULATION LEVELS OF CHEATGRASS REPRESENTED IN FIGURE 6.

Description	Equation
Seed bank persistence stochasticity	$b = N[0.015, 0.0026],$ $\text{where } 0 \leq b \leq 1$
Germination stochasticity	$g = N[0.30, 0.062],$ $\text{where } 0 \leq g \leq 1$
Seedling survival stochasticity	$s = N[0.82, 0.027],$ $\text{where } 0 \leq s \leq 1$
Density-dependent seed production	$f1_i = A_i * \left(\frac{77.9 * A_i}{1 + A_i^{1.36}} \right),$ $\text{where } 0 \leq f1_i \leq 10,000$
Number of seeds contributed to the seed bank at time i+1	$B_{i+1} = b * B_i + f1_i$
Number of reproductive plants at time i+1	$A_{i+1} = g * s * B_i$

Diversity of Rangeland Bird Populations

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Abstract

Most discussion and management of biological diversity occurs at the local population level, which can be defined as that group of organisms of one species that live in a specific area and that tend to interact more frequently with each other than with individuals from other populations. Loss of diversity always occurs first with the extinction of local populations, and, if the process continues long enough, will ultimately lead to extinction at the regional and global scales. Among animals, most changes in the biological diversity of western rangelands have involved local extinctions, and I summarize the general factors that determine whether a population will either persist through time or decline in numbers to local extinction. These include not only events that directly impact local birth and death rates, but also the ability of individuals to move between populations. I then discuss the changes that have occurred in the diversity of the bird community in a riparian area along the Lower Truckee River in west-central Nevada that was studied by Ridgeway in 1868 and over a century later by Klebenow and Oakleaf in 1972–76. A comparison of the species that were located in each study indicates that nearly half of the avian diversity that was originally present in this habitat has now disappeared. An analysis of the birds that are now locally extinct suggests four changes in the environment have been important: (1) loss of the total amount of habitat or subhabitats, such as marshy areas near the river; (2) loss of specific resources within the habitat, such as many native fish; (3) changes in the structure of the remaining habitat, such as loss of ground cover needed by ground-nesting species to protect their young from predators; and (4) loss of connectivity between remaining habitat patches. Restoration of local biological diversity in riparian habitats, for both birds and other animals, will require management actions to address each of these factors.

INTRODUCTION

Historically, much of the discussion concerning biological diversity on rangelands has centered around animal populations. Animals often are better known than plants to most people, including land users, managers, and the general public. As a result, changes in their numbers are usually easier to document, and the disappearance of one or more species in an area is more likely to result in a reaction of concern among the public, even though such disappearances also may be accompanied by, or be the result of, changes in local plant communities. For example, the extinction of nesting populations of osprey, bald eagles, and peregrine falcons in most rivers and streams in the western United States as a result of DDT poisoning was well known to the public, and it played an important role in the banning of most uses of this pesticide in the United States. The fact that these birds are now returning to many areas where they once nested is a major success story in the conservation of biodiversity.

In this paper, I review the basic elements of animal population biology as it relates to the management of biologi-

cal diversity. Since plant and animal populations share a number of characteristics in common,¹ I focus here primarily on those features of animal populations that will be most useful to managers. I then give a specific example of changes that have occurred over the past century in the diversity of bird populations occurring in a riparian habitat in western Nevada.

Many animals in arid and semiarid rangelands depend upon riparian areas for food and for places to have young; at the same time these habitats are heavily used for both recreation and livestock production. As a result, the management of these areas is very controversial. Birds often are very sensitive indicators of the overall ecological changes that occur in a local area; understanding the factors that may lead to changes in the diversity of bird populations in riparian habitats can serve as a useful guide to maintaining the health of riparian systems and restoring those areas that may have been degraded by past practices.

¹See Pyke, this volume, for a discussion of plant populations.

BIOLOGICAL DIVERSITY AND THE DYNAMICS OF ANIMAL POPULATIONS

LEVELS OF DIVERSITY

Although biological diversity has many components (genetic, community, landscape, etc.) one of the most fundamental is species diversity, which is a measure of the number and kinds of species that occur in a defined area (West 1993). Although the appropriate statistic that should be used to measure species diversity can be a matter of controversy, and depends upon the goal of the analysis,² most common approaches include two different components: species *richness*, or the number of different taxonomic categories (typically species) that occur in the area, and species *evenness*, or the extent to which individuals are evenly spread or distributed among those taxonomic units (i.e., the extent to which most species are rare or common in the area). The most diverse communities are those in which there are many species, and where most or all of those species are equally common; conversely, species diversity declines when there are fewer species (some go extinct), and/or many of the species that were once common become rare and consist of only a few individuals. The two components of species diversity are of course related in the sense that as each species becomes more and more rare (decreasing species evenness), each is more likely eventually to disappear entirely, decreasing species richness.

Some species are "naturally" rare and occur in low densities even in the absence of human-caused disturbances, while others are "naturally" common, and thus there is no ideal level of species evenness, or even species richness, in any particular habitat. However, rare species usually are able to maintain their populations through time just as well as common species. Thus there is considerable difference between the case where there are species that have always been rare, and one where many species that were once common have become rare as a result of human activity. The latter situation is the most common one on most rangelands, and understanding whether the sizes of animal populations are going up or down equals or exceeds the importance of knowing their current numbers.

A second important factor in biological diversity is the scale over which the measurement of diversity is made. For example, it has often been argued that very few species of animals have actually gone extinct over the past several hundred years in the United States, and thus concern over declining biodiversity in this part of the world is unwarranted. While this is true in the sense that a few representatives of most taxa may still survive somewhere (often either in very small and limited populations or in zoos), much of the diversity of animals that used to be present in many local areas has disappeared. For example, the river otter *Lutra canadensis* once was common in most of the medium and large streams and rivers in western rangelands. Although the otter still survives as a species, it is now extinct in almost all of its former haunts, and its disappearance probably has had a major impact on the diversity of the fish communities in the

²See West, this volume.

streams in which it once lived. It is therefore important to distinguish between the different levels at which changes in biological diversity can occur, including *local*, *regional*, and *global*.

Most animal extinctions in western rangelands have occurred at the local level, primarily as a result of changes in the structure and function of local habitats. While the losses of biological diversity at the local level often are the least noticed, they are extremely important because they change the functional dynamics of the local community, and because if the local extinctions continue long enough, the species will be lost over wide areas and may not recover without human intervention. Extinctions at the regional level have been less common to date than local extinctions, and usually result from either the widespread alteration of habitats or direct human persecution (e.g., grizzly bears *Ursus arctos* that are now extinct in most of the western United States; and Mexican wolves *Canis lupes mexicanus*, black-footed ferrets *Mustela nigripes*, and California condors *Gymnopyys californianus* that are now probably completely extinct in the wild).

Regional extinctions result in the permanent loss of considerable within-species genetic diversity,³ and often are the precursor to global extinction unless immediate and usually very expensive recovery efforts are undertaken. Changes in biological diversity are thus the result of a cascading effect from local to regional to global extinction. Management for diversity is likely to be most successful at the local level because most management decisions are made and implemented at the local level, and the results of different management options are most likely to become immediately apparent. Preserving or restoring biological diversity at the local level not only maintains local community structure and function, it also minimizes the chance of extinctions at the higher levels. Understanding the factors that impact animal populations at the local level is therefore probably the most important challenge to effective land management (West 1993).

ANIMAL POPULATION DYNAMICS

The consideration of biological diversity at the local level generally centers around the presence or absence of populations of particular species in a geographic area such as a stream course or valley. As with most biological phenomena, the exact makeup or boundary of a population is often hard to specify. In general, the population is considered to be made up of a group of animals that frequently interact with each other behaviorally, ecologically, and reproductively, while doing so much less frequently with individuals from other populations. In most western rangelands, patches of habitat that can be occupied by a species often are separated from each other by areas that are unsuitable for the animals. Thus riparian habitats often are isolated from each other by intervening grasslands, while grassland habitats in valleys are separated by forested mountain tops. In these situations, populations can be defined geographically as including all those individuals that live in a particular habitat patch.

³See McArthur and Tausch, this volume.

Most animals have the ability to move a considerable distance over their lifetimes. There are two general types of movement that impact population processes: *natal* dispersal, where juveniles move away from the area in which they were born to begin breeding, and *breeding* dispersal, in which adults move from one breeding season to the next. Local populations thus often are connected to each other through dispersal into a larger unit, termed a *metapopulation* (Levins 1976). Recent work (e.g., Gilpin and Hanski 1989, Stacey and Taper 1992) has indicated that the dispersal of individuals from one population to another, even when rare, can have a profound effect upon the dynamics of each individual population, and in many cases can prevent the local extinction (and loss of biodiversity) of these populations through time. This work suggests that maintaining the ability of animals to move among populations can be critical to managing for biological diversity even at the local level, and considerable effort is being spent to understand exactly how dispersal occurs, and the consequences of its disruption for population persistence (Pimm et al. 1993, Stacey and Taper, in preparation).

When a population goes extinct in an area, it means that the number of individuals of that species that live in the area has declined through time to zero (Figure 1). Unless the area is recolonized from other populations, the local extinction is permanent, and when all of the populations over a wide area have declined to zero, regional extinction has occurred. Thus a key question in managing for biological diversity is to determine the population trajectories of the different species that inhabit an area. Many (but not all) of the native species of animals in the rangelands of western North America appear to have experienced a substantial decline over the last several centuries. To reverse this trend, the factors leading to the declines must be understood and corrected; that is, the population trajectories that are now headed toward zero (extinction) must be reversed, and the population sizes restored to a stable level that will persist for extended periods (Figure 1).

In a population that is closed (i.e., completely isolated from other populations) the only factors that determine population size and its change through time (its trajectory) are the population birth rate and the population death rate (Figure 2). When these two rates equal each other, there is no net change in population size, and the population will remain stable indefinitely as long as the rates themselves do not change. In populations that are open, and exist within a metapopulation, there also will be the additional factors of immigration into and emigration out of the population; population size will remain stable when births plus immigrations equal deaths plus emigrations. In most cases, the local birth and death rates will be the most important; however, when populations are small and occur in isolated patches, immigration can be critical in maintaining a population (Stacey and Taper 1992, Rieman and McIntyre 1993).

One measure of birth rate is called the net reproductive rate, R_0 , or the average number of female offspring that the average female in the population produces over her lifetime. Many times it is not possible to measure this parameter directly because of the time required to follow a cohort of

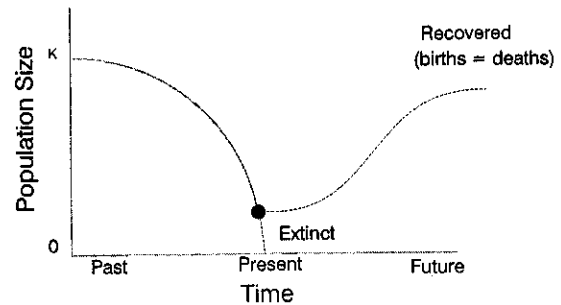


Figure 1. Potential population trajectories or changes in the size of a population through time. If a population of a species existed in the local area in the past, it probably had some relatively stable population size that was at or near the carrying capacity of that environment for that species (termed K). In many cases, human induced changes in the local environment have caused the size of the population to decline so that at present the species may be relatively rare in that area. Two future trajectories are then possible. If the decline continues, random events in the environment (e.g., droughts, floods, fires) will cause the population size eventually to drop to zero, causing local extinction and loss of biological diversity in that area. Management for biological diversity is designed to create the alternative trajectory, whereby the population decline reverses itself and it becomes large enough to avoid extinction from random events. At this point, the population may be considered to be recovered, in the sense that it will be likely to be able to survive in that environment for extended periods.

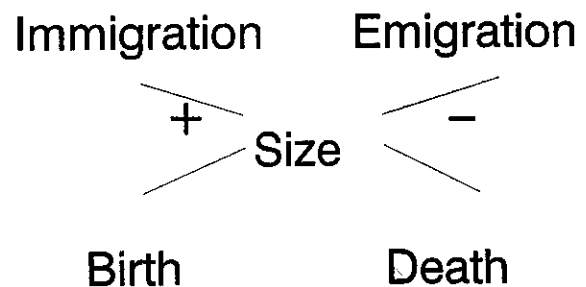


Figure 2. Factors or rates that will change the size of any population that is open, or where individuals can move into or out of the population. Birth and immigration will increase the size of the population; death and emigration will decrease its size. If a population is declining, it is necessary to determine which element(s) or change(s) in the environment have caused an increase or decrease in each rate.

females throughout their lifetimes. A useful approximation in many situations is λ , or the finite rate of increase. For example, if $\lambda=1.3$, there will be 1.3 individuals present in the population next year for every 1 individual present this year. Over the long term, when $\lambda<1$, the population will decline, when $\lambda=1$ the population will remain at constant size, and when $\lambda>1$, the population will increase. Of course, even in the best situations, real populations will not grow indefinitely, but eventually will reach some point where the resources required by that species for reproduction or survival begin to become limited. When this occurs, birth rates in most populations will tend to decline and/or death rates will increase, so that eventually $\lambda=1$ and the population more or less levels off and stops growing. This point, which is a particular population size, is called the *carrying capacity* of that environment

for that species (Figure 1), and is determined by the amount of resources available, including the food, water, shelter, places to reproduce, etc.

Each species in a community will have its own carrying capacity in each specific environment that may or may not be similar to other species in the community. And because similar species often use similar resources, the carrying capacity of an environment for one species will be affected by the number of individuals of all its competitor species in the same environment. For example, the population sizes of many of the native fish species in western rangelands like cutthroat trout (*Oncorhynchus clarkii*) have declined or gone locally extinct as a result of the introduction of non-native species that are able to outcompete the native fish. In general, any change in the environment that decreases the amount of resources that are available to a species, or increases the number of its competitors, will reduce the carrying capacity of the environment for that species, and eventually its local population size. If the carrying capacity declines far enough, the population itself will go extinct.

In addition to the local carrying capacity, a second factor that influences population trajectories is chance events in the environment. Because conditions change from year to year in an unpredictable way, birth and death rates in a population are not constant, but normally also vary from year to year. This means that in some years, as during a drought, deaths might be greater than births, while in a following year of greater rainfall, births might be greater than deaths. Thus natural populations are never absolutely stable, but fluctuate around some long-term mean value. (In a sense, each population may be considered to be "tracking" short-term changes in the local carrying capacity.) Another problem is that if a population gets too small, individuals may have trouble finding a mate, or there may be only males left in the local area (e.g., Simberloff 1988). These two phenomena are termed *environmental stochasticity* and *demographic stochasticity* respectively, and they will cause random variation in the population's λ from year to year. As a result, most natural populations will persist for substantially long periods of time only if they are large enough to be buffered from chance events like a series of drought years that will force otherwise healthy populations to extinction. This size of the population that is large enough to withstand such chance events is known as the *viable population size* and is frequently considered to be that size at which the population can survive at least 50 percent of the time for at least 500 years (which is essentially "forever" in terms of most management options). Viable population sizes are often considerably larger than would be expected by short-term studies of birth and death rates, and tend to increase as the variability of the environment increases (e.g., Soulé 1987). Of course, some catastrophic events such as large fires or extended droughts may so impact a population that it will go locally extinct, no matter what its original size. This is why most viability analyses are given in terms of specific probabilities of population survival (like the 50 percent chance of lasting for 500 years mentioned above), rather than in absolute numbers. It is in this context that movements between populations can become particularly important: if a functioning metapopulation is maintained in

a region, local extinctions from random or catastrophic events can be countered by recolonization from other populations. If it is no longer possible for animals to disperse between populations because of barriers to dispersal, or if the metapopulation structure no longer exists, current theory indicates that such random events will cause most populations to disappear eventually (Gilpin and Hanski 1989, Pimm et al. 1993, Stacey and Taper, in preparation).

AN EXAMPLE: THE DIVERSITY OF BIRDS IN RIPARIAN HABITATS

As discussed above, most of the changes in the biological diversity of animals in western rangelands have been the result of the extinction of individual populations in relatively localized areas. This trend recently has been of considerable concern (e.g., Finch 1991) because if enough local extinctions accumulate, the species is likely to be lost over a regional scale, and also because as each individual population is lost, there are fewer opportunities for recolonization of the area from elsewhere within the metapopulation. That is, loss of populations tends to be an accelerating phenomenon, and regional or even global extinction can occur with surprising rapidity during the final stages of decline. For example, the California condor probably inhabited much of the Pacific-coast region of western North America only 200 years ago, and collapsed into a single population in southern California, and is now extinct in the wild (Kiff 1990).

In the following section, I discuss factors that can influence the diversity of bird communities in local riparian or streamside habitats. The riparian zone is a valuable resource that has received increasing attention from research scientists and land use managers (Smith et al. 1991, Clary et al. 1992, Tellman et al. 1993). Although riparian habitats typically comprise less than 2 percent of total land area in the West (Pase and Layser 1977), they play critical roles in water quality, wildlife habitat, and livestock or crop production (Elmore and Beschta 1987, Hearne and Howard-Williams 1988, Minshall et al. 1989). In arid and semiarid regions like the Great Basin, the riparian zone is the major producer of vegetative growth because it is less dependent on local precipitation than the surrounding areas. Many wildlife species, from butterflies to ducks, depend on healthy riparian habitats, not only for food, but for places to raise young, for cover to avoid predators, and for areas to spend the night or avoid the heat of day.

Because riparian areas provide generally reliable sources of water, forage, and shade, these habitats also are heavily utilized by livestock, and the long-term impact of grazing on this ecosystem is of increasing interest and concern (Swanson 1988, Schulz and Leininger 1990). Because different species of birds often feed on different types of food and utilize different parts of the habitat for nesting, the bird community present in a riparian area can be a good indicator of the overall health of that area. Historically, the riparian communities surrounding most streams in western rangelands were dominated by a well developed and structurally complex understory of shrubs (primarily willows, *Salix* spp.), forbs, and grasses, and, in many cases, an overstory of cottonwood trees

(*Populus* spp.) or, at higher elevations, aspen (*P. tremuloides*). Watershed, agricultural, and livestock management practices singly and together can greatly alter this structure (e.g., DeBano and Schmidt 1990).

The first level of impact (primarily from grazing) results in removal of most of the understory while allowing large willows and mature trees to remain. Subsequent intensive grazing, channel modification, and water diversions can prevent the establishment of young scrubs and trees (Rood and Mahoney 1990). With the absence of any new recruitment and the die-off of the older woody plants, the original community will eventually be replaced by open grass or, in drier areas, scrub-dominated plant communities like sagebrush-steppe in the Great Basin. As a result of compaction and removal of the protective vegetative cover, soil and stream-bank characteristics may also change, leading to increased erosion, siltation, and water temperatures, as well as lower water tables and an overall reduction in water quality (DeBano and Schmidt 1990). Finally, areas near streams may be colonized by exotic plant species such as Russian olive (*Elaeagnus angustifolia*) and salt cedar (*Tamarix chinensis*). These species often prevent the recolonization of the disturbed habitat by native grasses, forbs, and trees through shading and other competitive interactions. Such species are of little value to either livestock or the native wildlife (Sedgwick and Knopf 1989, Howe and Knopf 1991).

Because of the importance of riparian habitats to wildlife—for example, riparian areas in the Southwest support a higher diversity of birds than all other western habitats combined (Anderson and Ohmart 1977, Johnson et al. 1977)—the potential impact of human use of areas on local and regional biodiversity has been of considerable interest. Perhaps the most important problem has been the widespread loss of the riparian habitat itself: for example, the amount of riparian gallery forest in Arizona has been reduced by 90 percent in the last three centuries (Krueper 1993). Such losses reduce both the population sizes and the distribution of species dependent upon riparian habitats, and fragment the remaining populations into smaller and more isolated units, which in turn makes them more vulnerable to extinction from random events in the environment (e.g., Rolstad 1991, Pearson 1993).

Other uses, such as livestock grazing and firewood production, can alter the structure of the riparian habitat as well as the component vegetation. Most riparian areas in western rangelands are grazed, and the impact of this use is often highly controversial (for recent reviews, see Bock et al. 1993 and Krueper 1993). Most, but not all, human impacts on riparian areas are suspected to lead to a decline in the number and types of bird species that depend on these areas, as well as in other wildlife (e.g., Szaro and Jakle 1985, Sedgwick and Knopf 1987, Tellman et al. 1993). However, documenting such changes is often difficult, because of the lack of long-term studies on riparian habitats (most studies last less than ten years) and the absence of clear information on the composition of the plant and animal communities prior to settlement (Bock et al. 1993).

Many changes in biodiversity are not apparent because the decline and eventual disappearance of a population in a

local area may be gradual rather than sudden (Figure 1), and the necessary data were not collected in the past to say with certainty that a particular species once occurred in an area but no longer does so at the current time (i.e., local extinction has occurred). There are exceptions, however, and one of the most interesting involves a study conducted by Klebenow and Oakleaf (1984) on the Lower Truckee River in the Western Great Basin, near Reno, Nevada.

In 1868 Robert Ridgeway surveyed the extensive riparian habitats on the lower Truckee as part of his work for the U.S. Biological Survey (Ridgeway 1877). He and his coworkers visited the area at the peak of the breeding season for birds between 15 May and 6 June, and they attempted to identify and estimate the abundances of as many birds as possible. Over a century later, between 1972 and 1976, D. Klebenow and R. Oakleaf studied the birds in the same locations as did Ridgeway, and compared their observations with what had been recorded earlier (Klebenow and Oakleaf 1984). Klebenow's and Oakleaf's data were collected during five different years, and as a result they were more likely to detect the presence or absence of a particular species than was Ridgeway during his visit. This is important because it means that any bias that might exist in comparing the results of two studies conducted more than a century apart would favor there being higher species richness (and biodiversity) in the more recent study rather than vice versa.

As a result of channelization, agricultural development, highway construction, and livestock grazing, the riparian areas along the Lower Truckee River have been extensively modified in the last 100 years. This has resulted in major changes in the biological diversity of birds inhabiting this area: for example, while Ridgeway observed 91 species of birds in three weeks of study, Klebenow and Oakleaf recorded only 61 species in five summers of work, a decline of nearly 27 percent in the total number of species. When the identity of the individual species involved is considered, the changes are even more extreme. Of the 91 original species of birds recorded by Ridgeway, 42 were not present at all in 1972–76, and 11 other species that had been either common or abundant in 1868 declined to the point that they had become very rare (a total of only one to three individuals observed over five summers). This represents a 58 percent change in the original bird communities in just over 100 years. There were 17 new species present in 1972–76, but many of these were either introduced or exotic species (e.g., European starlings, *Sturnus vulgaris*, and English house sparrows, *Passer domesticus*) or native birds that depend upon human garbage, open habitats, or extensive areas of dead or dying trees (including ring-billed gulls, *Larus delawarensis*, California quail, *Callipepla californica*, and downy woodpeckers, *Picoides pubescens*). In contrast, entire groups, or ecological guilds, of native species had disappeared since 1868, including most shorebirds (e.g., willets, *Catoptrophorus semipalmatus*, and American avocets, *Recurvirostra americana*), predatory birds (e.g., peregrine falcons, *Falco peregrinus*, and loggerhead shrikes, *Lanius ludovicianus*), birds that catch insects on the wing (e.g., Vaux's swifts, *Chaetura vauxi*, and bank swallows, *Riparia riparia*), birds that nest in riparian shrubs (e.g., willow flycatchers, *Empidonax traillii*, and song sparrows,

Melospiza melodia), many ducks (e.g., gadwalls, *Anas strepera*, American widgeons, *A. americana*, and northern shovelers, *A. clypeata*), birds that eat fish (e.g., double-crested cormorants, *Phalacrocorax auritus*, and osprey, *Pandion haliaetus*) and almost all the marsh birds (Virginia rails, *Rallus limicola*, marsh wrens, *Cistothorus palustris*, etc.).

Although none of these species have gone extinct on either a regional or global basis, the disappearance of so many different kinds of birds that once lived along the Lower Truckee before major human impacts constitutes an extraordinary loss of biological diversity at the local scale. Changes of this magnitude are of considerable concern for a number of reasons. First, as discussed above, if enough local populations continue to go extinct, the species is in danger of disappearing at larger geographic scales, and the trend may accelerate because of the disruption of the metapopulation structure and lack of immigrants to rescue declining populations. Secondly, at a local level, the loss of entire guilds of species (e.g., fish eaters, marsh birds) suggests that the riparian ecosystem itself has changed greatly, and that it may no longer function in the same way that it has in the past.

Although similar data were not collected by Ridgeway for other groups of animals, birds often are good indicators of the overall condition of the riparian system. If we can understand what factors have led to the loss of these species, we can perhaps manage the habitat in such a way as not only to restore the biological diversity of that habitat but also the overall health of the ecosystem.

As discussed above, when an individual population of birds goes extinct, it means that the number of births in that population has been lower than the number of deaths for an extended period of time, and that there have not been enough immigrants from other populations to make up the difference. If a management goal for a certain area is to maintain biological diversity in that area, then we can use population level theory as a guide to look for specific changes that may have already led, or are now likely to lead, to local extinctions. A consideration of the dynamics of bird populations in riparian areas suggests that at least four major factors may produce such large-scale losses of species: (1) loss of the total amount of habitat used by the species, (2) loss of specific resources needed by a species within the habitat, (3) change in the structure of the remaining habitat, and (4) loss of connectivity between existing habitat patches. Each of these can lead to a decline in birth+immigration rates and/or an increase in death+emigration rates. In terms of the populations models discussed above, the loss of the total amount of habitat effectively means there has been a decline in the amount of resources provided by that habitat for individual members of that population to either survive or reproduce. This means that the carrying capacity of the environment for the species in the local area is reduced, and in response, death rates will increase and birth rates will decrease until the population reaches a new equilibrium size with the available resources. However, if the amount of resources becomes too small, population sizes will decline to the point where demographic and environmental stochasticity become important, and the population is very likely to go extinct within a short time period.

Many people often assume that if we modify a habitat in such a way that it is no longer suitable for a species (for example, if a riparian forest is removed and it no longer provides the resources necessary for reproduction and survival), then animals that used to live in that habitat will simply go somewhere else. However, in most cases, the animals that exist in any other remaining suitable areas are themselves usually at or near their own carrying capacity, and as a result, most or all of the displaced individuals do not move, but simply die.

These types of changes can be illustrated by the Lower Truckee studies. For example, the marsh birds that used to occur along the Truckee probably nested and foraged in the wetland areas formed by oxbows and isolated meanders in the river, and these species disappeared when their habitat was destroyed by channelization of the riverbed or by the conversion of wetlands to agricultural fields. The absence of birds that specialized in eating fish (osprey, cormorants) is most likely the result of a decline of a specific resource—the native fish populations within the river, including two major species that themselves are now endangered: the Cui-ui (*Chasmistes cujus*), which once used the Truckee River during spawning runs, and Lahontan cutthroat trout (*Oncorhynchus clarkii henshawi*). In these situations, management to maintain or restore biological diversity is relatively straightforward: recreate the missing habitats (wetlands) in the riparian zones, or restore the specific resources (prey populations). Such actions will of course also restore the biodiversity of the many other animal and plant taxa that depend upon each habitat and/or resource.

In many cases, however, it may not be possible to determine a specific resource whose decline has led to the disappearance of a particular species. For example, many ground-nesting ducks had become locally extinct on the Lower Truckee by 1972, even though the food upon which these species depended presumably still was present. Similarly, a number of birds that feed upon insects were also gone, although there are many insects still found in the area. For these species, understanding the decline in biological diversity depends upon a consideration of the changes that occur in the riparian system, particularly as a result of grazing.

Herbivores such as cattle that feed in riparian areas will not only consume grass, they will also take any palatable forb, shrub, or small tree, including willows and young cottonwoods.⁴ For populations of cottonwoods and other trees in particular, continual consumption of seedlings by livestock prevents “births,” or new recruitment into the adult stages of the population. As a result, the age structure of the trees becomes older and older, until eventually the trees all die and are locally extinct. Thus the riparian area may change from a tree-lined stream or gallery forest to an open meadow, and eventually, if the water table also drops as a result of increased erosion, to a dry sagebrush or other shrubland. Not only will specific plants upon which many animal species depend disappear, the structure of the riparian habitat itself becomes radically different, changing from a structurally complex forest with a closed canopy and several intermediate vegetative layers to a very open and simple habitat comprised of small woody shrubs and sparse ground cover.

⁴See Pyke, this volume.

A number of studies, recently summarized by Martin (1992), provide strong evidence that changes in the structure of the vegetation itself can have a strong impact on the population level processes of many bird species. For example, many birds are more likely to be able to successfully reproduce in forest habitats than in shrub habitats: for example, in the studies surveyed by Martin (1992) the chance of producing a nest with one or more young for birds nesting on the ground in forest habitats was 60.3 percent compared to 47.4 percent for ground nesters in shrub habitats, and 46.3 percent versus 23.8 percent for birds nesting in the understory/shrub layers in the two types of habitats respectively. Similar differences exist in rates of nest parasitism by brown-headed cowbirds (*Molothrus ater*), a species that lays its eggs in the nests of other species. Because the host parents usually end up raising the young of the cowbirds (which are usually larger than the host young) at the expense of their own offspring, parasitism can have a major impact on the reproductive success of the host species. Martin (1992) found rates of cowbird parasitism tend to be much higher in birds nesting in shrub versus forest habitats: 12.2 percent versus 4.7 percent of the nests of birds nesting on the ground had cowbird young within them, and 23.3 percent versus only 1.9 percent of nests of birds using the understory/shrub layer.

Although the mechanisms behind these differences have not been demonstrated experimentally, it seems likely that predators and bird parasites have a more difficult time searching for and finding the nests of birds in the more structurally complex forest habitats. If grazing is intense in a riparian area, and the vegetation layers change throughout the system, rates of nest predation and parasitism will increase. And unless the resulting decrease in birth rates is balanced by an increase in adult survivorship (which is very unlikely, since the adults themselves also are subject to predation), then births will be less than deaths, and eventually the bird population will go extinct. This then suggests a second management goal: to restore structural complexity to the riparian system, in particular by ensuring that there will be sufficient ground cover, understory, and canopy layers to provide adequate nesting habitat that is safe from predators and avian parasites. As with the specific habitat and resource type restoration, the presence of structural complexity in a riparian area will also provide habitat and conditions necessary for the persistence of many other animal and plant species in addition to the birds themselves.

SUMMARY

Rangelands encompass a variety of habitats, each with their own particular community of animals. Much of the diversity of animals in western rangelands is found in riparian zones. These areas are usually extremely productive, and many different species of animal directly depend upon the resources provided by riparian habitats. In addition, because of their structural complexity, many other species that typically forage in upland areas also use riparian sites for cover, shade, and nesting sites. For example, recent study of the Mexican spotted owl (*Strix occidentalis lucida*) in the Southwest (Stacey and Hodgson, in preparation) indicates that this

species, which is normally thought of as strictly a bird of old-growth coniferous forests, may in fact be equally dependent upon mature riparian habitats as a place for the juvenile owls to hide from predators. It is possible that the widespread decline of this and many other species that we do not normally associate strongly with riparian areas may reflect changes in that habitat.

Because of their productivity, riparian habitats also are intensively used by humans. Many former riparian areas have been lost to rural and urban development, conversion to agricultural fields, and to highways and other transportation corridors. Most of the rest have been modified as a result of long-term use by livestock. This has led to four major changes that directly impact biological diversity of animal populations: (1) loss of total amount of habitat, (2) loss of specific subhabitats, such as the marshes that form in oxbows when the stream takes a new course, (3) loss of structural complexity, including entire vegetative layers such the tree canopy, and (4) loss of connections between habitats as the landscape becomes more fragmented. These changes often result in a major decline in local biological diversity, as in the Lower Truckee study discussed above. While very few species of higher vertebrates that occur on western rangelands have gone totally extinct on a regional or global scale (we know next to nothing about the status of most invertebrates), such widespread loss of local biodiversity is a cause for considerable concern. The basic functional unit of any species is the local population: when all local populations disappear the species itself is extinct. The process of regional and global extinction appears to accelerate as more local populations disappear (Stacey and Taper 1992, Stacey and Taper, in preparation). Management almost always occurs at the local or population level, and understanding the factors that influence local population processes, such as birth and death rates, and the ability of individuals to move between populations, can provide the land manager with specific tools and goals with which to maintain local biodiversity, and to restore populations of different species where they have disappeared (West 1993).

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Diversity Indices Applied in Desert Grassland Communities of Otero Mesa, New Mexico

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Abstract

To describe plant community (alpha) diversity on rangelands, managers are confronted with a variety of commonly used indices. The choice, performance, and interpretations of these indices are often not clear. Biodiversity indices were computed for a variety of plant communities in a desert grassland of southern New Mexico. Data consisted of reported importance values, range transect data for both grazed and ungrazed pastures, and search-and-find data specifically addressed to plant community diversity. Occurrence of threatened and endangered plants was considered by a weighting procedure. Performance of each diversity index was evaluated by ranking plant communities from low to high and comparing the rankings yielded by the various indices. Data based upon importance or dominance that omit plant species of lesser importance or dominance should not be the basis of comparisons for alpha diversity. Communities described by range transect data ranked differently depending upon the index used. The most practical measure of plant species diversity may be the number of species found by search-and-find procedures.

INTRODUCTION

Diversity is a characteristic of plant communities that indicates variation among a combination of properties such as number of species, life forms, cover values, patchiness, or densities. Diversity at the community or alpha level is defined as the number of plant taxa present in the community together with some measure of how common, abundant, or dominant these taxa are relative to each other (Magurran 1988). Sometimes usage of the term *diversity* is limited simply to the number of taxa present in the community (richness). Range managers acknowledge the importance of plant diversity in helping evaluate range condition or health (West 1993).

For describing diversity in plant communities, ecologists are confronted with numerous indices (Magurran 1988). It is not uncommon for managers to apply these indices to data already reported from inventories not expressly designed for estimating diversity, a fallacious practice as we illustrate in this paper. Different indices portray different attributes of the plant community and are sensitive to methods of sampling. Selection of a particular diversity index can support an underlying bias in favor of or against particular range community plant assemblages (West 1993). Can we speak of

plant diversity alone, without regard to other organisms, and make sense out of plant assemblages? In what ways are diversity measures value laden? How can managers or investigators use diversity indices for establishing management objectives? For example, how can the existence of threatened or endangered plants, clearly an important diversity element, be quantitatively assessed? Can diversity be used to describe "abundance" aspects of range communities, such as cover or biomass of forage plants?

One way of gaining familiarity with diversity indices and evaluating their usefulness is to compare the performance of some common indices across a variety of plant communities. Then diversity becomes a kind of "scorecard," somewhat akin to more familiar scorecards, such as ecological condition or forage production.

Here expressions of some common measures of community diversity are evaluated in a variety of desert grassland communities. Different measures are examined to rate both grazed and ungrazed communities, with and without adjustments for rare or endangered species. Several data sources are used to illustrate the kinds of data available to range managers and from which diversities are often computed. Results are compared by ranking different communities from low to high diversity according to the various diversity indices.

Indices are then evaluated for effectiveness in management interpretation.

METHODS

THE STUDY AREA

Otero Mesa is a vast (209,000 ha) grassland in the lower Tularosa Basin of southern New Mexico. Vegetation generally corresponds to the Shrub-Mixed Grass and Plains-Mesa Grassland Series (Dick-Peddie 1993). Only small portions of this grassland were studied, namely a 349-ha tract of ungrazed (by domestic livestock) grassland along State Road 506 and the two adjoining pastures known as McGregor range units 7 and 9 (BLM 1980). Details of the plant synecology in the ungrazed area were described by Stewart (1982) and Ludwig and Moir (1987). Range conservationists from the BLM (Bureau of Land Management) measured range condition in the pastures for purposes of computing allowable livestock numbers used in their lease bidding system (BLM 1980).

Vegetation in the areas studied is dominated by perennial grasses, mostly *Bouteloua eriopoda*, with a mixture of shrubs, succulents, perennial forbs, and annual plants (Table 1). The climate is semiarid, with summer rains accounting for over 50 percent of the mean annual precipitation of about 34 cm. Winter precipitation is erratic, but is especially important for C_3 plants (Neilson 1986). Mean annual temperature is about 14° C. A pedon in the ungrazed area of the study site indicated the soil to be a moderately deep, very cobbly Aridic Ustochrept developed from limestone parent material. Four soil series were described within the preserve tract (administered by New Mexico State University under a cooperative agreement with BLM and the Department of Defense). All soils are calcareous throughout their profiles. The principal differences between these steppic soils are primarily the solum depth, texture, and development and erodibility of the A1 horizon (Soil Conservation Service data contained in BLM 1980).

DATA SOURCES AND COMPUTATIONS

Several vegetation data sources were used in this study (Table 1). The proportionate values in the body of Table 1 can be multiplied by totals at the bottom of each column to obtain actual values reported in the different data sources. Data for five plant communities came from summary tables in Stewart (1982). Her tabular reports included only those plant taxa having the greatest importance, calculated as the sum of relative density, relative frequency, and relative cover for each plant taxon. We use these data as an example of available data from which diversity is sometimes computed. The second source of data was BLM transects from permanent Parker three-step clusters in pastures grazed by cattle. The transect indicated as BLM-8 was in the McGregor Range unit known as the Mesa Horse Camp (MHC) pasture; transect BLM-9 was in the unit known as the Rutherford Winter pasture. Range conditions of the plant communities represented by these transects were respectively "good" and "fair" as calculated using BLM standards.

Finally, in late July 1990 several areas were sampled by procedures expressly designed for obtaining estimates of vascular plant community (alpha) diversity. These were time-controlled search-and-find techniques. The first exercise was to search exhaustively (by essentially random walking) an approximately 0.2-ha area in the Mesa Horse Camp pasture (Plot MHC-1). All vascular plants were tallied during two hours of searching (computed on the basis of one person searching). Canopy coverage (Daubenmire 1959) was assigned to each plant taxon using subjective visual estimates rather than measurements from quadrats. This method seemed justified, since interest resided in both the richness and evenness components of diversity rather than actual cover, biomass, or frequency. This sampling "overkill" was far in excess of the time that would be spent measuring range condition and trend by the standard procedures used by BLM. The intention was to obtain a seasonal measure of maximum alpha diversity.

The second search-and-find procedure took place in paired 0.2-ha plots, one of them (MHC-2) in the Mesa Horse Camp pasture and the other one (NA-506) in the natural area along highway 506. Each search was limited to 20 minutes (by a single searcher). At the end of that time each plant taxon was assigned a subjective abundance class based on cover (5 = abundant, 4 = very common, 3 = common, 2 = uncommon, 1 = rare). We consider this method more practical than that used in the first search-and-find procedure, because a range conservationist could sample the diversity of numerous plots during a working day.

The search-and-find exercises occurred July 19, 1991, about eight days after the onset of summer rains. Warm-season vegetation was greening up, and one ephemeral species, the zephyr lily (*Zephyranthes longifolia*), was in fruit dispersal phenology.

We computed several conventional indices of diversity (Magurran 1988) for each data set using AID (analysis of information and diversity) programs developed by Overton et al. (1987). The diversity indices are given in Table 2, using notation of Overton et al. (1987). Diversities were computed from proportionate values of each taxon (Table 1) in order to minimize differences in sampling or reporting methods.

Rare, endemic, or threatened plants are major biodiversity concerns among many biologists and publics. One of these in particular, *Toumeyia papyracantha* (grama grass cactus), is considered a diversity element warranting special management to ensure that adequate numbers will be maintained *in situ* (Spellenberg 1993). For computing weighted measures, a coefficient, w_j , was assigned to all plant taxa. This allowed additional weights to be assigned to *Toumeyia*, such that the sum of the weights is equal to N_j , the total number of taxa in plot j . The exact weight given to *Toumeyia* is not important for our purposes, although we note the probability of occurrence, p_j , is very small, and therefore the weights to be effective must be relatively large. We assigned weights of 1.0, 7.5, and 15 to this cactus. The results are reported respectively as plots MHC-1w0, MHC-1w1 and MHC-1w2 in Table 3.

If *Bouteloua eriopoda* declines on poor ranges, so does *Toumeyia*, which depends especially upon the cover of this grass for survival (Fletcher and Moir 1992). Since this grass

TABLE 1. PLANT COMMUNITIES AT OTERA MESA, NEW MEXICO. THE VALUES IN THE BODY OF THE TABLE ARE PROPORTIONATE VALUES. TO COMPUTE REPORTED VALUES (BY DIFFERENT WORKERS), MULTIPLY THE PROPORTION FOR EACH TAXON BY THE TOTAL AT THE BOTTOM OF EACH COLUMN.

Taxa by growth forms	SPAINOS	EULALAT	LATRBO1	LATRBO2	LATR-FL1	BLM-8	BLM-9	MHC-1	MHC-2	NA-506
SHRUBS > 0.5 m tall										
Atriplex canescens					0.007					0.016
Ephedra trifurca				0.003	0.030			0.001	0.015	0.032
Flourensia cernuum		0.135	0.001	0.075	0.180			0.049	0.076	0.079
Larrea tridentata								0.005	0.080	0.016
Prosopis juliflora										0.016
Senecio longilobus								0.005	0.030	0.016
Yucca elata	0.001	0.001	0.001	0.001						0.016
SHRUBS < 0.5 m tall										
Croton pottsii		0.039	0.001	0.010	0.005			0.097	0.076	0.064
Dalea formosa		0.001	0.001							0.016
Dyssodia acerosa		0.002	0.035	0.051			0.034	0.010	0.046	0.032
Eurotia lanata		0.021						0.005	0.030	0.048
Gutierrezia sarothrae		0.011	0.091	0.074	0.057	0.177	0.283	0.073	0.076	0.016
Parthenium incanum					0.002			0.001	0.015	0.016
Zinnia grandiflora								0.001	0.015	0.016
BUNCH GRASSES										
Aristida arizonica										0.032
Eriogonum pulchellum	0.034							0.010	0.080	0.016
Hilaria mutica										0.016
Muhlenbergia porteri										0.048
Setaria macrostachya										0.048
Sporobolus airoides	0.527							0.073	0.046	0.048
Sporobolus flexuosus										0.048
Unidentified										0.048
Aristida sp.										0.048
MAT GRASSES										
Bouteloua eriopoda		0.554	0.746	0.582	0.122	0.543	0.031	0.487	0.076	0.079
Bouteloua gracilis		0.071	0.050	0.044	0.086	0.008	0.125	0.010	0.030	0.064
Bouteloua hirsuta							0.018			
Unidentified						0.004	0.005			
Muhlenbergia arenacea				0.046	0.168		0.019	0.001	0.015	0.032
Muhlenbergia arenicola						0.021	0.050	0.010	0.030	0.016
Muhlenbergia torreyi						0.017	0.027	0.001	0.015	
Panicum obtusum							0.019			
Scleropogon brevifolius	0.069				0.166					
RHIZOMATOUS FORBS										
Leersia ericoides										0.016
Perezia nanum	0.037		0.003					0.010	0.030	0.064
Desmanthus								0.049	0.061	0.032
Polygala sp.		0.036						0.073	0.046	0.016
Sphaeralcea sp.								0.001	0.015	0.016
Unidentified										0.016

TAPROOTED FORBS Haploappous spinulosus Lesquerella fendleri Lesquerella montana Lepidium sp. Linum sp. Thelyperma sp.	0.015 0.045	0.010 0.001 0.001 0.001	0.030 0.015 0.015 0.015	0.048 0.016
BULBOUS FORB Zephyranthes longifolium		0.001	0.015	0.016
TALL SUCCULENTS Opuntia leptocaulis Opuntia spinosior Opuntia phaeacantha	0.052	0.010 0.005	0.046 0.030	0.016 0.016 0.032
DWARF SUCCULENTS Echinocereus viridiflorus Tourneya papyracantha		0.001 0.015	0.015	
NON-VASCULAR PLANTS Cryptogams				
		0.177		
		0.114		
		88.0 10	72.0 9 good	
		0.072		
		77.9 9	87.4 11	
		0.128		
		92.4 11		
		0.218		
		94.8 7		
Total Count (all taxa)		100.0 30	101.0 29	102.7 32

was already dominant, a special weight for it was considered unnecessary for maintaining the endangered cactus.

After computing diversities for each community sample, the communities were ranked from low to high for each diversity index within each of the data sources. The rankings are given by the sequence of communities (abbreviated as numbers) in the columns of Table 3. The last column gives an averaged rank order from low to high of the numbered communities across all the indices.

RESULTS

The easiest measurement to obtain in the field is the number of taxa present, or simple richness. To be useful in comparing different sites, count rules must be fixed, because the number of plant taxa counted will depend upon time spent observing as well as the area covered. Communities one through five in Table 3 were sampled by Stewart (1982) using fixed rules, but her tabular reports included only those plant taxa having the greatest importance values. Community five (LATR-FL1 in Table 3) was ranked the most diverse by all measures; this community was high in reported taxa, and most taxa had relatively even and rather low importances ($p=.002-.177$). Community three (LATR/BOER1) was ranked least diverse by most measures. This community had low evenness, expressed particularly by the high importance of *Bouteloua eriopoda* ($p=.746$). We note that the Simpson and McIntosh evenness measures (J[SDI] and J[MDI]) have opposite interpretations, the former ranking community three relatively high, the latter ranking community three low. The other communities were sequenced four, two, one between communities three and five by Simpson's diversity index (SDI) and the McIntosh evenness measure (J[MDI]). By contrast, the information measure (HE) and McIntosh diversity (MDI) ranked these communities in opposite order between communities three and five. The Simpson evenness measure (J[SDI]) ranked communities one through four in a sequence different from rankings under the other measures.

What does all this mean? When few taxa are reported, community diversity measures (except richness) become overly sensitive to evenness (given in Table 1 as proportionate importance). Evenness, and thus diversity, can be reported as high or low, depending on the choice of measure used (e.g., J[MDI] or J[SDI]). Because Stewart reported so few taxa in each community, each of the seven diversity measures in Table 3 is unreliable. Community one with the fewest reported taxa jumps around in the rankings depending upon the diversity measure. Community five consistently ranks highest. For censored data, i.e., reports that omit plant taxa, different interpretations of diversity could be made for any plant community. For this reason (which was not clear at the onset of this study), data in which plant taxa inclusion is based upon importance or dominance and that clearly underrepresent the number of plant taxa in the community should not be the basis for comparisons of diversity.

The two BLM plots had nearly consistent ranks relative to each other, with the community rated as fair (BLM-9) mostly ranking above (more diverse than) the community rated as good (BLM-8). We note that the Simpson evenness

TABLE 3. RANKINGS OF NUMBERED PLANT COMMUNITIES BY VARIOUS DIVERSITY INDICES (COLUMNS 2-8). THE RANKINGS ARE WITHIN EACH OF THREE DATA SOURCES INDICATED BY THE SEPARATED ROWS. THE LAST COLUMN RANKS THE NUMBERED COMMUNITIES BY AVERAGING OVER ALL THE INDICES.

Numbered Community	Individual Rank Order							Average
	N	HE	SDI	MDI	J(H)	J(SDI)	J(MDI)	Rank Order
1 SPAI/Nostoc	1	3	3	3	3	2	3	3 LATR/BOER1
2 EULA/LATR	3	1	4	1	2	4	4	4 LATR/BOER2
3 LATR/BOER1	4	2	2	2	4	1	2	2 EULA/LATR
4 LATR/BOER2	2	=4	1	4	1	3	1	1 SPAI/Nostoc
5 LATR-FLCE	=5	5	5	5	5	5	5	5 LATR-FLCE
6 BLM-8 good	6	6	6	6	6	7	6	6 BLM-good
7 BLM-9 fair	7	7	7	7	7	6	7	7 BLM-fair
8 MHC-1w0	11	8	8	10	8	9	8	8 MHC-1w0
9 MHC-1w1	8	9	9	9	9	8	9	9 MHC-1w1
10 MHC-1w2	=9	10	10	8	10	10	10	10 MHC-1w2
11 MHC-2	=10	11	11	11	12	11	12	11 MHC-2
12 NA-506	12	12	12	12	11	=12	11	12 NA-506

SPAI=*Sporobolus airoides*, EULA=*Eurotia (Ceratoides) lanata*, LATR=*Larrea tridentata*, BOER = *Bouteloua eriopoda*, FLCE=*Flourensia cernua*, MHC=Mesa Horse Camp pasture, NA=natural area along state road 506, w = weighted for *Toumeyia papyracantha*, numbered communities preceded by = have the same diversity as the community above.

Ranks within community groups (1-5,6-7,8-12) are ordered from lowest to highest diversity.

measure reversed the ranking: the community with greater dominance (in this case BLM-8 with *Bouteloua eriopoda* having $p=0.543$) ranked higher than the community (BLM-9) with greater evenness. The chosen diversity measure again affected the ranking. Unlike the five communities with censored data, the ranked differences in the two BLM communities can be explained most simply by differences in the number of reported taxa. BLM-9 had considerably more reported taxa than BLM-8 (Table 1). Unfortunately the BLM plots suffer the same problem as the data of Stewart. Only those plants measured along the transect are reported. Finally, we note that the BLM ratings of good and fair, based (in those days) upon the presumed successional status of the community, are not the same as ratings based upon diversity. The better of the two samples from a livestock forage viewpoint (which was assumed to relate to successional status) was the poorer on the basis of plant diversity.

The Mesa Horse Camp plots (MHC-1, MHC-2) and the natural area plot (NA-506) were specifically sampled for diversity, and had considerably more reported taxa than the

plots discussed above. Interestingly, plot MHC-1, which had a two-hour search, was the least diverse by all except the richness measure (N) of Table 3. This was the case regardless of assigning various weights to the endangered cactus, *Toumeyia*. Plots MHC-2 and NA-506, which were measured by a time-limited search-and-find technique, appeared in the field to have about the same plant diversity. However, NA-506 ranked higher by all the measures except the McIntosh and Pielou evenness measures (J[MDI] and J[H]). Since each had about the same number of taxa (30-32), the relative scores reflected the evenness (or dominance) component of diversity. The MHC-2 plot had four dominant taxa (*Larrea tridentata*, *Bouteloua eriopoda*, *Croton*, and *Gutierrezia*); the NA-506 plot had one dominant taxon (*Bouteloua eriopoda*) and thus was more uneven in diversity. We also note that plots MHC-1 and MHC-2 contained small cacti, but not NA-506, which had a higher diversity ranking in most instances. Structural diversity is not provided for in the equations of Table 2, although it may influence other kinds of diversity such as avian community diversity.

DISCUSSION AND CONCLUSIONS

Diversity indices at the plant community level have their interpretative limitations (West 1993), and this study shows no exceptions. Nevertheless, it is becoming increasingly important for managers to know the kinds of biological diversity existing on lands they manage (Probst and Crowe 1991). The performance of indices across the various communities in this study has yielded different results. How do managers choose an index without some bias? We propose that the simplest measure is perhaps the most useful in yielding interpretations and making comparisons. Simply count the number of plant taxa present using a standardized procedure. The richness column of Table 3 (N) is easily understood and easiest to obtain for an individual familiar with the flora.

However, a mere count of the number of taxa is also of limited interpretative or management value. A grassland with mostly adventive plants has a meaning different from that of another with the same number of mostly native plants. Undesirable taxa (for whatever reason) are no different in their count than preferred taxa (although one approach would be to give them negative weights). Indeed, all the indices studied here have a similar disadvantage: the index gives no insight to the content of the sample, but it is the content that we are most interested in. A pasture dominated by *Gutierrezia* and with little *Bouteloua* might have the same evenness and richness measures as a pasture dominated by *Bouteloua* with little *Gutierrezia*. But each pasture has different management implications.

This study reveals other limitations to common diversity measures. If estimates of alpha diversity are specifically intended, then data collected to sample productivity, range condition, or ecological status (conventional scorecards) seem inappropriate as surrogates. If diversity estimates as such are needed, then a single visit to a sample plot may also be insufficient, because of the seasonality of plant expression (e.g., West and Reese 1991). For example, *Toumeyia*, which mimics grama grass in form, is best sampled when flowering, because of the difficulty of finding it at other seasons.

Can diversity scorecards be developed that provide for specific elements of diversity according to some kind of social or cultural standard? We increased values of community diversity in community MHC-1 by giving more and more weight to the endangered grama grass cactus (but the higher weights did not change its rank). It remains to be tested how far one can go with weighting. Instead, maintaining a viable population of the endangered cactus may in itself be a sufficient diversity criterion for management not requiring any diversity index. A desired landscape description might include maintaining special populations, or high alpha plant

diversity with a stand, or high overall primary production each in different areas. This elevates the description of diversity to a landscape (or beta) level where various social and cultural values can be accommodated. In such a case community diversity must be evaluated in the context of landscape diversity.

The performance of diversity measures across different communities suggests that sampling only for diversity cannot replace sampling for other community properties such as productivity or ecological succession (West and Reese 1991).

In summary, there was no single diversity index that served as a best measure of the true diversity (as defined in the introduction) in the desert grassland communities examined. In our opinion the most practical estimates of site or pasture diversity can be obtained by simply counting the number of plant species present in the samples. This is emphasized because of the common approach taken today: that of using various equations with species cover or biomass data in indices of diversity. Yet, the output of these equations bears no relationship to the true diversity of a given community. For instance, one gram of biomass of one species is not ecologically equivalent to one gram of biomass of another species. The same is true for units of species ground cover. Is the function of the two species in the system the same? Are the two species ecologically equivalent within the system? Presently, diversity indices are not related to any known ecological or community theories. Neither do these indices provide "value" (i.e., importance) in comparison of plant communities. Yet, this is precisely what is needed.

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Diversity of Animal Communities on Southwestern Rangelands: Species Patterns, Habitat Relationships, and Land Management

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Abstract

The rangelands of the southwestern United States comprise a mosaic of biome types, including deserts, grasslands, chaparral, woodlands, forests, subalpine meadows, and alpine tundra. Taken together, these ecosystems support exceptionally high numbers of vertebrate and invertebrate animal species. Biogeographic patterns of mammal, bird, and reptile species across North America show trends of increasing species numbers from the Arctic to Central America. Within the conterminous United States, maximum species numbers for these vertebrate groups, and some invertebrate groups, occur in Texas, New Mexico, Arizona, and California, especially in the border region with Mexico. Underlying causes of the region's high biodiversity are related to (1) the elevational variability inherent in the basin-and-range topography, with its concomitant range of climatic conditions, (2) the diverse biogeographic history of the region, particularly with respect to the merging of major faunal groups during glacier retreats, and (3) the architectural variations in vegetation structure across the region's component ecosystems.

Climate dynamics and disturbance also play major roles in maintaining a habitat mosaic, promoting greater regional faunal diversity. Disturbances affect animal diversity at many scales, from individuals' home ranges to continental species' distributions. Human activities have generated new suites of disturbances (livestock grazing, timber harvesting, mining, agriculture, prescribed fires, construction of roads and buildings), many of which contribute to the habitat patchiness of the landscape. Studies have shown that these disturbances prove beneficial to some species and detrimental to others. Hence, local increases in biodiversity can be orchestrated by creating or maintaining habitat diversity and disturbance regimes. Such management strategies can be scaled up to regional landscapes, in which areas of intensive human land use and disturbance are interspersed with regions of little or no human interference. Historically, this has been accomplished at local or state levels on an ad hoc basis (i.e., crisis management), with little evidence of long-term, large-scale, regional planning or coordination.

If faunal biodiversity is to be preserved and enhanced on southwestern rangelands, human activities must be managed in a fashion that integrates faunal biology, resource requirements, and movement patterns with landscape scale attributes. Therefore, the task of the modern land manager will be to balance carefully the various scales and intensities of human activities, for the purpose of promoting sustainable use of natural resources and assuring the maintenance or enhancement of biodiversity. Future regional planning for biodiversity attributes will clearly require extensive communication and close cooperation among concerned citizens, private landowners, scientists, and government land managers.

INTRODUCTION

Variation and diversity are essential elements in the maintenance of populations, species, communities, ecosystems, and the entire biosphere. The natural complexity of biological systems serves as a buffer against dramatic change, as well as maintaining the necessary ingredients for life. This diversity also plays a significant role in the affairs of our

species, as we extract foods, medicines, fibers, and fuels from plants, animals, and microbes. However, the level of diversity for many important groups of organisms is unknown even in North America, and the mechanisms that sustain many important groups of organisms remain problematic. At the same time we are experiencing a loss of biological diversity that is unprecedented. The National Science Board (1989) has estimated that at current rates of extinction, 25 percent or more of the Earth's species will be lost during the next decade.

This paper provides a review of species diversity patterns of some of the terrestrial animals across the western United States, and discusses some of the causes for these patterns. In addition, the role of disturbance in creating new assemblages of animal species is discussed. Finally, we provide a summary of management implications for land use planners and managers with respect to the maintenance of faunal biodiversity.

SPECIES PATTERNS IN TERRESTRIAL VERTEBRATES

At a regional scale, animal species diversity in the Southwest is among the highest in the United States. This is perhaps best illustrated by continent-wide or nationwide "contour maps" of species richness. These maps, which are now available for mammals (Simpson 1964), birds (Cook 1969), reptiles (Kiestler 1971), and some groups of arthropods (Otte 1981, Noonan 1990, Pearson and Cassola 1992), are based on the total number of species that occur within the squares of an arbitrary grid, usually 160 or 241 km (100 or 150 miles) on a side. These maps show that species diversity in all of the above groups is high in the southwestern and Intermountain states.

In virtually all groups of animals and plants that have been studied, there is a pronounced gradient of increasing diversity from the Arctic to the tropics. Within the United States many groups attain their highest diversity along the border between Mexico and Arizona/New Mexico/west Texas. In mammals, species richness in this region is equaled only

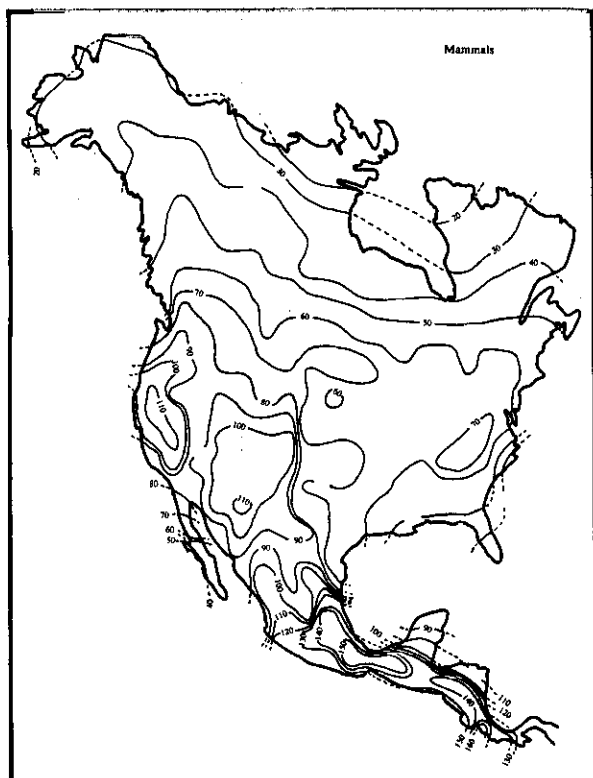


Figure 1. Contour map of mammal species richness in North America (from Simpson 1964, with permission).

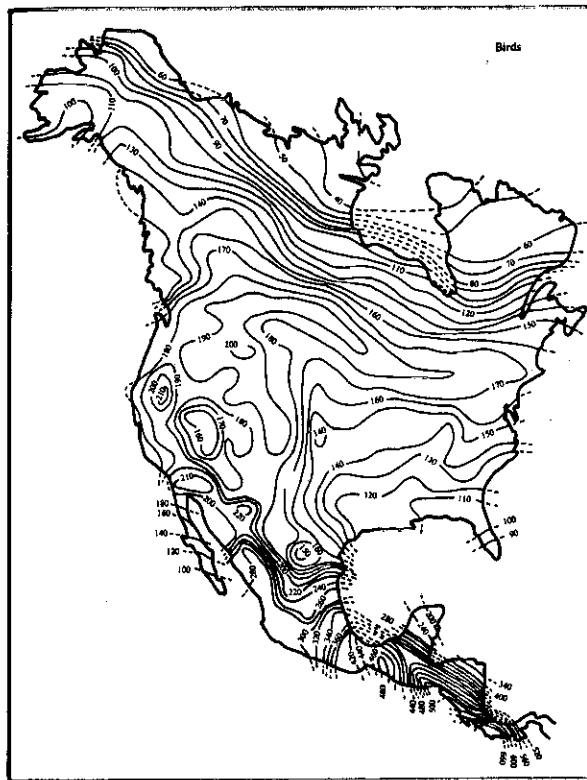


Figure 2. Contour map of bird species richness in North America (from Cook 1969, with permission).

by that in central California (Figure 1). Birds show a similar pattern, with species diversity along the Mexican border equaled only by that in central California and in extreme southern Texas (Figure 2). Again, in reptiles, species diversity is very high along the Mexican border, perhaps slightly higher only in eastern Texas (Figure 3).

These geographic patterns are obviously very similar in the different groups of terrestrial animals. They probably also hold for many groups that have not yet been studied. The only kinds of animals that exhibit conspicuously different geographic patterns of diversity are aquatic and semiaquatic, and perhaps some kinds of organisms occurring in mesic environments. Thus, for example, freshwater fishes and amphibians attain their greatest diversity in the United States in the southeastern states.

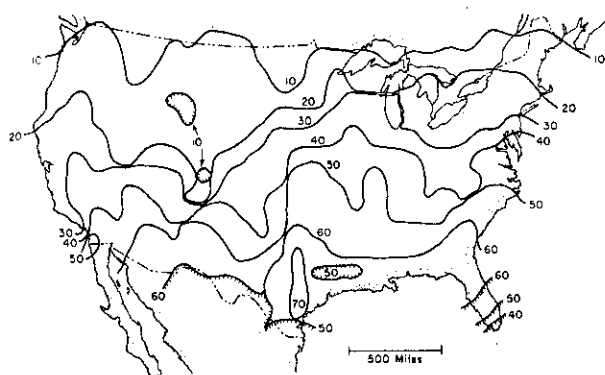


Figure 3. Contour map of reptile species richness in North America (from Kiestler 1971, with permission).

TABLE 1. SPECIES RICHNESS ON THREE SPATIAL SCALES IN THE SOUTHWESTERN UNITED STATES.

Patch Size	Mammals	Land Birds	Lizards
Study plot, Portal, AZ (~ 1 km ²)	36	102	21
Chiricahua Mountains, AZ (~ 320 km ²)	58	221	30
Sevilleta LTER Sites, Socorro Co., NM (~ 12,800 km ²)	70	284	25

Diversity of terrestrial animals in the Southwest is also spectacularly high at smaller spatial scales. This is illustrated in Table 1, which compares the number of terrestrial mammal, land bird, and lizard species on three scales: (1) within small patches containing one square kilometer or less of relatively uniform habitat in southeastern Arizona or southwestern New Mexico; (2) within the Chiricahua Mountains and the immediately surrounding desert and grassland, an area of about 320 km² in southeastern Arizona; and (3) within the 12,800 km² of Socorro County, New Mexico (site of the National Science Foundation Sevilleta Long-Term Ecological Research Program [LTER]). Note that the number of species of both mammals and birds increases with the increasing area sampled. The exception, the smaller number of reptiles in the Sevilleta site than in the Chiricahua Mountains, presumably reflects the high diversity of reptiles in warm, low elevation, desert shrub habitats since mountainous habitat is not included there.

The spectacular diversity on small scales is also illustrated by the following anecdote. An experimental research area in extreme southeastern Arizona, studied by J. H. Brown, contains just 20 ha (about 50 acres) of relatively homogeneous Chihuahuan Desert shrub habitat. In 15 years of trapping and observation at this site, 23 species of native rodents have been recorded (see Brown and Heske 1990a). This number equals the total number of rodent species in the entire states of Michigan and Pennsylvania, and the totals for these latter states include two introduced species (house mouse and Norway rat) and two semiaquatic species (muskrat and beaver).

SPECIES PATTERNS IN TERRESTRIAL ARTHROPODS

Little is known about the diversity of arthropods on southwestern rangelands. The available data indicate that species diversity for most groups of rangeland arthropods is higher in the Southwest than in other parts of the country. The discussion below will focus on certain groups of arthropod herbivores (grasshoppers), predators (spiders, ants, ground beetles), and detritivores (tenebrionid beetles, termites, millipedes).

The above-listed members of the three trophic groups are not only important components of rangeland ecosystems, but are also some of the most extensively researched arthropods

in the Southwest. Insects of the southwestern rangelands are often thought of as agricultural pests because of the economically costly forage consumption by some species. Rangeland entomology is a field of research aimed at understanding the biology and management of rangeland insect pests. Good reviews of important rangeland insect pests and research on those insects are found in Capinera (1987) and Watts et al. (1982, 1989).

The pest species that are included in the above-cited literature represent only a small fraction of the insects and other arthropods that occur on southwestern rangelands. Most species are not agricultural pests, many are rare, and many are beneficial components of rangeland ecosystems. Arthropod detritivores have important roles in the decomposition of dead plant material and nutrient cycling (Crawford 1981, 1986, Walter 1987, MacKay 1991, Zak and Freckman 1991). Plant-feeding insects may even have an important role affecting the rates of nutrient cycling (Lightfoot and Whitford 1990).

HERBIVOROUS ARTHROPODS—GRASSHOPPERS

Many different species and trophic groups of plant-feeding insects occur on southwestern rangelands (Wisdom 1991, Crawford 1981, Watts et al. 1989). Of these, grasshoppers are among the most prevalent and conspicuous. A considerable amount of research has been conducted on grasshoppers throughout the Southwest, and more is known about the diversity and biology of grasshoppers than about other rangeland plant-feeding insects. For these reasons, the following discussion will focus on grasshoppers as representative rangeland herbivores.

In North America, grasshopper species diversity is highest in the Southwest. Otte (1981) demonstrates that species densities of slant-faced grasshoppers (Gomphocerinae, primarily grass-inhabiting and -feeding grasshoppers) average around 30 species for locations in the Southwest, compared to 5–20 for most of the rest of North America (Figure 4). The numbers of all grasshopper species recorded in the states of California (211 spp. [Strohecker et al. 1968]), Arizona (175 spp. [Ball et al. 1942]), and New Mexico (166 spp. [Richman et al. 1994]), are higher than numbers from other western states, e.g., Colorado (133 spp. [Capinera and Sechrist 1982]), Nevada (88 spp. [LaRivers 1948]), Montana (93 spp. [Hebard 1925]), and South Dakota (96 spp. [Hebard 1928]).

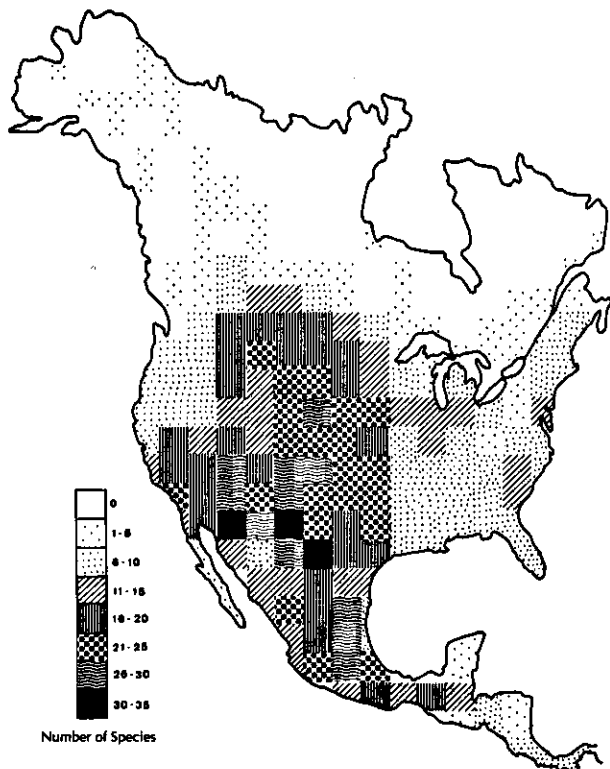


Figure 4. Map of species richness patterns of gomphocerine and acridine grasshoppers in North America (from Otte 1981, with permission).

PREDATORY ARTHROPODS—SPIDERS, BEETLES, AND ANTS

Spiders form a major part of the arthropod fauna of the Southwest, but, as is the case with many other arthropod groups, the total number of species in the region is still unknown (Gertsch 1979). In a study of desert shrublands, spiders comprised 25 percent to 40 percent of arthropod species (Chew 1961). Over 100 ground-dwelling spider species have been collected from Socorro County, in central New Mexico, in habitats ranging from riparian areas to mountain tops (S. Brantley, unpublished data). In a recent review of the status of arthropod systematics, Schaefer and Kosztarab (1991) estimate that most of the United States species of arachnids (and insects) that are still undescribed occur in the desert and montane Southwest and Great Basin areas.

The carabids are a large and diverse group of ground-dwelling beetles, with more than 2,200 species in North America (Borror et al. 1981). Species in the genus *Harpalus* reach their highest species richness (31 species) in the southern Rocky Mountains (Figure 5), where the beetles are found on mountain slopes or mesa tops at elevations of 2,000 m or higher (Noonan 1990). The distribution of the beetles seems to be limited by the higher temperatures and lower precipitation of the desert regions between the mountains. The higher elevations of this region also hold the largest numbers of endemic species in North America (Noonan 1990).

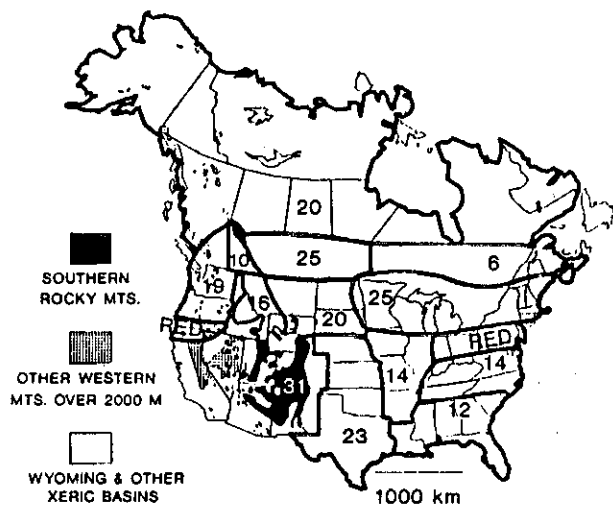


Figure 5. Map of species richness patterns of the ground beetle genus *Harpalus* (Carabidae), in North America (from Noonan 1990, with permission).

The tiger beetles (Cicindelidae) are relatives of the Carabidae and are also predators. The family is found worldwide, but many species have restricted distributions. In North America, the Rocky Mountains and Great Plains contain the highest numbers of species, 15–20 (Figure 6), compared with 10 for New England and 15 for the Middle Atlantic states (Pearson and Cassola 1992).

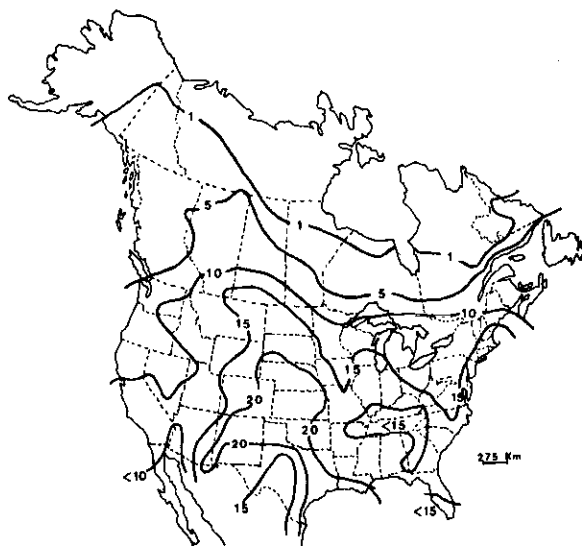


Figure 6. Contour map of tiger beetle (Cicindelidae) species richness in North America (from Pearson and Cassola 1992, with permission).

Ants are the dominant arthropod predators (on other arthropods and on plant seeds) in some ecosystems (Hollдобler and Wilson 1990). In some areas of the Chihuahuan desert there may be as many as 4,000 ant colonies per ha. In arid regions the numbers of species range from 23 to 60 (MacKay 1991), with 59 species found in one California canyon alone (Wheeler and Wheeler 1973). Ants originated in tropical areas and spread into temperate habitats. Many of the species found in the western United States are not unique to the region (Hollдобler and Wilson 1990).

DETRITIVOROUS ARTHROPODS

Darkling beetles (Tenebrionidae) are more diverse in western arid lands than elsewhere in North America and are major detritivores in the Southwest (Crawford 1990). Other southwestern macrodetritivores that compare favorably in richness with similar species in wetter zones include camel crickets (Hubbell 1936), scarab beetles (Scarabaeidae), and click beetles ("wireworms," Elateridae) (Crawford 1990). Native cockroaches comprise several genera, fewer than in other parts of North America (Crawford 1990). Millipedes are represented by a few very large-bodied species and more small-bodied species, but species richness is greater in wetter regions (Crawford 1979). Introduced isopods also have lower richness than in mesic areas (Muchmore 1990), but are very abundant in restricted habitats. Termites have low species richness (up to a dozen species in the southwestern United States) but may be the greatest regional consumers of net primary production (NPP) (MacKay 1991). Bristletails (microcoryphians) and silverfish (thysanurans) are well represented in the American Southwest, but poorly known taxonomically (Crawford 1990, Ferguson 1990). Pulmonate gastropods are an inconspicuous but species-rich group of omnivores/detritivores in the Southwest (Crawford 1990).

Soil- and litter-inhabiting mites and nematodes (in all consumer guilds) (Zak and Freckman 1991) and collembolans (springtails—mainly fungivores) (Crawford 1990) occur in vast numbers and are species-rich in nearly all southwestern habitats. The ratio of prostigmatid to cryptostigmatid (oribatid) mites in the Southwest, as in other arid regions, is relatively high (MacKay 1991).

GENETIC BIODIVERSITY IN THE SOUTHWEST

The southwestern region of North America harbors an exceptionally rich biota due to the complexity of habitat variation and the complex geological history of the region. Most range managers or even amateur naturalists are aware of the changes in species diversity across the Southwest and of the variation that is evident in color and size of organisms within a species from different parts of these species' ranges. What this variation means from a diversity standpoint has long been an area of debate among scientists, and many suspected that, once sufficient technology became available to allow an examination of the underlying genetics of these species, much of this variation would be found to be environmentally induced. During the past decade, however, the technology became available to allow a critical examination of diversity at the level of the gene, and, surprisingly, the opposite was found to be true in many cases. For example, a little over 4,000 species of mammals were recognized worldwide when the first edition of *Mammal Species of the World* (Honaki et al. 1982) was published. Ten years later, over 4,600 species are recognized, and the number is still growing.

If one applies this level of genetic analysis to all groups of organisms, the biodiversity analysis problem quickly becomes enormous. Approximately 1.4 million species of plants and animals have been named worldwide, but many biolo-

gists believe the actual number may be from 5 to 80 million (National Science Board 1989). Although many of the newly described species are from poorly known regions of the world, such as tropical rain forests, many are from well-studied and developed portions of the world, including the southwestern United States.

The degree to which variation in phenotype can be used as an accurate measure of species diversity varies from group to group. There are many cases where it can be highly misleading. For example, pocket gophers (Geomyidae) are common mammals in southwestern rangelands. Morphologically they are highly cryptic and difficult to distinguish without careful examination (Figure 7). Genetically, pocket gophers are among the most variable of mammals, especially chromosomally (Patton and Sherwood 1983). Three genera and seven species occur in New Mexico alone, and new species are still being described (Baker et al. 1989).

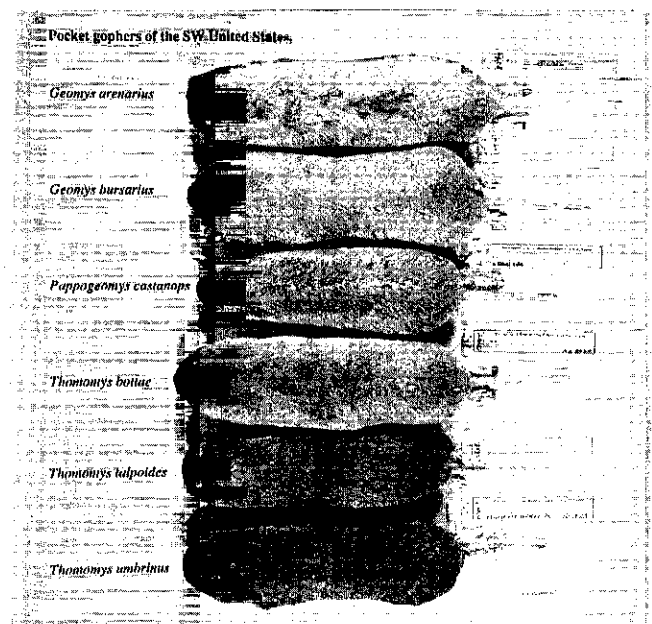


Figure 7. Museum specimens of pocket gophers (Geomyidae) of the Southwest (not shown: *Geomys atwateri*).

Numerous species of mammals have been discovered in the Southwest over the last decade using modern genetic analyses. For example, those found to occur in New Mexico include a new species of grasshopper mouse, *Onychomys arenicola*, a new form of meadow-jumping mouse, *Zapus hudsonius* (Hafner et al. 1981) along with a new species of parasite from the new host (Duszynski et al. 1982), and a new species of deer mouse, *Peromyscus gratis* (Modi and Lee 1984). Species from the latter genus represent another morphologically cryptic group, and yet there are currently 11 species that occur in New Mexico and Arizona (Figure 8). Not only are these species morphologically difficult to distinguish but, in contrast to pocket gophers, all have the same number of chromosomes ($2n=48$), requiring even more refined techniques to distinguish them (Yates et al. 1979).

The Southwest has many other examples of species that are highly variable morphologically but conservative genetically. Figure 9 offers three such examples. Within some

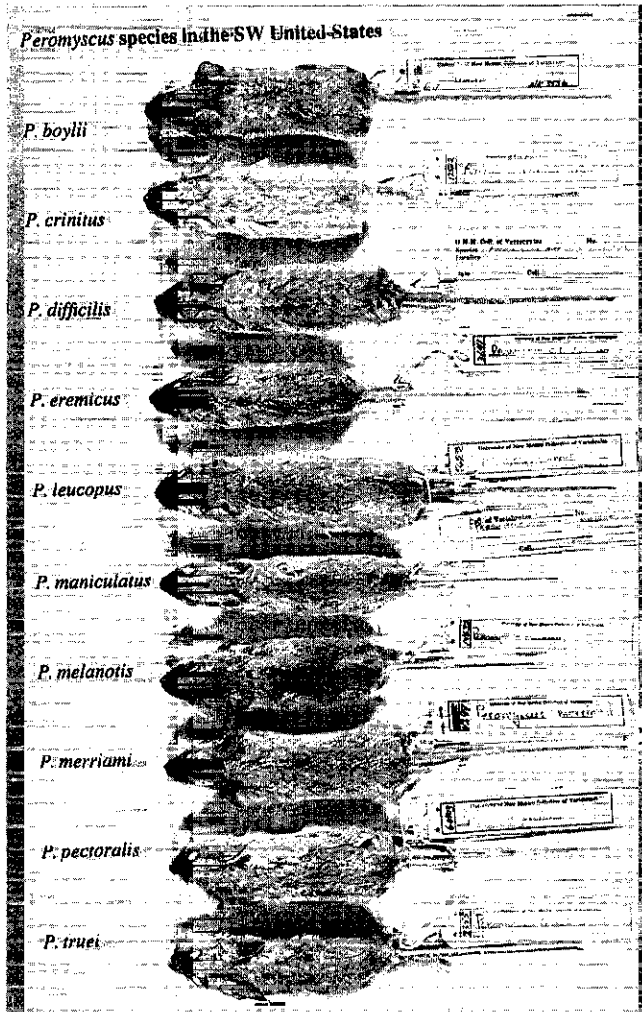


Figure 8. Museum specimens of mice in the genus *Peromyscus* from the Southwest (not shown: *P. gairdneri*).

species, it is common for populations living on different substrates to vary greatly in color and yet remain genetically very similar. In New Mexico, for example, populations of woodrats (*Neotoma mexicana*), rock mice (*Peromyscus difficilis*) and pocket mice (*Perognathus intermedius*), frequently have dark and light forms in geographic proximity where different-colored substrates such as lava flows and light-colored sands exist.

Melanism in rodents of the SW United States

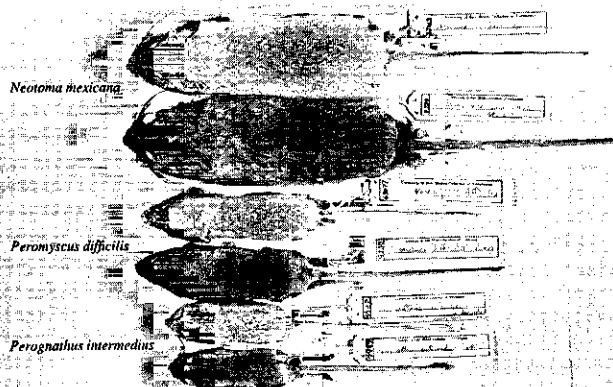


Figure 9. Examples of melanism in rodents from the Southwest.

Similar patterns of genetic variability are known among arthropods in the Southwest. Dobzhansky's research on genetic variation among races of fruit flies demonstrated striking geographic variation in chromosome polymorphisms across the Southwest (Dobzhansky 1944, Dobzhansky and Levene 1948). White (1949, 1951) found geographic variation in races of *Trimerotropis* grasshoppers in the Southwest. The large grasshopper genus *Trimerotropis* is particularly diverse in the Southwest (Rentz and Weissman 1980). One subdivision of the genus, Section A, is represented by species that are phenotypically quite different, yet have almost identical karyotypes (Weissman and Rentz 1980). The other subdivision, Section B, is represented by species of similar phenotypes, but with different and variable karyotypes (Weissman and Rentz 1980). Several cryptic species, belonging to Section B, are almost identical in appearance, but have different karyotypes.

These examples clearly illustrate the magnitude of the problem. If we are finding new species in one of the best-known groups of organisms (mammals) in well-studied areas such as the Southwest, the magnitude of our lack of knowledge in other groups must be enormous. In addition, variation below the level of species (as in grasshoppers and mammals) is also of great value from the standpoint of biological diversity, and must be considered when planning management strategies.¹

CAUSES OF HIGH SPECIES DIVERSITY IN THE SOUTHWEST: BIOGEOGRAPHIC HISTORY

The Southwest is a biological "melting pot," where historically distinct faunas of several major geographic regions come into contact and intermingle. Many species are derived from the distinctive faunas of these regions, and co-occur in the anastomosing habitats present in today's southwestern rangelands.

The modern assemblages of terrestrial vertebrate species have been derived from several sources. The boreal fauna characteristic of the coniferous forests, wet meadows, and alpine tundra of the Rocky Mountains and Sierra Nevada has contributed species such as red squirrel, pika, Steller's jay, and spotted owl. Several forms characteristic of the arid grasslands have expanded into the Southwest from the Great Plains. These include the western box turtle, Great Plains skink, black-tailed prairie dog, northern grasshopper mouse, Swainson's hawk, and lark sparrow. The Sierra Madre of Mexico has contributed many middle-elevation species that follow the oak woodland and savanna habitats across the border into the isolated mountains of southeastern Arizona, southern New Mexico, and southwestern Texas. These include Yarrow's spiny lizard, rock rattlesnake, coatimundi, pygmy mouse, elegant trogon, and Montezuma quail. Three major desert regions that were historically isolated in lowland areas as recently as the end of the last Ice Age, about 10,000 years ago, now come into contact in the Southwest, bringing their distinctive species with them. Thus the Chihuahuan Desert to the southeast contributes Texas horned lizard, Trans-Pecos rat snake, silky pocket mouse, banner-tail kan-¹See Stacey, this volume.

garoo rat, scaled quail, and Cassin's sparrow. The Sonoran Desert to the southwest contributes the collared lizard, sidewinder, desert kangaroo rat, southern grasshopper mouse, Gila woodpecker, and Bendire's thrasher. The Mojave/Great Basin Desert to the west and north contributes the short-horned lizard, chisel-toothed kangaroo rat, sagebrush vole, sage thrasher, and sage sparrow. Finally, the distinctive pinyon-juniper woodland that is so widespread throughout the Southwest and Intermountain region contributes its own distinctive species, such as pinyon mouse and pinyon jay.

As with vertebrates, the invertebrate fauna on southwestern rangelands has been derived from several major biomes. Using grasshoppers as an example, the Great Basin, Mojave, Sonoran, and Chihuahuan Deserts all contribute taxa in the Southwest region (see grasshopper geographic distributions in Otte 1981, 1984, and Helfer 1953). The Great Plains grasslands contribute many taxa, especially to New Mexico and eastern Arizona. The Rocky Mountains to the north, and the Sierra Madre to the south, both contribute different taxa to the mountainous areas of the Southwest.

Darkling beetles (Tenebrionidae) are major detritivores in arid regions throughout the temperate world (Crawford 1981). Presumably, the mix of species in the Southwest is due to the coming together of previously distinct assemblages. The response of many groups of beetles to rapid climate change, such as the warming at the end of the last glaciation, has been to move to more suitable habitats or to become locally extinct. Elias (1991) suggests that the species composition of these groups in the West is changing most of the time. Camel crickets and native cockroaches in the Southwest may occur for similar reasons. In addition, large "desert" spirostreptid millipedes are the northernmost representatives of a widespread New World and African genus (Crawford 1979, Crawford et al. 1987). "Desert" atopetholid millipedes are in a family restricted to southwestern North America (Hoffman 1979). Other, more high-elevation millipedes in at least three orders may be residual populations of both Rocky Mountain and Sierra Madrean origin. The common isopods

are all Old World (originally Mediterranean) imports since Columbus (Muchmore 1990). The termites are all subtropical in origin (MacKay 1991). Ants have moved into the region mostly from the south and have taken advantage of the variation in topography to extend their ranges (Holldobler and Wilson 1990).

TOPOGRAPHIC RELIEF AND RESULTING ENVIRONMENTAL HETEROGENEITY

The varied and uplifted geology of the Southwest and the resulting variation in climate and soils has created a wide diversity of abiotic and biotic environments. Most conspicuous is the elevational gradient from desert shrubland, through grassland or chaparral, woodland, coniferous forest, to alpine tundra (Figure 10). This is also a gradient of climate, of decreasing temperature, and usually of increasing and then decreasing precipitation. This gradient has long been recognized as playing a central role in the distribution and diversity of species in the Southwest.

On the one hand, the classification of ecosystems along this gradient into zones (such as Merriam's classic life zones: Lower Sonoran, Upper Sonoran, Transition, Canadian, and Hudsonian) or biomes (desert shrub, grassland, chaparral, woodland, coniferous forest [often further subdivided into Ponderosa pine, mixed conifer, and spruce-fir forest], and alpine tundra) is convenient. These ecosystem types are easily recognized by their dominant plant life forms and species, and they support distinctive species of terrestrial vertebrates (Table 2) and invertebrates (Table 3).

On the other hand, the recognition of discrete life-zone ecosystem types is misleading. It divides a relatively gradual gradient of abiotic conditions and vegetation and individually distributed plant and animal species into units that are not at all discrete and coincident. Most contemporary ecologists reject the idea that there are discrete habitat types and plant and animal communities. At the same time, they

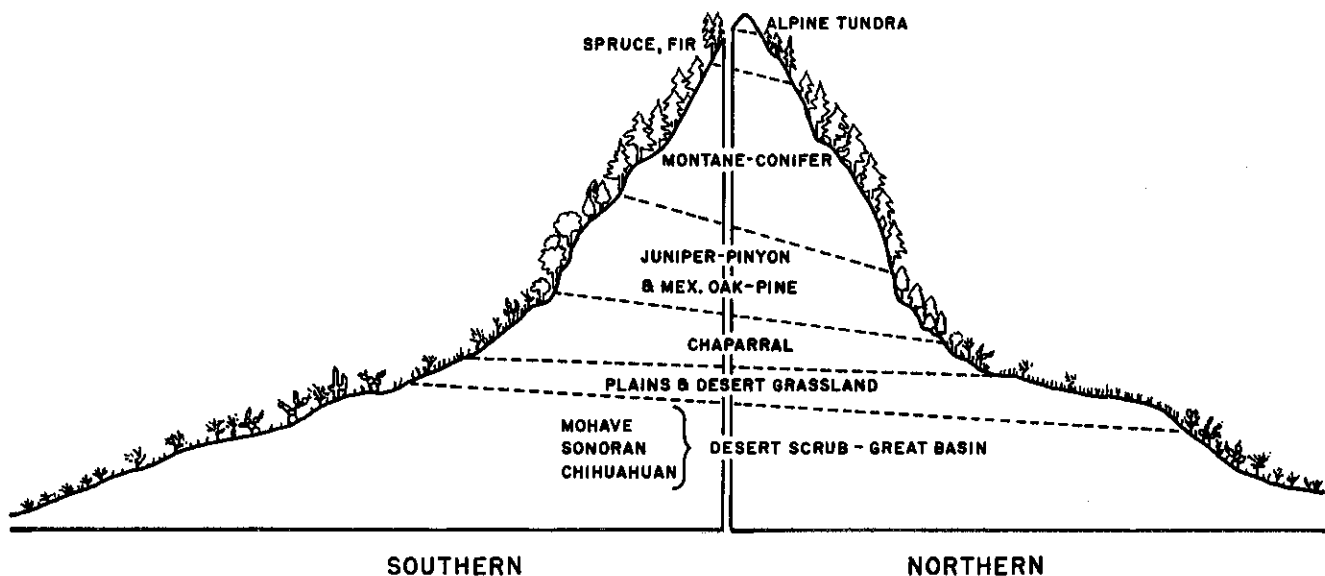


Figure 10. Diagram of the distribution of plant communities across a typical elevation gradient in the Southwest (from Hoffmeister 1986, with permission).

TABLE 2. HABITATS AND HABITAT-SPECIFIC TERRESTRIAL VERTEBRATES OF THE WESTERN UNITED STATES.

HABITAT	BIRDS	MAMMALS	REPTILES
DESERT	CACTUS WREN BLACK-THROATED SPARROW HARRIS' HAWK	KIT FOX MERRIAM'S KANGAROO RAT LONG-NOSED BAT	DESERT IGUANA DESERT TORTOISE GILA MONSTER
GRASSLAND	HORNED LARK CASSIN'S SPARROW APLAMADO FALCON	WHITE-SIDED JACKRABBIT PYGMY MOUSE PRONGHORN ANTELOPE	MASSASAGUA WESTERN BOX TURTLE GREAT PLAINS SKINK
PINYON-JUNIPER	PINYON JAY MONTEZUMA QUAIL BUSHTIT	PINYON MOUSE CLIFF CHIPMUNK BOYLE'S MOUSE	MOUNTAIN KINGSLAKE
CONIFER FOREST	STELLAR'S JAY SPOTTED OWL RED-CROSSBILL	RED SQUIRREL PINE MARTIN RED-BACKED VOLE	
SUB-ALPINE/ALPINE	PTARMIGAN ROSY FINCH	PIKA	
RIPARIAN FOREST	VERMILION FLYCATCHER HOODED ORIOLE ELEGANT TROGON	JUMPING MOUSE YELLOW-BELLIED COTTON RAT	WESTERN WATER SNAKE
SAND DUNES		DESERT KANGAROO RAT	FRINGE-TOED LIZARD

still recognize the importance of the elevational gradients in climate and vegetation in influencing the distribution of species and patterns of diversity. Characteristically, the highest diversity in most groups occurs at intermediate elevations, presumably reflecting the limiting effects of aridity below and low temperature above.

Interspersed among the distinctive environments determined by elevational gradients are other distinctive habitat types caused by the patchy distribution of geological, hydrological, and microclimatic conditions. Examples include the deciduous forests that form riparian corridors along the rivers and streams throughout the Southwest, and other patchy habitats, such as sand dunes, playa lakes, and lava flows. Most of these support distinctive invertebrate species (Table 3, bottom), and some even have unique species of terrestrial vertebrates (Table 2, bottom).

Perhaps one of the best illustrations of the role of habitat variation on faunal diversity can be found in species patterns of grasshoppers. Studies of grasshopper assemblages from different habitats in the same area tend to demonstrate high species diversity within habitats, and differences in species composition between habitats. This pattern exists in the Southwest (Tinkham 1948, Joern 1979, and Rivera 1986), and in other parts of the country (Scoggin and Brusven 1973,

Alexander and Hilliard 1969, and Cantrall 1943). Because habitats are more heterogeneous in the Southwest than in other parts of the country, regional habitat diversity and corresponding grasshopper diversity tend to be higher in the Southwest than elsewhere. Table 3 lists some of the habitat-specific grasshopper species found in some of the more common and specialized habitats in the Southwest. Table 3 also illustrates the changes in common grasshopper species across an elevational/environmental gradient in central New Mexico. Alexander and Hilliard (1969) found a similar pattern, but with different species in Colorado. The Southwest also has higher plant-species diversity than elsewhere in the country (Brown 1982), and Otte (1976) demonstrated a strong positive relationship between plant- and grasshopper-species diversities.

Differences in species-habitat affinities also contribute to the high diversity of other arthropods. Darkling beetles on the whole have moderate habitat specificity (therefore moderate beta diversity) (Doyen and Tschinkel 1974). This is probably less true for most of the region's common but less species-rich macrodetritivore families (e.g., certain camel cricket species occurring in rodent burrows [Hawkins and Nicoletto 1992] and another in riparian woodland). Native cockroaches are found in sandy soils throughout the Southwest, and, being highly fossorial, commonly occur in rodent

TABLE 3. HABITATS AND HABITAT-SPECIFIC TERRESTRIAL ARTHROPODS OF THE WESTERN UNITED STATES.

Habitat	Grasshopper/crickets	Beetles	Other Arthropods
Desert	<i>Boottettix argentatus</i> <i>Cibolacris parviceps</i> <i>Trimerotropis pallidipennis</i> <i>Ceuthophilus pallidus</i>	<i>Eleodes armatus</i> <i>Eusattus muricatus</i>	<i>Orthoporus ornatus</i>
Grassland	<i>Ageneotettix deorum</i> <i>Melanoplus occidentalis</i> <i>Paropomala pallida</i> <i>Ceuthophilus lamellipes</i>	<i>Eleodes hispilabris</i> <i>Pasimachus obsoletus</i>	<i>Atopethalid</i> millipedes
Pinyon-Juniper Woodland	<i>Mestobregma plattei</i> <i>Shistocerca alutacea</i> <i>Trimerotropis cyaneipennis</i> <i>Ceuthophilus utahensis</i>	<i>Eleodes obscurus</i>	<i>Apacheiulus</i> spp.
Conifer Forest	<i>Melanoplus franciscanus</i> <i>Trimerotropis cincta</i> <i>Trimerotropis modesta</i> <i>Styrocosceles neomexicanus</i>	<i>Scaphinotus snowi</i>	<i>Utadesmus hoffi</i>
Subalpine Alpine	<i>Chorthippus curtipennis</i> <i>Melanoplus magdalenae</i> <i>Melanoplus snowii</i>	<i>Eleodes nigrinus</i> <i>Carabus taedatus</i>	<i>Aniulus</i> spp. <i>Hekeiulus</i> spp.
Riparian	<i>Chortophaga viridifasciata</i>	<i>Calosoma scrutator</i>	<i>Armadillidium vulgare</i>
Forest	<i>Melanoplus differentials</i> <i>Trimerotropis maritima</i> <i>Ceuthophilus gertschi</i>	<i>Blapstinus fortis</i>	<i>Porcellio laevis</i>
Sand Dunes	<i>Cibolacris samalayucaae</i> <i>Trimerotropis barnumi</i> <i>Trimerotropis whitei</i> <i>Ammobaenetes phrixocuemoides</i>	<i>Eleodes hispilabris</i>	<i>Schizocosa</i> spp.

burrows (Crawford 1981, Hawkins and Nicoletto 1992). Large-bodied spirostreptid and atopetholid millipedes tend to occur in arid shrubland (Crawford et al. 1987), whereas small-bodied parajulid, polydesmid, and spirostreptid species tend to occur at higher elevations (C. S. Crawford, personal observations). Isopods are common in moist (mainly riparian) habitats; the few native species are very habitat-restricted, as are bristletails and silverfish. Termites, being essentially subterranean, appear relatively tolerant of habitat differences but are less diverse in cool, northern climates.

Soil and litter mites and springtails show variable habitat specificity. Some mites especially are ubiquitous. A recent unique discovery in central New Mexico revealed that large numbers of predatory epigeal mites occur in grassland/shrubland. Many are unknown species and of unexpected families. Different groups of mites exhibit seasonal differences in activity, including winter (C. Welbourn, Ohio State University, personal communication).

MICROHABITATS AND FAUNAL DIVERSITY

Within habitats, small-scale variations in vegetation, soils, slope, aspect, and moisture can create a suite of microclimates and resource conditions to which animals selectively respond. These microhabitat characteristics can significantly influence the diversity of faunal assemblages. For example, the presence or absence of shrubs on southwestern rangelands has been shown to affect the species composition and abundances of small mammals (Rosenzweig 1973, Price 1978, Whitford et al. 1978, Holbrook 1979, Parmenter and MacMahon 1983). In southwestern deserts, the shrub open-space mosaic of shrubby habitats supports a high diversity of rodents and lizards, because different species use the microhabitats in different ways to forage, escape from predators, and cope with the extremes of the abiotic environment (Figure 11).

Arthropods provide many instances of species-specific habitat requirements. For example, spiders are extremely

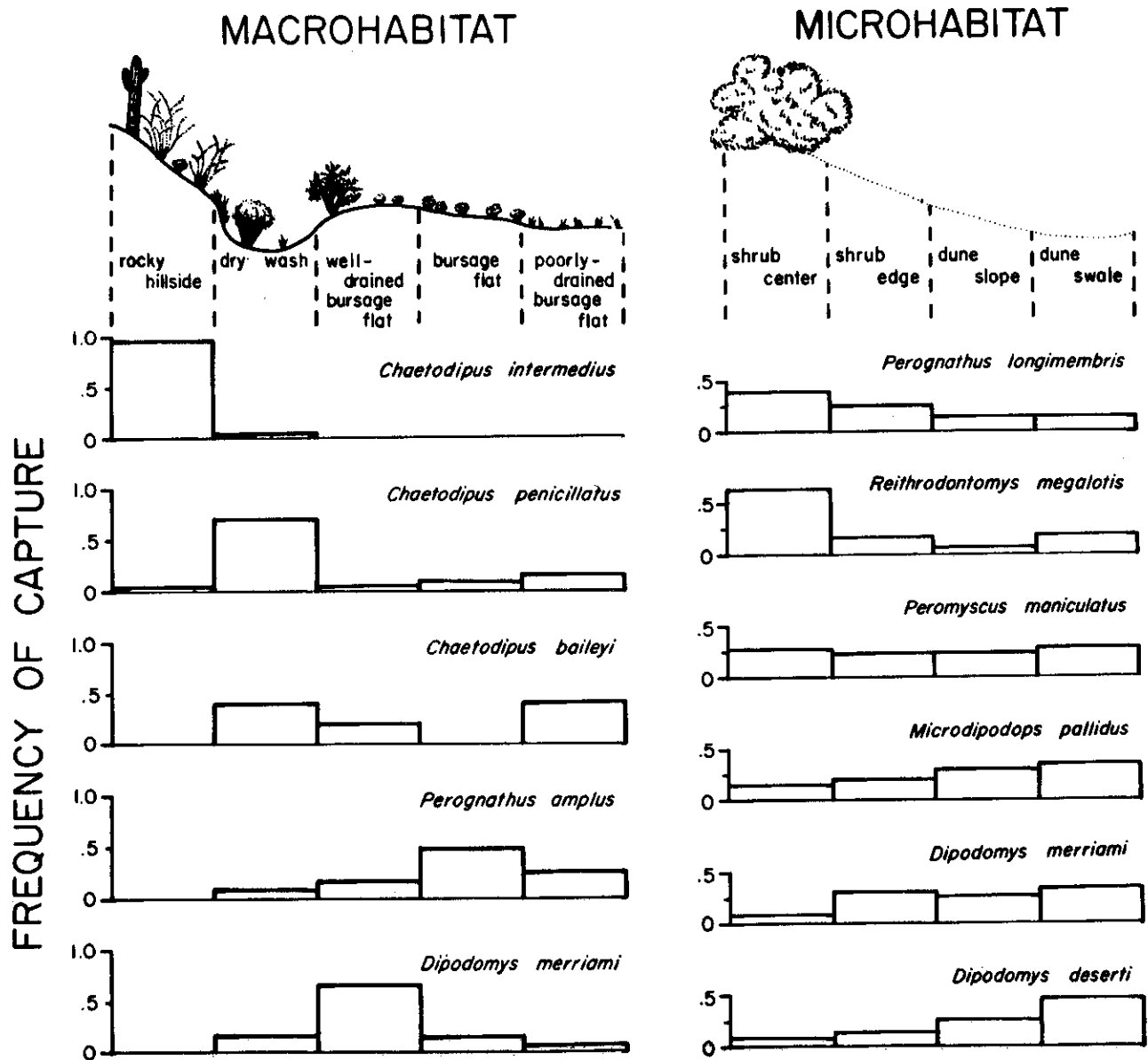


Figure 11. Distribution of desert rodent species among different macrohabitats and microhabitats based on trap capture frequency data. Data from J. H. Brown.

sensitive to variations in microhabitat structure, due for the most part to their various techniques for capturing prey. Crab spiders (Thomisidae) use plant litter for ambush sites, the larger wolf spiders (Lycosidae) are found more often in open spaces, and web-building species (e.g., the orb-weavers, Araneidae) require the proper anchor points for their webs (Gertsch 1979). As a group, then, spiders respond to the vegetation of an area, not so much to particular plant species but to plant architecture (Robinson 1981). During one case study in the sagebrush steppe of northern Utah, Abraham (1983) collected 83 spider species from ground, herb, and shrub layers. The percentage overlap in species between shrub and herb layers was 73 percent, but the overlap between ground and plant layers was only 17 percent.

Beetle distributions are also influenced by microhabitat factors. For example, the distribution of bombardier beetles

(Carabidae: *Brachinus* spp.) in southeastern Arizona along an elevational gradient varies with local environmental features (Juliano 1985). *Brachinus lateralis* is found around permanent ponds, while *B. mexicanus* and *B. javalinopsis* inhabit margins of temporary ponds at high and low elevations, respectively.

Darkling beetles (Tenebrionidae) also demonstrate distinct microhabitat partitioning among different species. Topographic relief and soils, as well as natural and anthropogenic disturbances, are all related to the distribution and structure of these detritivores (Crawford 1991). These assemblages can be relatively habitat-specific, but levels of diversity within them can change dramatically from year to year (Rogers and Rickard 1975). The importance of climate in the maintenance of assemblage structure is difficult to assess, but temperature may be at least as important as precipitation

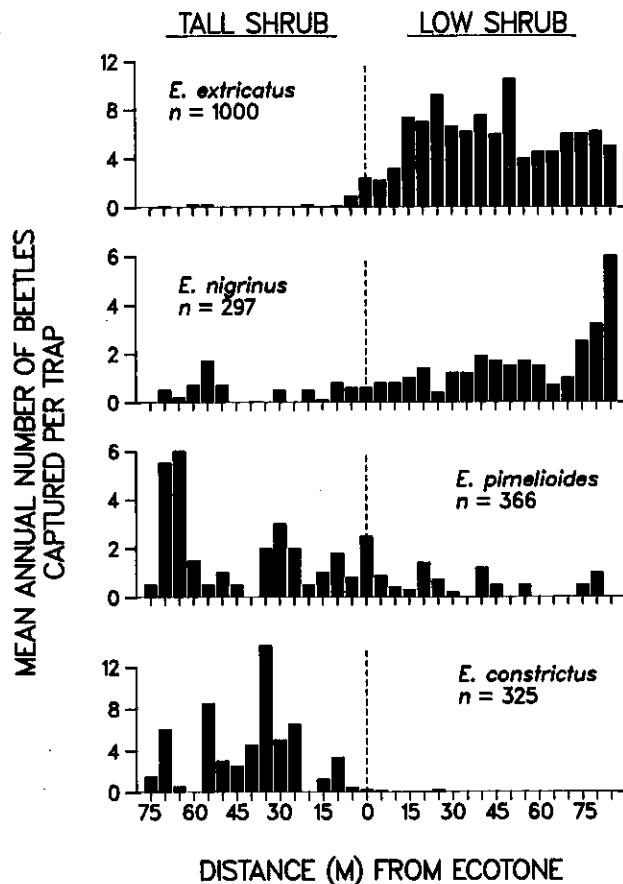


Figure 12. Numbers of darkling beetles (*Tenebrionidae*: *Eleodes* spp.) captured in pitfall traps in low and tall shrub microhabitats in sagebrush-steppe rangelands near Kemmerer, Wyoming (from Parmenter et al. 1989a, with permission).

(Crawford 1988). For example, in sagebrush-steppe habitats, *Eleodes* spp. partition microhabitats based on shrub canopies that influence temperature and moisture regimes (Figure 12, Parmenter et al. 1989a). These beetles search out microclimates beneath or between shrubs that are favorable to their preferred temperature tolerances (Parmenter et al. 1989b).

While differences in animal-species compositions occur among habitats, the faunal assemblages supported by various habitats are not always comparable in species diversity. An excellent example of this is found in spider assemblages of New Mexico grasslands and pinyon-juniper woodlands. Muma (1980) found that, while numbers of individuals were approximately equal in both habitats, the higher elevation pinyon-juniper site supported greater numbers of families, genera, and species.

DISTURBANCE AND ANIMAL BIODIVERSITY

NATURAL DISTURBANCES

Disturbances are common occurrences in nature, and have substantial influence in determining the structure and functioning of ecosystems. Disturbances vary in type, intensity, timing, size, and areal extent, and cause significant

impacts on biodiversity and ecosystem processes (e.g., succession, Pickett and White 1985). As a result of the obvious importance of disturbance in ecosystems, considerable scientific effort has gone into understanding the ecological role of disturbances.

Rangelands in the southwestern United States are subjected to a variety of natural disturbances. In view of the arid nature of the climate and the frequent thunderstorms, natural lightning-caused fires are a major form of disturbance in nearly all habitats except extreme desert and alpine tundra. By removing a large fraction of the existing species and vegetation, initiating secondary succession, and creating a spatial mosaic of patches on the landscape, fire promotes the regional coexistence of species. In addition to wildfires, thunderstorms also cause flooding and soil erosion/deposition, which are important forms of disturbance in certain habitats (e.g., riparian woodlands and some deserts).

Animal disturbance of many types (beaver dams, grazing and trampling by large native mammals, and burrowing by some rodents, reptiles, and invertebrates) are also important forms of disturbance that enhance spatial heterogeneity and species diversity. For example, several vertebrate and invertebrate species are strongly associated with banner-tail kangaroo rat mounds (Hawkins and Nicoletto 1992). The deep burrows and the humid, thermally moderate microclimates provided by these mounds may be essential for the several species of Great Plains reptiles (western box turtle, Great Plains skink, massasauga rattlesnake), whose geographic extension into the Southwest corresponds closely with the range of banner-tail kangaroo rats, and also for the several species of roaches, crickets, and beetles that are found almost exclusively in the kangaroo rat mounds (Hawkins and Nicoletto 1992).

ANTHROPOGENIC DISTURBANCES

Aboriginal and modern humans have changed the landscape, habitats, and microenvironments of the Southwest in ways that can enhance as well as decrease diversity. We are increasingly learning that the habitats and landscapes of the Southwest encountered and described by the first European explorers a few centuries ago were not "natural." They had already been modified to varying extents by "Native Americans," who had colonized North America from Asia at least 20,000 years ago. Some of the impacts of aboriginal humans, such as their contribution to the extinction of giant mammals (see Martin and Klein 1984, Owen-Smith 1989), the deforestation of the lands around Chaco Canyon, and the dense settlements and irrigation agriculture along the lower Rio Grande and Colorado Rivers, undoubtedly had large effects on local and regional biological diversity.

These changes continued and intensified with the settlement of the Southwest by Europeans and with the introduction of domestic livestock and exotic plants (e.g., cheatgrass and salt cedar). Not all impacts of either aboriginal or modern humans have been detrimental to diversity, however. Some activities enhance diversity by creating or augmenting spatial and temporal heterogeneity. For example, adjacent patches of cut and uncut timber, grazed and ungrazed grassland, "re-

TABLE 4. NUMBER OF ARTHROPOD SPECIES ON UNDISTURBED AREAS AND RECLAIMED SURFACE MINE SITES IN SAGEBRUSH RANGELAND, SOUTHWESTERN WYOMING. BEETLE DATA FROM PARMENTER AND MACMAHON (1987), GRASSHOPPER DATA FROM PARMENTER ET AL. (1991), SPIDER DATA FROM S. BRANTLEY (UNPUBLISHED DATA).

	Undisturbed	Mined	Total
Total Beetle Species	45	86	98
Unique Beetle Species	12	53	
Total Grasshopper Species	21	22	25
Unique Grasshopper Species	3	4	
Total Spider Species	55	58	76
Unique Spider Species	18	21	

claimed" surface mines and unmined lands, agricultural fields, and undisturbed areas often support more species in combination than would large areas of uniformly unaltered habitat (e.g., Table 4).

Other human activities provide species resources that enable certain species to survive where they otherwise could not. Examples include urban, suburban, and agricultural habitats and associated food resources that support dense populations of certain vertebrates and invertebrates (crows, honeybees, and other insects associated with ornamental and crop plants). Increases in abundance and expansion of the winter and breeding ranges of several hummingbird species in the Southwest can be attributed to people's bird feeders and to the planting of exotic plants in urban and suburban areas.

Humans have always modified their environment and will continue to do so. The increasing world population, however, coupled with unprecedented technological advancements, has tipped the balance grossly to one side. The constant degradation of natural habitats is causing environmental destruction and species extinctions on a scale never before seen on this planet. The problem is complex but relates to environmental patchiness and total amount of habitat. It has been hypothesized (MacArthur and Wilson 1967) that when natural communities are reduced to 10 percent or less of their original habitat, 50 percent of the species in the community are at risk. Although such a reduction sounds like a lot, it is exactly what is being approached by old-growth forest reduction of boreal forest on southwestern mountain tops. Grasslands in south Texas have been reduced by agricultural cultivation to such a level that Attwater's prairie chicken is now on the verge of extinction, even though a refuge was established for its preservation. Apparently, the remaining native habitat was not sufficient to maintain the necessary diversity in native plant species, and the limited protected area served to attract predatory species (W. Kessler, personal communication).

Reducing habitats to small patches via human activities also is detrimental to diversity, especially if the patches are not interconnected. The newly discovered jumping mouse (*Zapus hudsonius*) in New Mexico, mentioned above, is now considered endangered by the state and may receive future Federal listing due to habitat fragmentation along the Rio Grande and in the Sacramento and White Mountains. It has

been shown in central and South America that when forests are reduced to patches of 20 square miles or less, 10 percent or more of the bird species are lost within ten years (Terborgh 1974, Willis 1979, Simberloff 1984, Wilson 1988). Similar models may well apply to southwestern rangelands.

MANAGEMENT PRACTICES, LAND USE, AND BIODIVERSITY

Human activities on rangelands of the western United States have clearly had considerable impact on the abundances and distributions of animal species. Anthropogenic ecosystem disturbances, resulting from mining, grazing, chaining, dam building, agricultural development, road construction, fires, and construction of human communities, have altered the composition of biotic and abiotic resources within virtually all western biomes. Understanding the ecosystem responses to such disturbances, especially in regard to biodiversity patterns, has become a critical aspect of current and planned management strategies.

CONCEPTUAL BACKGROUND

With respect to animal biodiversity patterns, and how they are altered by human management practices, scientists have long recognized that the faunal component of the ecosystem both influences and responds to a number of biotic system properties. First, animals require a number of habitat resources, including food, shelter, and reproduction sites. A major component of an animal's habitat is the architectural structure of the vegetation. This includes both vertical architecture (grass vs. shrub vs. tree) and horizontal architecture (patch size and spatial distribution of vegetation types). Because animal species vary tremendously in their vagility and movement patterns, horizontal vegetation architecture is an important resource factor at a number of scales, ranging from landscapes (km²) through stands (m²) to individual plants (cm²).

Animals also contribute a trophic structure to ecosystems. Through feeding activities, animals influence the plant community in a number of ways (e.g., herbivory, granivory, pollination, and seed dispersal) (e.g., see Brown and Heske 1990b). In addition, animals transport spores of beneficial

mycorrhizal fungi (Rothwell and Holt 1978, Ponder 1980, Warner et al. 1987). Animal trophic interactions also influence nutrient cycling and energy flows; numerous invertebrate species (e.g., earthworms) are detritivores and play important roles in decomposition and soil development (Abbott 1989, Hutson 1989).

Faunal diversity (species richness and evenness) and biomass are additional properties of ecosystems that have significant influence on ecosystem processes. Species richness and diversity are ecologically important attributes of an ecosystem, as they can be a measure of the amount of redundancy in functional groups and trophic guilds. High levels of species' functional redundancy may promote a greater stability of ecosystem functioning (e.g., numerous species of detritivores may increase decomposition rates and efficiencies, enhancing nutrient availability to vegetation.)² Animal biomass will, to some degree, determine the amount of herbivore pressure on the floral assemblage, and may ultimately influence the dispersion and species composition of the plant community.

SUCCESSIONAL PROCESSES AND ANIMAL DIVERSITY

Following an ecosystem disturbance (be it "natural" or human), successional change is perhaps the most important ecological process influencing the biodiversity of a site. While numerous models of successional processes have been developed (see MacMahon 1981), Clements's (1916) classic succession model serves as a conceptual framework in which to discuss ecosystem development on disturbed lands. In Clements's scheme (which applies to both flora and fauna), the ecosystem sustains a disturbance ("nudation") that reduces or eliminates resident populations. Surviving species ("residuals") undergo the process of establishment ("ecesis"), during which some species that are unable to cope with the new environment are eliminated. Through time, newly colonizing species ("migrants") join the residuals. Species that successfully establish alter the abiotic environment ("reaction"), thereby influencing the potential establishment of future migrants and the survivorship of the offspring of both residuals and past migrants. Biotic interactions ("coactions," e.g., competition, predation, parasitism, etc.) also influence the species composition of the community. These successional processes continue until an equilibrium ("stabilization") is attained among the extant species and the environment. This state is often termed the "climax."

In arid deserts, semiarid shrub-steppe, and grasslands, the successional process can be viewed as a simple accumulation of species, in which plants and animals are sequentially added to the community without extensive losses or replacement (species turnover). This is because arid lands generally do not progress beyond shrub-dominated vegetation patterns. This type of succession, based predominantly on the initial species list, can be termed auto-succession. In contrast, succession in more mesic, forested regions follows a pattern of distinct species turnover (or relay succession) as a site goes from a forb/grassland system through shrubland into forest. Such patterns have been well documented for small mammals

²However, see Whitford, this volume.

(Yeager 1942, Verts 1957, Kirkland 1976, Sly 1976, Hansen and Warnock 1978) and birds (Karr 1968, Chapman et al. 1978, Crawford et al. 1978, Bejcek and Turner 1980, Kremetz and Sauer 1982, Schaid et al. 1983) during primary and secondary succession on reclaimed mine lands.

Studies of the successional development of arthropod communities on disturbed sites have shown that initial colonization and dominance is generally accomplished by scavenging and omnivorous species, and that the herbivore assemblage changes as a function of vegetation diversity and abundance (Bulan and Barrett 1971, Teraguchi et al. 1977, Southwood et al. 1979, Butt et al. 1980, Force 1981, Hawkins and Cross 1982, Majer et al. 1982, Brown and Southwood 1983, Majer 1985, Parmenter and MacMahon 1987, Parmenter et al. 1991). Disturbances that alter plant species composition or vegetation structure will affect various faunal compositions. For example, the composition of plant species in an area is important to grasshopper diversity because many grasshoppers specialize on certain plants for food (Otte and Joern 1977, Gangwere et al. 1989). Vegetation structure is also important to grasshopper diversity, because many grasshopper species specialize on certain microhabitats resulting from vegetation architecture (Anderson 1964, Joern 1982).

In addition, numerically dominant species in postdisturbance environments are oftentimes exceedingly rare in the undisturbed community; such opportunistic "pioneer" species typically exhibit large and rapid population increases following a disturbance. These successful colonizers benefit not only from a suite of newly available food resources, but also from a combination of changes in the abiotic (e.g., temperature and moisture regimes) and biotic (e.g., predation and competition pressures) environments. Given the importance of insect pollinators, herbivores, predators, and detritivores to ecosystem functioning, and the potential for economic impact on management efforts, knowledge of insect recolonization and successional patterns would be useful to ecologists and land managers in their attempts to develop successful strategies of managing disturbed ecosystems.

In general, ecosystem disturbances will favor certain species that can opportunistically use the altered suite of environmental resources. The actual assemblage of species occupying a disturbed site will depend on a number of factors, including the severity of the disturbance, the site's proximity to potential recolonizing populations, the number of residual species, and biogeographic history of the surrounding area. Observations of changes in biodiversity following a variety of disturbance types have demonstrated reciprocal shifts among species based on habitat-specific requirements of resident and immigrant species. For example, livestock grazing can have significant effects on vegetation composition, percentage cover, and physical architecture, which in turn favors population increases of particular vertebrate and invertebrate species over others (for examples, see Jones 1981; Bock and Webb 1984; Bock et al. 1984, 1986; Jepson-Innes and Bock 1989; Hunter 1991; Stangl et al. 1992). Some of the favored species are considered economic pests; for example, livestock grazing, and the associated reduction in grass cover, has been found to lower grasshopper species diversity and increase the dominance of a few species (Pfadt 1982, Jepson-Innes and

Bock 1989, Quinn and Walgenbach 1990, Joern 1982). Grasshopper species that dominate disturbed habitats tend to be generalist feeders, have good dispersal capabilities, and exhibit high reproductive potentials. These are all characteristics of agricultural pest species. There is abundant evidence that human-caused disturbances on rangelands, especially overgrazing by livestock, alter the environment in such a way as to favor pest grasshopper species (Hewitt 1977, and references therein). Other types of human disturbances such as forest cutting and road construction (Lightfoot 1986, Scoggan and Brusven 1973), and surface coal mining (Parmenter et al. 1991), have also demonstrated a reduction in grasshopper diversity, and an increase in pest-species dominance.

With respect to detritivores, natural and anthropogenic disturbances may alter detritivore diversity and assemblage structure over long periods of time if the nature of the habitat's soil is distinctly changed. For example, Crawford (1988) has documented changes in detritivore assemblages on sand dunes vs. adjacent habitats in central New Mexico. Detritivores are sufficiently tolerant of food availability shifts, even though they can be quite selective of food choice (Crawford 1991). This dietary plasticity allows them to survive in disturbed sites exhibiting considerable food resource change. Stochastic effects may well determine their diversities as much as anything else, judging from unaccountable assemblage differences in otherwise similar appearing habitats (riparian, grassland). Also, long-term climate changes should cause expansion and contraction of some species' ranges, as suggested by the present distributions of some millipede species (Crawford et al. 1987, C. S. Crawford, personal observations). But other millipede species seem impervious to climatic differences (Shelley 1987). Use of certain detritivores (e.g., camel crickets, isopods, millipedes, tenebrionids) as indicators of climate change may be productive.

Wildfires and controlled burns influence habitat characteristics and alter animal biodiversity. Fires in shrublands and chaparral change the vegetation architecture, nutrient dynamics, and plant species composition, thereby influencing animal species, e.g., elk (Jourdonnais and Bedunah 1990), deer (Klinger et al. 1989), tortoises (Bury and Smith 1986), and arthropods (Hansen 1986, Scifres et al. 1988). For example, fire in tallgrass prairie communities may increase or decrease grasshopper species diversity depending upon fire frequency (Evans 1984, 1988a,b); however, little is known about the effects of fire on grasshopper assemblages on southwestern rangelands.

Habitats can be altered mechanically as well, resulting in concomitant changes of the faunal assemblages. The clearing of mesquite shrubland and pinyon-juniper woodlands in the western United States by "chaining" or bulldozing has been shown to alter vertebrate species composition and abundance, particularly birds and small mammals (Germano and Hungerford 1981, O'Meara et al. 1981, Szaro 1981, Germano et al. 1983), although use of chained areas by larger mammals is only marginally affected (e.g., Skousen et al. 1989). In addition to rangeland modification, other human-directed mechanical disturbances occur. Roads, highways, and power

lines, with spacious rights of way, constructed through deserts, shrublands, and forests, favor species normally found in open grasslands (e.g., Adams and Geis 1983, Butt et al. 1980). Development of human settlements, along with buildings, landscaping, and agricultural crops, contributes to the habitat diversity of an area, permitting the survival of a wide variety of opportunistic species. Nor is this a recent phenomenon; evidence for enhanced bird species diversity around ancient Pueblo sites in the Southwest has been documented by Emslie (1981), and apparently was a result of the irrigation systems and increased grain and insect productivity associated with the agricultural activities of the native peoples.

Mining activities are perhaps one of the most intense disturbances in western ecosystems. Reclamation of mine sites has received considerable attention from ecologists and land managers, due in part to increased public awareness and interest in restoring mined lands to productive and aesthetically pleasing natural communities. As a result, studies have addressed factors influencing the recolonization of both reclaimed and unreclaimed mine lands by various groups of vertebrates (e.g., Yeager 1942, Verts 1957, Karr 1968, Kirkland 1976, Sly 1976, Chapman et al. 1978, Crawford et al. 1978, Hansen and Warnock 1978, Bejcek and Tyrner 1980, Kremetz and Sauer 1982, Schaid et al. 1983, Parmenter et al. 1985, Sieg et al. 1986). In addition, some studies have examined arthropod community development on reclaimed mine sites (e.g., Neumann 1971, Usher 1979, Hawkins and Cross 1982, Majer et al. 1982, Urbanek 1982, Schrock 1983, Majer 1985, Nichols and Burrows 1985, Parmenter and MacMahon 1987, Sieg et al. 1987, Parmenter et al. 1991; see also references in Majer 1989).

ENDANGERED AND PROTECTED SPECIES

A direct consequence of land management practices, without regard for native animal species or their habitats, is that many animal species are threatened or endangered by extinction. The Federal Endangered Species Act provides guidelines for the protection of such species. However, implementation of the act has been slow and inadequate for species in the Southwest.

The Southwest supports a higher diversity of animals than most other parts of the country, as illustrated above. However, the recognition of threatened and endangered species in the Southwest appears to be lagging behind other parts of the country. A tabulation of terrestrial vertebrate animal species listed as threatened or endangered (U.S. Fish and Wildlife Service 1992), or recommended for listing (candidates, category 1; U.S. Fish and Wildlife Service 1991), reveals that only 34 species, or 18 percent of all species listed, are from the Southwest region (Table 5) (see Federal Register 1991 for regional boundaries). A total of 54 (28 percent) species are listed from the West Coast region, and 56 (29 percent) from the Southeast region (Table 5).

A similar pattern is evident for terrestrial arthropods. Only 5 (14 percent) of all listed and candidate 1 species are from the Southwest, while 20 (55 percent) are from the West Coast region (Table 6). Hafernik (1992) has summarized data from the 1989 Federal Register for all invertebrate species,

TABLE 5. ALL ENDANGERED (E), THREATENED (T), AND PROPOSED CANDIDATE (C1 AND C2) TERRESTRIAL VERTEBRATES IN THE U.S. FEDERAL REGISTER BY REGION. PERCENTAGES ARE OF COLUMN TOTALS.

Region	Listed (E,T,C1)	Candidates (C2)	Total Considered
West Coast ¹	54 (28%)	118 (38%)	172 (34%)
Southwest	34 (18%)	73 (24%)	107 (22%)
Rocky Mtns.	13 (7%)	42 (14%)	55 (11%)
Midwest	18 (9%)	9 (3%)	27 (5%)
Northeast	18 (9%)	19 (6%)	37 (8%)
Southeast ²	56 (29%)	46 (15%)	102 (20%)
Totals:	193	307	500

¹ Excluding Alaska, Hawaii, and Pacific Islands.

² Excluding Caribbean Islands.

and presented numbers by state. The same pattern is evident: relatively few listed or candidate taxa are from the southwestern states; most are from California and Hawaii (Figure 13). Hafernik (1992) further demonstrates that the listing rate for threatened or endangered invertebrate species since 1976 has been inadequate when compared to plant and vertebrate animal species (Figure 14).

There is an obvious discrepancy between the actual biodiversity of the Southwest and the proportion of Federal listed or candidate threatened or endangered species that are from the Southwest. California is indeed a biologically diverse state, and a state with a rapidly growing human population that is threatening native plant and animal species. Concomitant with the human population growth in

California is a public awareness and concern for identifying and protecting threatened and endangered species. The Southwest region is also undergoing a rapid human population increase with associated environmental impacts. Although the Southwest has a comparable or greater faunal diversity than the West Coast or Eastern regions, proportionately fewer species have been examined and evaluated for threatened or endangered status in the Southwest. We believe that this discrepancy is due largely to the fact that the invertebrate faunas of the eastern United States, and of the West Coast, are better known and studied than the invertebrate fauna of the Southwest.

This latter point can be illustrated using southwestern grasshopper species. Many of the grasshopper species in the

TABLE 6. ALL ENDANGERED (E), THREATENED (T), AND PROPOSED CANDIDATE (C1 AND C2) TERRESTRIAL INVERTEBRATES IN THE U.S. FEDERAL REGISTER BY REGION. PERCENTAGES ARE OF COLUMN TOTALS.

Region	Listed (E,T,C1)	Candidates (C2)	Total Considered
West Coast ¹	20 (55%)	178 (43%)	198 (44%)
Southwest	5 (14%)	36 (9%)	41 (9%)
Rocky Mtns.	2 (6%)	14 (3%)	16 (4%)
Midwest	3 (8%)	22 (5%)	25 (5%)
Northeast	4 (11%)	67 (16%)	71 (16%)
Southeast ²	2 (6%)	99 (24%)	101 (22%)
Totals:	36	416	452

¹ Excluding Alaska, Hawaii, and Pacific Islands.

² Excluding Caribbean Islands.

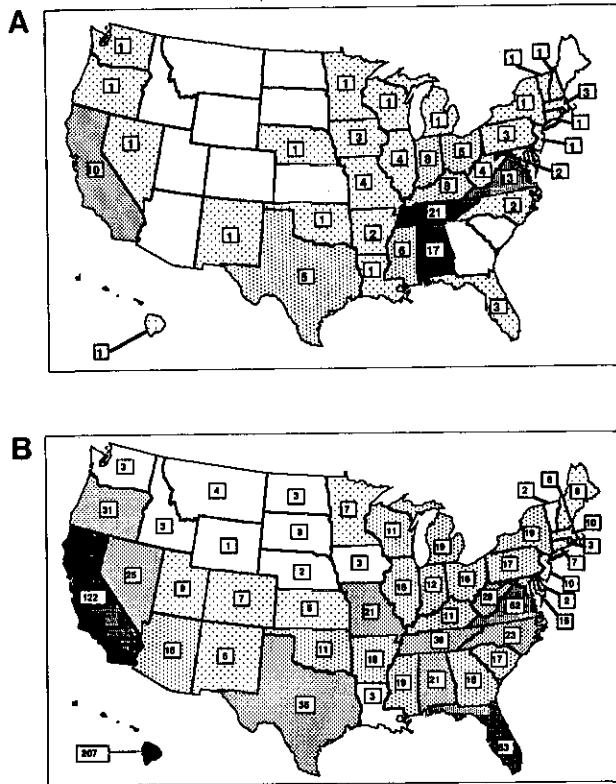


Figure 13. Numbers of invertebrate species in each state that are listed as (A) Federal threatened or endangered species, and (B) category 1 and 2 candidate species for Federal listing (from Hafernik 1992, with permission).

Southwest are rare and have localized distributions. Some examples of localized species include *Trimerotropis whitei* and *Cibolacris samalayuca*, found only on certain sand dunes, *Shotwellia isleta* and *Anconia hebardii*, which are limited to isolated playas, and *Melanoplus magdalenae*, *Melanoplus chiricahuae*, and *Melanoplus pinaleno*, which are found only on some high mountain peaks. Many other species are equally rare, or more so, and habitat restricted. None of these species are recognized by land or wildlife management agencies as rare, and no evaluations have been made as to whether or not any of these grasshopper species may be threatened or endangered.

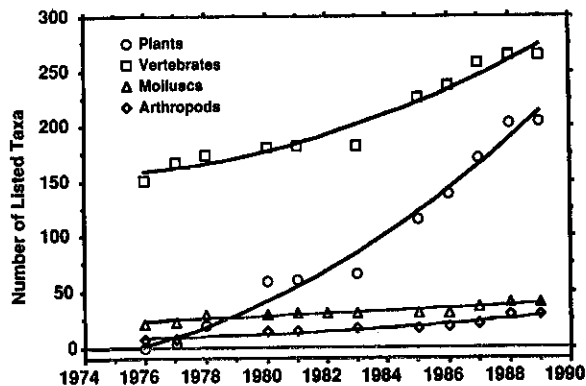


Figure 14. Rate at which taxa have been listed as Federal threatened or endangered species since 1976 (from Hafernik 1992, with permission).

MANAGEMENT RECOMMENDATIONS

Given the foregoing discussion on faunal biodiversity on southwestern rangelands, we offer the following observations concerning policy strategies for maintaining and enhancing animal diversity on managed lands.

1. Maintenance of biological diversity should be a specific goal of management of public lands (and often of private lands as well).

2. There is a need to recognize the patterns of diversity and the ecological processes that promote and sustain diversity. This will require considerable increases in research funding for systematic surveys of public lands, particularly in regions that heretofore have been missed in scientific studies.

3. The conscientious use of natural resources by humans (e.g., grazing, timber and fuel wood harvest, hunting, and recreation) can be performed without serious detrimental impacts on biological diversity. If natural resources are actually utilized on a multiple-use, sustained-yield basis, most threats to endangered species and biological diversity can be avoided.

4. One of the most serious threats to diversity in the Southwest is the gradual "nibbling away" of habitats, which permanently destroys critical habitats and resources required by resident wildlife. Examples include the cumulative impacts of telescopes, ski areas, and campgrounds on the highest mountaintops of the Southwest, or the additive effects of damming small streams (for irrigation agriculture, livestock watering, and flood control) on riparian habitats and species. Because each of these "nibbles" is relatively small, it can be difficult to marshal convincing arguments why it should not be permitted. The collective effect of many such developments, however, can be severe. Most mountains in southeastern Arizona now have telescopes on the peaks and campgrounds in the watered canyons; most of the once permanent streams now have diminished flows.

5. Manageable disturbances, such as livestock grazing, forestry, and mining, might be regulated in such a way as to contribute to overall species diversity of an area. Patches of variable grazing levels, or grazing at light to moderate levels, might maintain more habitat diversity than overall heavy grazing or no grazing at all. However, consideration must also be given to the ecological characteristics of the species responding to such disturbance. It may not be desirable to create habitats for "pest" or alien species. Considerations must also be given to rare, and potentially threatened, species.

6. Human-caused global climate change potentially poses one of the most severe threats to southwestern biological diversity in the coming century. If there is a substantial increase in average temperature, and especially if precipitation remains low, then rangelands will become desertified, suffer reduced productivity, and lose many of their present animal species. Effects should be especially severe on isolated mountain ranges, where warming will eliminate entire habitat types, causing extinction of many animal populations (e.g., McDonald and Brown 1992, Brown 1993).

7. Finally, there is a growing need for regional com-

munication and coordination of biodiversity strategies among private landowners, the concerned public, the scientific establishments, and the government agencies responsible for administering public lands. At present, the various components of regional biodiversity plans are being developed in a piecemeal, *ad hoc* fashion, based on local issues and using "crisis management" approaches. Examples include many endangered species identification and protection efforts, wilderness area designations, and assignments of grazing allotments and forest harvests within political, rather than ecological, boundaries (although the spotted owl and gray wolf strategic planning programs are notable exceptions). A regional, landscape approach would certainly be a more effective and efficient way to accomplish the goals of a southwestern biodiversity program.

Management of natural resources, including rangeland, in a sustainable way must take all levels of biotic diversity into account. At present, the greatest threat to southwestern biodiversity is the loss of local and regional species diversity. If this occurs, the remaining populations of each species will be reduced and fragmented, and will accrue an increased risk of global extinction. Further, changes in population structure will cause increased loss of within-species genetic diversity. Not only is within-species diversity the ultimate source of biodiversity at higher levels (Bawa et al. 1991), it represents an important resource that cannot be replaced once eliminated. As our knowledge of genetics and evolution continues to expand, the potential economic value of the natural gene bank in southwestern rangelands increases as well. Management plans that include sustainability and manage for biological diversity promise to provide the greatest long-term dividends.

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The Intersection of Ecosystem and Biodiversity Concerns in the Management of Rangelands

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Abstract

Maintenance of ecological functions and disturbance regimes within ecosystems is as important as preserving species populations or their genetic structure, biotic communities, and landscapes. There is considerable dispute as to how species diversity influences productivity and stability of various ecosystem structural and dynamic attributes. Some view each and every species as making an incremental contribution to these features. Others assume that some redundancy exists. Addition or loss of species can be anecdotally shown to influence ecosystems in proportion to the role such organisms have in altering microclimate, capturing energy, cycling nutrients, and serving as food and habitat for other organisms. Subtle but essential interactions are easy to overlook, however. We should try to keep all the parts until more definitive research is available on this topic. Sustainable development will require balancing resource use with maintenance of our natural legacies. Ecosystem perspectives must contribute to decisions on where the balance exists.

INTRODUCTION

Maintenance of ecological functions, processes, and disturbance regimes is as important as preserving species, their populations, genetic structure, biotic communities, and landscapes. Hence ecosystem-level processes, services, and disturbances must be considered within the arena of biodiversity concerns.

In the following, we will define ecosystems, illustrate ecosystem structure, function, processes, and disturbance regimes, and consider whether equilibrium and integrity exist. We will also review how diversity relates to stability and productivity. We will then conclude with recommendations to land managers interested in this topic and researchers who wish to help them.

ECOSYSTEM DEFINED

An ecosystem is defined as the biological community plus the physical environment with which it interacts. One can view ecosystems as either abstractions emphasizing

processes such as energy flow, biogeochemical cycles, hydrological relationships, etc., or as bounded, concrete places on the earth's surface. Ecosystems may be as small as a single plant with its associated soil, atmosphere, and fauna or as large as a watershed or a geographic region. While it is comparatively easy to define a watershed and the hydrological cycle of that area, it is impossible to capture completely all of the interactions between the atmosphere, biota, soils, etc. A test of this statement is the challenge to try to map just one part of an ecosystem, e.g., the nitrogen cycle (Allen and Hoekstra 1992).

Ecosystems remained abstractions as long as land management was focused on goods rather than services or processes (Table 1). Now that management perspectives have shifted from goods only to include services and processes (Kessler et al. 1992), it is essential that we determine what functions are occurring and at what rates in order to gauge the integrity of an ecosystem (Rapport 1989). In addition, it is necessary to understand how that ecosystem contributes as a source or sink of energy and materials within its larger region and even in the global context.

ECOSYSTEM FUNCTIONS

Ecosystem functions translate into vital services (Table 1) to human society such as water conservation, balance of atmospheric gases, and waste degradation. Society is beginning to understand the need to sustain intact and productive wildlands, not just for their extractable goods, but also as life support systems.

TABLE 1. VALUES OF ECOSYSTEMS

Goods (Materials)
Foods
Fibers
Fuels
Medicines
Building Materials
Industrial Products
Genetic Resources
Aesthetic, Cultural, Spiritual Renewal
Services (Life Support Systems)
Maintenance of Atmosphere and Hydrosphere
Amelioration of Climate
Origin and Maintenance of Soils (and their buffering capacity)
Absorption and Degradation of Wastes
Natural Control of Pathogenic and Parasitic Organisms
Processes
Production of Organic Matter
Decomposition of Organic Matter
Nutrient Cycling
Grazing Regime
Fire Regime
Hydrologic Regime
Infiltration
Runoff
Evapotranspiration
Soil Erosion Regime

A large segment of human society now questions management approaches that simplify ecological systems by concentrating nutrients and energy into efficient production of desired goods. The full array of values (goods, services, processes) of wildlands may be compromised by ecological simplification. Ecosystem structure and function, rates of ecosystem processes and disturbance regimes, and their stability are influenced by biotic diversity from the genetic to landscape levels (Solbrig 1991a). The quantitative interrelationships are, however, unknown for the most part and therefore the subject of considerable controversy (Pimm 1991).

ECOSYSTEM PROCESSES

Examples of major ecosystem processes are flow of energy, cycling of nutrients, fire, soil erosion, and hydrologi-

cal regimes. Climate may be the principal driver of these processes, but interactions between land use and biotic influences and their feedbacks may markedly alter these processes. Abundance of particular species can have disproportionately large effects on these processes. For instance, Vitousek (1990) has shown how the invasion of a single species of nitrogen-fixing tree into Hawaii is beginning to alter everything else about those ecosystems. The invasion of cheatgrass (*Bromus tectorum*) into the Great Basin is another example of how ecosystem-wide alterations can occur with the addition of only one exotic species (Billings 1990). Hobbs and Huenneke (1992) review this topic more generally, illustrating how maximal diversity is usually found at intermediate frequencies of disturbance. Thus, if managers wish to maintain such diversity and limit local extinctions and invasions, more than passive protection is needed.

Dramatic changes in entire ecosystems are generally slow. Because we can rarely observe impacts species by species, ecologists have often resorted to concepts such as guilds, functional groups, leagues, and minimal structure, while recognizing the necessity to consider keystone species, critical link species, and exotic species.

It is impossible to prevent all environmental degradation, species extinctions, and species invasions. The human population of the planet is already too large, especially in view of the increasing demand for goods and services as populations in less developed parts of the world raise their expectations for living standards. In addition, the extreme mobility of humans and their penchant for transporting organisms with them makes it impossible to diminish further movement of organisms to new locales. The establishment of non-native species will generally relate to the degree of landscape fragmentation and variable disturbance (Hobbs and Huenneke 1992) and have impacts in proportion to the adventives' roles at the ecosystem level (Vitousek 1990).

Because of the inevitability of both environmental and biotic change, it is essential that we alter our unrealistic focus on the past, particularly the supposed equilibrium condition of the pristine. We will not go that way again (Allen and Hoekstra 1992, Hobbs and Huenneke 1992). We need to shift focus from the pristine and equilibrium condition to nonequilibrium or nonsteady state ecosystems in which future pathways of change may be different, stochastic, and even chaotic. Given that ecosystems do not behave as equilibrium conceptual models predict, the question becomes, can we maintain their biological and ecological integrity?

ECOSYSTEM INTEGRITY

Some prefer to talk of ecosystem "health" (Rapport 1989). We contend that this is not a good metaphor because it leads to superorganismic thinking. We prefer the expression "ecological integrity." Establishment of standards for ecosystem integrity will revolutionize the management of wildlands because we will be forced to confront the ethical questions of how humans fit with nature (Grumbine 1992).¹

There is no agreement about what is meant by ecological integrity. Cairns (1977) defines biological integrity as "the

¹See West, this volume.

maintenance of community structure and function characteristics of a particular locale deemed satisfactory to society.” West (1993) defined ecosystem integrity as preservation of the remaining soil profile, plus reasonable levels of the critical ecosystem functions of energy flow and nutrient cycling such that human society maintains options, mainly for food production.

Salwasser (1994) defines ecosystem integrity as “possession of a full set of natural parts and processes in good working order.” Can ecosystem integrity be defined through purely biological data or need environmental factors and their interactions with biota be monitored? In order to answer that question, it is necessary to review briefly current theories of community-ecosystem interactions.

THEORIES OF COMMUNITY-ECOSYSTEM INTERACTION

DIVERSITY/STABILITY

For diversity, we here mean taxonomic richness of the biotic community at the alpha level.² We are thinking of stability in this context as maintenance of rates of function (e.g., net primary production, nutrient cycling).

RIVET HYPOTHESIS

Most ecologists have held to the notion that increased diversity results in increased stability. Ehrlich and Ehrlich (1981) called this notion the “rivet” hypothesis. This hypothesis assumes that each species plays an incrementally important role (like that of rivets in holding an airplane together). Thus, after the loss of a certain set of species, a threshold is crossed and rapid degradative change occurs (the airplane crashes). This is really a restatement of Aldo Leopold’s first rule of ecological tinkering—save all the pieces. The assumption that all species need to be retained is at the core of Grumbine’s (1994) view of ecosystem management.

REDUNDANCY

Another approach, the theory of structural and functional redundancy, conceptualizes communities as composed of a few structural and functional groups, each of which is composed of several ecologically equivalent species. In such communities, some species may be lost with little or no effect on ecosystem processes (Walker 1992). Thus, redundancy at the species level can be thought of as “insurance” or “backup” because each species within the group is functionally equivalent.

Which is the more reliable model?

Common sense favors the rivet hypothesis. The logic used is that although each of the species within a group can tolerate only a limited range of climatic and biotic conditions, the tolerances of each species probably differ at least somewhat from those of all other species within the group. The logic of those favoring redundancy is that with several species in each structural and functional group, those structural and

functional features are more likely to persist under global environmental change. However, Odum (1992) points out that maybe the backup components are not as efficient as the primary ones.

The modeling efforts of May (1973) showed no increase in stability with increased species diversity and food web complexity. May’s definition of stability was, however, quite restrictive. Peters (1991) reviews this topic, including the modeling, and concludes that it is hopelessly confused.

Very little direct experimental data yet exist to favor one theory over the other (Simpson 1988, Solbrig 1991a, Chapin et al. 1992). A lot of research on this topic is now under way, however (Anon. 1993, Baskin 1994). Tilman and Downing (1994) reexamined some data from fertilized Minnesota grassland recovering from drought and concluded that more diverse grassland plots showed greater resistance to and recovered more fully from drought. Each additional species lost from their grasslands had a progressively greater impact on drought resistance. Further long-term detailed observations of ecosystems (Holdgate 1991, Walker 1992, Solbrig 1991b, Frank and McNaughton 1991, Heal et al. 1993) will be required before greater generality can be reached. Until the results of such studies are published for a variety of ecosystems, we are reduced to either logical or historical arguments, a style of research with distinct problems (Peters 1991).

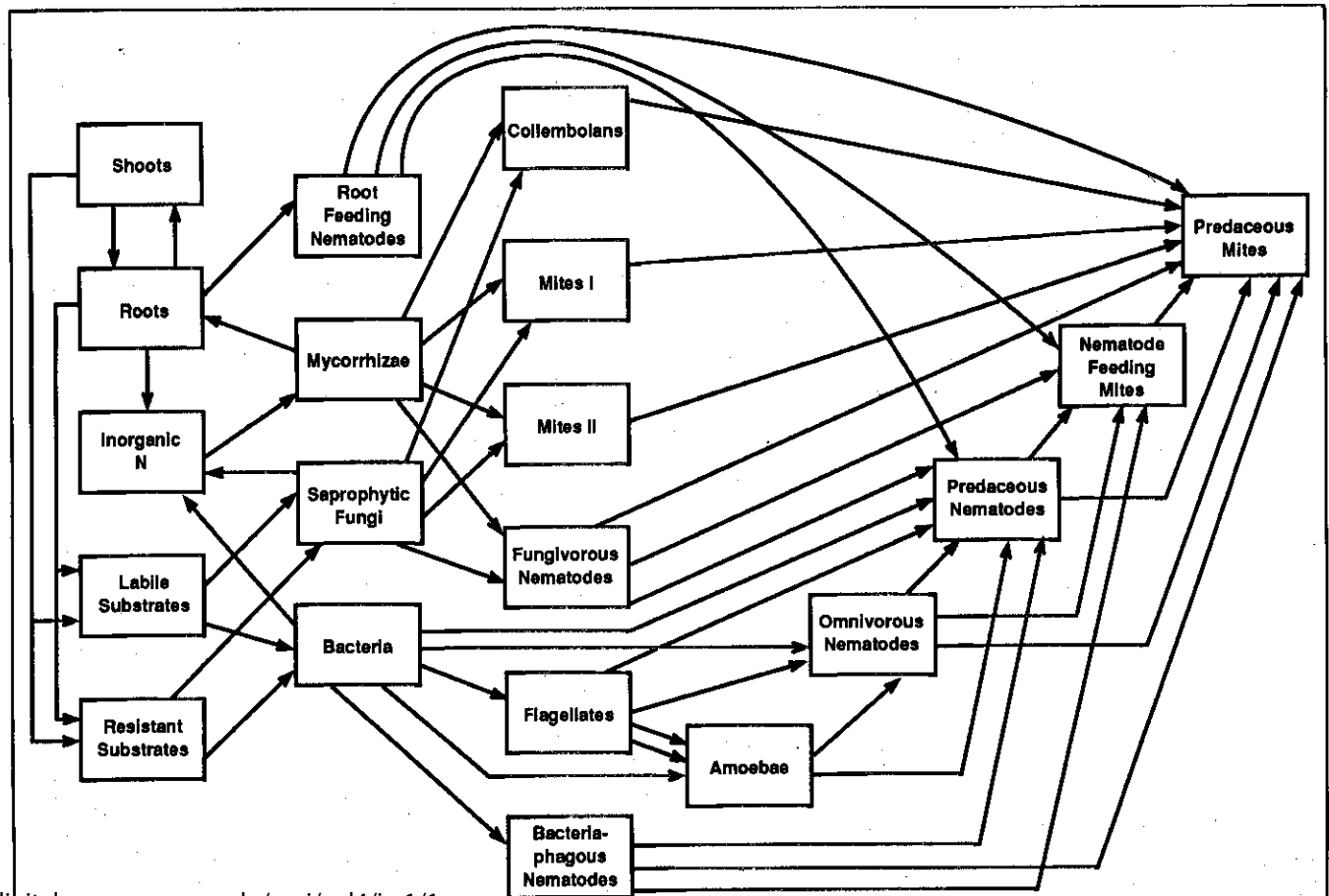
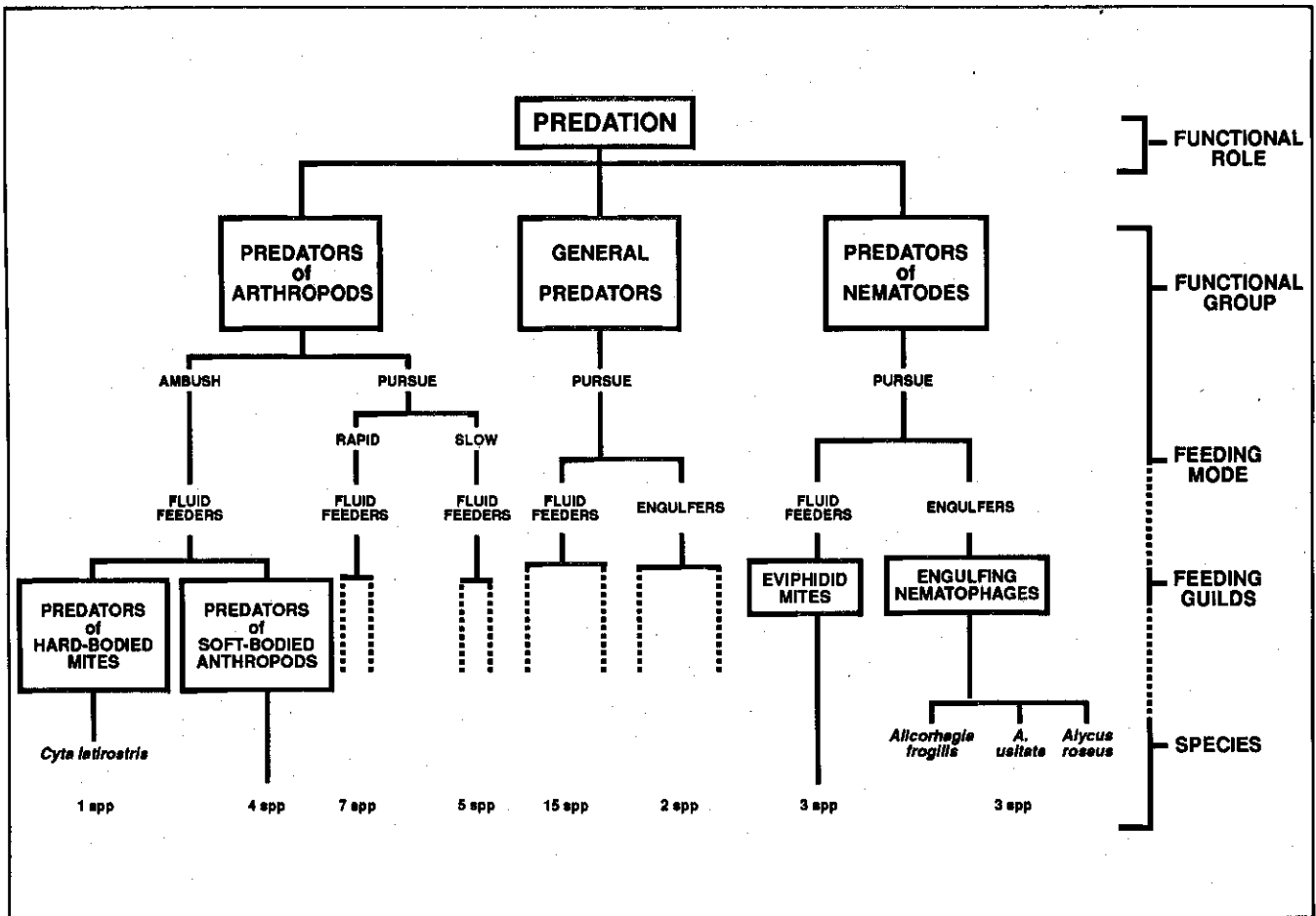
DIVERSITY/PRODUCTIVITY

Earlier workers believed that increased diversity inevitably led to increased productivity, thinking that as more species appeared there were self-augmented appearances of organisms at higher trophic levels. Marshes, however, are systems with low plant species richness but with considerable trophic diversity (complexity of food webs) yet with some of the highest levels of overall productivity. Most ecosystems, however, have species richness higher than that required for efficient biogeochemical and trophic functions (DiCasteri 1991). Functional groupings have been proposed as a means of aggregating species having similar effects on ecosystem processes (Walker 1992). The term *functional group* defines a species assemblage in which all of the species perform a certain functional role in the ecosystem. Functional group contrasts with guild, which has come to mean all species using some resource (Simberloff and Dayan 1991). Because we can never determine how each species affects all ecosystem functions, aggregates such as “functional group” may be a practical necessity. In functional groups with more than one species, there is the implication that one or more of the species may be equivalent or redundant. Implicit in this is the assumption that the ecosystem could function equally well with fewer species in that functional group. A species, however, doesn’t just fit in one functional group. It may be a critical member in another grouping that wasn’t examined. Faber (1991) has introduced the concept of “league,” which assembles organisms by their exploitation of or processing in more than one habitat.

Many examples of the use of functional groups in ecological research come from studies of the biological control of biogeochemical cycles. This is largely because of severe

²See Moir and Bonham, this volume.

West and Whitford, Figure 1. The top half of the figure was omitted. Below is the correct and complete figure.



deficiencies in taxonomic determinations of organisms living belowground (Klopatek et al. 1992). Thus, much of the research on belowground processes has of necessity focused on functional groups, and on guilds such as bacterial-feeding nematodes and fungus-feeding mites (Ingham et al. 1986a, b, Parker et al. 1984, Elliot et al. 1988, Whitford and Parker 1989) (Figure 1). These functional groups contain many species and the biogeochemical processes proceed in what appears to be a "normal" fashion in microcosm studies in which the diversity of species in any functional group was greatly reduced (Cole et al. 1978). Even when a single functional group such as predatory mites was broken down into finer subdivisions, most of the subdivisions remained characterized by multiple species (Elliott et al. 1988), implying that many species within each functional group may be equivalent or redundant.

Anecdotal, historical evidence also appears to support the idea of redundancy in functional groups. For example, while the loss of American chestnut trees and passenger pigeons from the eastern deciduous forests of the United States led to some short-term economic impacts for that small segment of the population that harvested these species for food or fiber, other species filled in the space and drew on the resources that those species once utilized. The end result of those extinctions was that no undesirable long-term changes

in total productivity and watershed protection were noticed (Johnson and Mayeaux 1992).

Proponents of the rivet hypothesis would counter that loss of any species is important and forever. The genomes of passenger pigeons cannot be used to improve the world's genetic options via any technology that we now possess (but scenarios like that in Michael Crichton's book *Jurassic Park* may become real some day). Furthermore, devising any structural or functional categories results in arbitrary overgeneralizations that possibly mask the structural and functional uniqueness of any individuals or species populations.

As is the case with the passenger pigeon and chestnut, because we generally lack sufficiently detailed data on the conditions before and at the time of the extinctions, we could be overlooking subtle associated losses or consequences. For example, we have no knowledge of the ecosystem connections of the seven species of lepidopterans that fed exclusively on American chestnut and thus have become extinct (Opler 1977). There were concomitant impacts on the forests besides the chestnut blight, e.g., timber harvesting, air pollution, excessive hunting, livestock grazing (particularly by hogs), etc. These may have uniquely interacted with the loss of the tree and the pigeon.

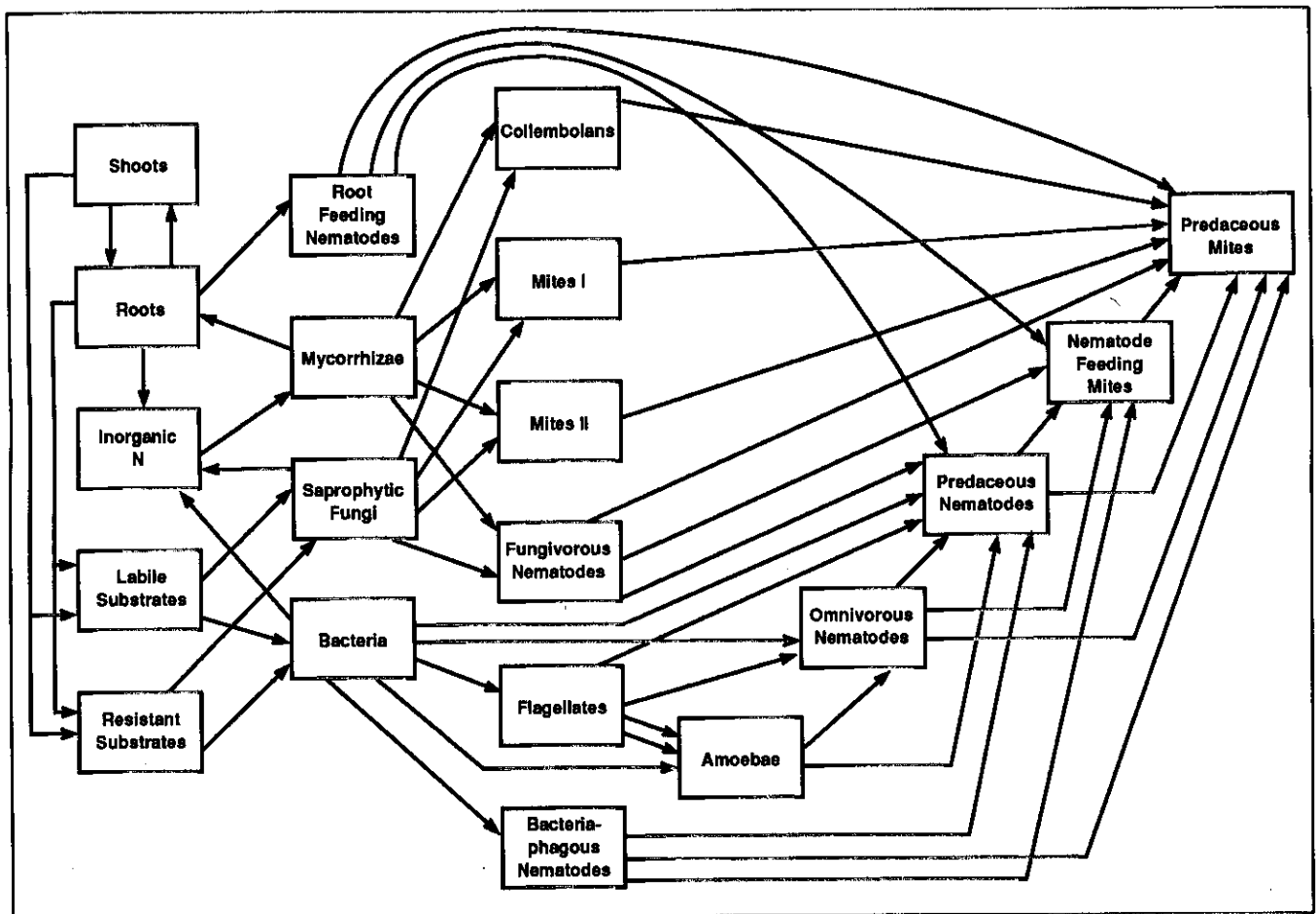


Figure 1. Belowground food webs

ACTIONS NEEDED

Analysis of past incidences of extinctions suffers from inadequately detailed data and lack of replication and control. Studies of only the past will thus never defuse the debate over hypotheses of community-ecosystem interactions. Well-designed experimental studies are needed where they are tractable and ethical. However, most ecosystems are too large and unique to find replicates. Furthermore, control and manipulation of just one factor at a time is unreasonable (Eberhardt and Thomas 1991). Thus, what is currently needed is to combine management and research in an approach called adaptive resource management (Walters 1986, Allen and Hoekstra 1992) and monitor some management units closely enough to allow us to see if simplified ones are functionally less desirable than the biotically richer "controls."

All species are not created equal. Some are "drivers" and some are "passengers" (Walker 1992). The extent of change will largely depend upon the tightness of the linkage of major species to others in the food web (Pimm 1991). Considerable effort must be invested in the identification of these major linkages. Until convincingly demonstrated otherwise, Leopold's axiom should prevail—save all the pieces possible.

LIFE FORMS AND ECOSYSTEM ARCHITECTURE

Biological communities are frequently described on the basis of dominant life forms or structural dominants, e.g., bunchgrass steppe, open woodland, thorn scrubland, etc. The life form of such dominant species affects important ecosystem properties and processes. These dominants are the organisms that directly interface with climate and modify microclimates associated with them in their immediate environment (e.g., Pierson and Wight 1991). These are the species that Solbrig (1991c) refers to as "structural" species that by virtue of their size, abundance, and structural features influence the local environment. "Structural" species may have direct influences on ecosystem services such as ground water and stream water. For instance, from a recent study in Great Britain, stem flow water from trees on wooded hillslopes was shown to bypass the soil matrix by rapidly following root channels (macropores), accounting for the major characteristics of stream hydrographs (Crabtree and Trudgill 1985). Vetaas (1992) reviewed the contributions of trees and shrubs in savannas to water and nutrient distribution patterns and on species composition and community diversity. That review points to the importance of these "structural" species in influencing ecosystem properties. Obviously there may be redundancy in species that are the "structural" dominants, e.g., pinyon and juniper in those woodlands. However, the potential importance of such dominants and the frequently overwhelming importance of a single "structural" species in an ecosystem suggests that structural species should be carefully considered with respect to their effects on ecosystem goods, services, and processes.

KEYSTONE SPECIES

Species whose direct or indirect effects on the survival of other species or on ecosystem function is disproportionately large in relation to their abundance are called "keystone" species (Westman 1990). Keystone species fall into three general classes: (1) keystone predators, (2) keystone mutualists, and (3) keystone resource species. Keystone predators are carnivores, herbivores, parasites, or pathogens that allow the maintenance of diversity among competing organisms by reducing the abundance of dominants and thus prevent competitive exclusion. An example of a keystone predator is the wolf in many North American and Eurasian wildlands with abundant ungulates. Keystone mutualists are organisms such as mycorrhizae and honey bees that link the fate of many partner species. Keystone resource species provide resources during bottlenecks of resource availability or chronically low resource availability. A rangeland example would be prickly pear cacti serving as a food resource for animals as diverse as javelina and coyotes, and even cattle during drought. Another example of a resource species is the N-fixing plants in semiarid to arid regions. By definition, there is no redundancy in the critical function of a "keystone" species.

The keystone-species concept has been expanded to include guilds or functional groups of species (Simberloff and Dayan 1991). For example, Brown and Heske (1990), in a long-term experimental study in the Chihuahuan Desert in eastern Arizona, found that without kangaroo rats (*Dipodomys* spp.), there was a significant reduction in shrubs, but a significant increase in grass cover. Investigations by Chew and Whitford (1992) and Hawkins and Nicoletto (1992) have reinforced this view of kangaroo rats as a keystone group.³

Another keystone functional group in many subtropical deserts, grasslands, and savannas is subterranean termites. These animals process more than 50 percent of the dead organic matter and herbivore dung in the Chihuahuan Desert, as well as physically modifying the soil and thereby affecting infiltration, water storage, and nutrient cycling. Elimination of termites on experimental plots has resulted in marked changes in species composition and/or productivity of annual forbs, perennial grasses, and shrubs (Whitford 1991).

Given the constraints of the experimental designs in the cases discussed above, it is not possible to say unequivocally that the keystone species in these examples are Merriam's kangaroo rats (*Dipodomys merriami*) and termites (*Gnathamitermes tubiformans*), despite their relatively high abundance with respect to other potential species in the group. Mills et al. (1993) warn us to use care in defining what we mean by keystone species. Different questions will require different approaches (Allen and Hoekstra 1992). Man could be considered to be the major keystone species in most present contexts (Salwasser and Pfister 1994). Obviously considerable work is necessary to identify keystone species and their effects on ecosystems. These species are of obvious importance to land managers, but there is scant knowledge of them for rangeland ecosystems.

³See Parmenter et al., this volume, for further detail.

EXOTIC AND ALIEN SPECIES

Policies calling for removal of all exotic, alien, or introduced species appear to rest on the old notion of a totally interdependent community in which any change in abundance of any species is a threat to the entire community (the "rivet" hypothesis). However, wildland communities continuously receive new arrivals. The consequent readjustments don't always result in a net loss of species. Indeed, plant species richness of the California annual grasslands is probably much higher today than it was prior to the coming of European man (Johnson and Mayeaux 1992).

The introduction of exotics is not always as innocuous as the annual grasses in California's central valley (Hobbs and Huenneke 1992). For instance, the imported fire ant has certainly affected the biotic communities in many areas in the southeastern United States, where it occurs in high densities (Porter and Savignano 1990, Tschinkel 1993). The imported fire ant is also a good example of how an introduced species can change genetically, thereby changing its role in the ecosystem (Mann 1994). The introduction of salt cedars (*Tamarix* spp.) into the southern Great Plains and Southwest, and their consequent monopolization of riparian zones, is definitely a case of undesirable simplification of an ecosystem (Graf 1978), possibly endangering the willow flycatcher. It is indeed difficult, if not impossible, to evaluate the consequences of a species introduction during its early stages because we generally lack detailed information on the biology of such species.

Most communities do not consist of highly coevolved species pairs, but exhibit some substitutability by species within groups (Westman 1990). This is not to deny mutualism and the existence of keystone or critical link species, but rather to acknowledge that not all species play these roles. We need to differentiate between the exotics to worry about and those that are of less worry, based on what they do. Vitousek (1990) makes a good case for concentrating on exotics that play a strong role in energy flow or nutrient cycles or that change disturbance regimes. A good example on western rangelands is cheatgrass (Billings 1990). Introduction of this winter annual grass has led to a shortening of the interannual fire cycle by about an order of magnitude. Furthermore, fires now come earlier within the year so that the chances of soil erosion are increased. The consequent lack of recovery of native perennial bunch grasses and nonsprouting shrubs such as sagebrush leads to enormous change in the biotic communities and the accompanying environments (West 1995).

CRITICAL LINK SPECIES

Critical link species are those that play a vital role in ecosystem function, regardless of their biomass, place in a food web, or possible role as a keystone species (Westman 1990). Mycorrhizal fungi are an example of a group of critical link species on rangelands. These organisms exchange carbon fixed by green plants for enhanced uptake of phosphorus. The absence of appropriate mycorrhizal species may severely inhibit the establishment and growth of the vascular plants that depend upon them. Approximately 90 percent of all

vascular plants are thought to depend upon mycorrhizal mutualists. The importance of these species in rangeland ecosystems is demonstrated by the studies of Wicklow-Howard (1989), who found that repeated fires promoted by cheatgrass on land formerly covered by sagebrush steppe can lead to extinction of mycorrhizae over vast areas and impede attempts to reestablish shrubs and perennial grasses there.

It is necessary, but not sufficient, simply to identify critical link species. Quantitative knowledge of their ecological interactions and substitutability will be required if such species are to be considered in management policy. For instance, the effectiveness of the mycorrhizal-plant symbiosis can be affected by other organisms in the system. Soil collembola have been found to reduce the effectiveness of phosphorus transfer to grasses by grazing on the VA mycorrhizal hyphae (McGonigle and Fitter 1988). The same species of collembolans that graze on mycorrhizal fungi may be essential in the mineralization of nutrients immobilized in the hyphae of saprophagic fungi. Firmly establishing critical links will require addition or subtraction experiments.

The concepts of minimal and configurational structure (Pickett et al. 1989) are also worth considering. Species composition (configurational structure) within functional groups (minimal structure) may vary widely without collapse of biotic communities or ecosystems. Stenhouse (1991) has recently demonstrated how qualitatively defining stability as the maintenance of minimal structure is a practical approach to assessment of ecosystem change. Grabherr (1989) gives an example of how to proceed to identify keystone species, modules, guilds, or functional groups on rangelands, but see also the warnings of Mills et al. (1993) before undertaking this type of work.

Another possible way of quantifying ecosystem diversity is through food web complexity (Kikkawa 1986). This is because the number of feeding links reflects total productivity plus the number of links that can develop between all trophic levels in the ecosystems of interest. We have barely begun this kind of research on rangelands.

CONCLUSION

We hope to have convincingly demonstrated that diversity of services, processes, and disturbances within ecosystems is another important facet of biodiversity to consider. The importance of extinction and invasion is not equivalent for all species; it depends on what those organisms do within ecosystems. We have barely begun to understand rangelands as ecosystems. The linkage of biodiversity to ecosystem function is scarcely known in these as well as most other ecosystems (Schulze and Mooney 1993). Considerably more effort should immediately go toward identifying functional groupings, relative importances, connections, and the impacts of additions or subtractions. Loss of species is inevitable, loss of functions need not be if we understand our rangeland ecosystems well enough to prioritize our management and protection efforts. The ecosystem-level concerns are, however, but one facet of biodiversity. We acknowledge that there will be situations where preservation of species

with no obviously important role in ecosystems takes precedence (e.g., the charismatic megafauna). Such decisions will involve ethics and aesthetics more than functionality.

If sustainable development is ever to be realized, we need to find ways that natural resources can be both used and maintained. Finding balancing points would be easier if we better understood the roles that both species and other groupings play in ecosystem structure and function.

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Landscape Diversity in the Western Great Basin

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Abstract

The biological diversity that is supported by a particular area is generally a positive function of the degree of environmental heterogeneity occurring over space and time within that area. Because heterogeneity or patchiness can occur from very small to very large spatial scales, biodiversity at the extensive scales covered by landscapes can be affected by heterogeneity occurring in a nested series of smaller-scale patches. We discuss this relationship between patchiness and biodiversity in the context of nonequilibrium models of community organization, such as source/sink and metapopulation models, and contrast this with the traditional equilibrium view of ecological communities. We provide empirical examples from western Great Basin landscapes demonstrating that animal species diversity is a positive function of heterogeneity in the local vegetation. We then extend this to consider stand renewal processes in Great Basin plant communities, especially effects of anthropogenic changes in these processes on landscape-level heterogeneity. Under pristine conditions small-scale and infrequent herbivory may have been the predominant mechanism of stand renewal, but this process has been overshadowed during this century by large-scale, catastrophic fires. A promiscuous burning period in which fires were intentionally set characterized stand renewal shortly after European settlement of the West. For the past several decades this has been replaced by frequent unintentional range fires carried by fine fuels provided by introduced annual weeds. These changes in the spatial and temporal patterns of stand renewal reduce environmental patchiness and associated biodiversity across Great Basin landscapes.

INTRODUCTION

Most past considerations of diversity at the landscape level have concerned geographic areas with very limited variability in the basic soils and landforms where highly developed crop production has been imposed for a considerable period of time. In such an environment, features such as farm wood lots, drainage ways, wetlands, and corridors that connect such features become of paramount importance in assessing landscape level diversity. In the western United States there are many examples where a patchwork of intensively farmed areas and rangelands creates similar landscapes, but at different scales from that found in humid climates. Irrigated agriculture in semiarid and arid environments can cause dysfunction of range landscapes or create extensive new landscapes, depending on scale.

In this presentation we will discuss biodiversity at the landscape level from a general perspective, but will concentrate on specific examples from the range landscapes of the western Great Basin, an area where we have the most experience. This is an environment where less than 5 percent of the total landscape has been subjected to intensive agriculture and where almost all of the nonagronomic landscapes are rangelands. Our rationale aims for originality at the expense of reiteration of the experiences from other landscapes.

HETEROGENEITY AND ASSESSING LANDSCAPE DIVERSITY

The extensive areas classified by ecologists as "landscapes" can be considered to consist of a nested hierarchy of different-sized patches (Kolasa 1989, Kotliar and Wiens 1990). Patch sizes vary substantially, ranging perhaps from a few square centimeters to many square kilometers. The sizes of patches important to individual organisms are also quite variable, and depend on ecological requirements and natural history characteristics such as the organism's size and mobility. Thus, for a specialized phytophagous insect, relevant patch types may be restricted in size range from a single leaf to a single shrub, while for a generalized mammalian browser, patch sizes may vary from a small stand of shrubs to a vast expanse of rangeland encompassing an entire valley or more. The smallest patches recognized by a particular organism are referred to as its "grain," while the "extent" of the organism refers to the largest patches utilized (Kotliar and Wiens 1990). For example, the extent of an animal, covering its entire lifetime home range, may include various smaller-scale patches down to its grain, which may be specific foraging microsites. While a variety of patch sizes may occur between the extremes represented by grain and extent, organisms differ in the degree to which they perceive and respond to this intermediate-level patchiness. These

terms are also applied to studies conducted at the landscape level, but in this case the grain corresponds to the sampling unit and the extent to the area encompassed by the study (Turner 1989).

The degree of heterogeneity within a landscape is determined by two properties of its constituent patches: landscape heterogeneity is directly correlated with "contrast," or the distinctness of different patch types, and is inversely correlated with "aggregation," or the spatial clumping of patches (Kotliar and Wiens 1990). The sensory abilities of an organism determine how it perceives the heterogeneity or patchiness of its environment. As human observers, we perceive patchiness in terms of visual discontinuities in structural components of our environment. An animal with well-developed olfaction may perceive patchiness based instead on chemical discontinuities or gradients. Although a landscape is really a mosaic of different types of patches, an organism that specializes on particular patch types may perceive the landscape as a small number of suitable patches arranged in a matrix of unsuitability.

Superimposed on this spatial patchiness are temporal effects on landscape patchiness arising from disturbance and successional changes. Indeed, it is partly because of the patchy nature of these temporal effects that landscapes appear spatially heterogeneous. If disturbances generally occurred over vast areas and if successional recovery of these disturbed areas occurred in a uniform fashion, landscapes would be composed of highly aggregated patches with little contrast and would therefore be very homogeneous.

Considerable theoretical and empirical evidence indicates that biological diversity is a direct function of the patchiness or degree of heterogeneity of a landscape. Therefore, the necessary tools for assessing landscape biodiversity include a variety of techniques for characterizing and analyzing environmental heterogeneity (cf. Magurran 1988, Turner 1989, Turner and Gardner 1990, Johnson et al. 1992). Although traditional ground-level approaches for sampling and quantifying spatial patchiness are still applied in many situations, the use of remote sensing techniques, which allow one to visualize structural patchiness based on discontinuities in spectral reflectance, has obvious applications for assessing heterogeneity and associated diversity at the scale of landscapes (Pickup 1989). However, remote sensing places a lower limit on the grain size that can be resolved, and the technique can reveal heterogeneity only on the basis of reflectance; nonvisual sources of patchiness are not identified. Ground-based sampling may be required to overcome such problems.

A comprehensive review of landscape diversity assessment and potential interpretation techniques for remotely sensed data has recently been published in the proceedings of the symposium "Evaluation of Reclamation Success: The Ecological Considerations" (Tueller 1992). In this paper Tueller suggests: "Each landscape that we work on has both vertical and horizontal dimensions. The horizontal dimensions are the polygons that we describe when we map the various ecosystems. The vertical dimensions are the geology, soil, soil chemistry, ground water systems, lake and river

depths and other variables encountered in the earthward dimensions. The structure of the vegetation and its various layers constitutes another vertical dimension as does the atmosphere." This quotation alludes to another potential limitation of remote sensing: it reveals heterogeneity in the horizontal dimension to a much greater extent than in the vertical dimension. Fortunately, this is less of a problem in studies of desert landscapes, where vegetation layering is not pronounced, than in landscapes with complex vertical structure such as forests.

Tueller cites an often quoted definition from Pickett and White (1985): "Landscape patterns are the consequence of numerous disturbances or perturbations creating patches. Patch implies a relatively discrete spatial pattern, but does not establish any constraint on patch size, internal homogeneity, or discreteness." Landscape heterogeneity is thus largely determined by spatial and temporal patterns of disturbance, or how plant communities are renewed. The death of a plant community foretells its future. In forested areas such as the Pacific Northwest, the connection between the stand renewal process by timber harvesting procedures such as clear cutting and landscape heterogeneity is apparent. In temperate deserts of the Great Basin, where vegetation is very sparse, layers few, and biomass relatively slight, the influence of stand renewal is far more subtle.

SPATIAL HETEROGENEITY AND ANIMAL BIODIVERSITY

What is the underlying ecological basis for the purported correlation between environmental heterogeneity and biological diversity? In this section, we discuss theoretical and empirical support for this correlation and use animal examples to illustrate how spatial heterogeneity can promote biodiversity. Although we follow the convention of emphasizing the species richness aspect of biodiversity, the direct relationship between environmental heterogeneity and biodiversity is equally applicable to concepts such as species evenness and to structural, demographic, and genetic diversity within species, and to functional processes and structural features of landscapes as well.

Traditional equilibrium models of species coexistence in ecological communities that assume the operation of deterministic species interactions in a uniform environment often underestimate the diversity observed in natural communities (DeAngelis and Waterhouse 1987). For example, simple two-species models may fail to predict the coexistence of competing species or of predator and prey populations that actually do coexist, or alternatively such models may predict coexistence only under unrealistically restrictive conditions. When one considers the concepts of species interactions and species-specific ecological niches in the landscape framework of nested patch hierarchies, however, it is intuitively clear that persistence of competitive or predator/prey systems is not only possible, but likely.

At any particular scale within the patch-size hierarchy, the number of ecologically similar species that can coexist without competitive exclusion occurring is correlated with

the number of "ecological opportunities" available, and each distinct patch type can be considered to provide a different opportunity. In the simplest case, each individual species is most successful in a different patch type, so the number of species is equal to the number of ecological opportunities that is in turn equal to the number of patch types. Similarly, the persistence of predator/prey systems will be enhanced with increasing patchiness, because certain patches will provide good opportunities for predator hunting while other patches (i.e., those with better refuges) will provide good opportunities for predator avoidance by prey. Our use of the term *opportunity* here is similar to the concept of the ecological niche as articulated by Grinnell (1917), but in a more restrictive sense. We imagine different ecological opportunities arising through qualitative differences in the patch types that comprise a landscape. Thus, at any given time these opportunities can be delineated solely in terms of space. By contrast, species' ecological niches can differ not only through interspecific differences in the use of space, but through differences in any particular axis that is included in the multidimensional niche. In reality, then, two or more ecologically similar species can coexist in a particular patch type because of interspecific niche differences that do not involve spatial use.

The combined effects of patch hierarchies and patch contrast or distinctness in promoting biodiversity can be further appreciated in light of the concepts of alpha, beta, and gamma diversity (Neilson et al. 1992) by considering some intermediate size of patches within a landscape to constitute "communities." Based on the above argument, the degree of smaller-scale patchiness within each community will directly affect the diversity of that community (α -diversity). The distinctness of each community will directly affect the amount of species turnover among communities (β -diversity). The combination of increasing α -diversity within communities and increasing β -diversity among communities that occurs with increasing environmental heterogeneity will necessarily yield increased gamma-diversity at the landscape level.

These intuitive arguments regarding effects of patchiness on biodiversity have been formalized in various analytical models. Pulliam (1988) imagined that animal populations are composed of subpopulations, some of which occur in productive "source" habitats while others occur in "sink" habitats where reproductive success is too low to offset local mortality. Sink habitat subpopulations are maintained by immigration of excess individuals produced in source habitat subpopulations. Pulliam's model demonstrates that such a system can persist in some cases even when only a small proportion of the overall population occurs in source habitats. Danielson (1991) extended the source-sink model to consider a two-species system in which the source habitat for each species is the sink for the other, and demonstrated that although the two species share a common resource they can coexist at the landscape level with competition, commensalism, or even mutualism resulting from their interaction.

The idea of populations being subdivided into productive and unproductive patches has been further generalized in "metapopulation" models (e.g., Gilpin and Hanski 1991, Stacey and Taper 1992) that consider temporal as well as

spatial variance in a species' reproductive success. A metapopulation consists of a number of smaller populations with decoupled dynamics that occur in disjunct patches across a landscape. A given patch may represent a source habitat during locally favorable times and a sink habitat during unfavorable times. If a population crashes or goes extinct in a patch, it can be rescued by immigrants from other patches within the metapopulation. In a landscape consisting of communities of interacting species undergoing separate metapopulation dynamics, a nonequilibrium coexistence is likely in spite of the prevalence of unstable species interactions at a local patch level. Even in the absence of the patch quality variation assumed in more recent metapopulation models, den Boer's (1981) "spreading of risk" model demonstrates that asynchronously fluctuating subpopulations are more likely to persist than either a fluctuating composite population or than subpopulations fluctuating synchronously.

Empirical evidence for a direct relationship between environmental heterogeneity and animal biodiversity comes from a variety of systems ranging from deposit feeders in deep-sea-sediment communities (Etter and Grassle 1992) to the well-known correlation between bird species diversity and foliage height diversity (MacArthur and MacArthur 1961, Willson 1974). Although the latter correlation was established from comparisons of bird species residency in habitats ranging from simple grasslands to complex multi-layered forests, bird communities in sparsely layered Great Basin landscapes also exhibit this pattern (Wiens and Rotenberry 1981, McAdoo et al. 1989). Specifically, McAdoo et al. (1989) demonstrated that bird species richness is lower in both shrub-dominated and grass-dominated habitats than in habitats with a relatively even mixture of shrubs and grasses, even though overall bird abundance did not differ significantly among these three habitat types (Table 1). While shrub- and grass-dominated habitats contained only species whose nesting habits require shrubs and grass respectively, mixed habitats contained virtually all species from both the shrub- and grass-nesting groups.

Additional support for a heterogeneity/biodiversity correlation comes from studies of small mammal community responses to disturbance (mainly wildfire) in the western Great Basin. Early- and late-successional plant communities, which are dominated by herbaceous and shrub species respectively, tend to harbor fewer small mammal species than more heterogeneous midsuccessional plant communities (Longland, in press; unpublished data; Table 2). Those species that remain immediately following reduction of food supplies and protective vegetation cover by fire (kangaroo rats, *Dipodomys* spp., and pocket mice, *Perognathus* spp.) are both more efficient foragers and superior at evading predators relative to those species that disappear. Experiments at the Red Rock site represented in Table 2 showed that when vegetation cover is removed without reducing the availability of food (mainly seeds for these rodents), rodent species composition changed in a manner very similar to changes induced by fire. Thus, rodent species composition in early-successional Great Basin environments may be driven by predation risk. One rodent species in the unburned habitat at Red Rock, the western harvest mouse (*Reithrodontomys megalotis*) has still not

TABLE 1. SHRUB COVER, HERBACEOUS COVER, AND BIRD ABUNDANCE, SPECIES RICHNESS, AND REPRESENTATION OF SHRUB- VERSUS GRASS-NESTING BIRD SPECIES IN THREE HABITAT TYPES IN CENTRAL NEVADA (1982-83). SEE McADOO ET AL. (1989) FOR FURTHER DETAILS.

Habitat (# sites)	VEGETATION COVER (%)		Total % abundance ^a	BIRDS Shrub % nesting	Grass nesting	Species richness ^b
	Shrubs	Herbaceous				
Sagebrush (3)	19.9A	2.0A	99.3A	79.8A	20.2A	6.3
Sagebrush/Crested wheatgrass (2)	9.9B	6.8B	93.8A	48.3B	51.7B	9.5
Crested wheatgrass (2)	2.6C	12.4C	114.1A	18.0C	82.0C	7.0

^amean # individual birds/transect-day averaged among sites. Transects were 2700m long.

^bmean # bird species/site.

Values in same column followed by a common letter are not significantly different ($P > 0.05$) based on ANOVA.

TABLE 2. RELATIVE ABUNDANCES (%) OF VARIOUS RODENT SPECIES OCCURRING IN DISTURBED AND UNDISTURBED HABITATS AT THREE WESTERN GREAT BASIN STUDY SITES. FIRE CAUSED THE DISTURBANCE AT THE RED ROCK AND FLANIGAN SITES; EXTENSIVE USE BY DOMESTIC SHEEP DISTURBED THE NOBLE SITE. SUCCESSIONAL STATUS OF EACH HABITAT AT EACH SITE IS CATEGORIZED AS EARLY, INTERMEDIATE (MID), OR LATE BASED ON ELAPSED TIME SINCE DISTURBANCE AND ON RELATIVE EVENNESS OF SHRUB AND GRASS COMPONENTS OF VEGETATION.

Study site	Rodent species	Percentage of captures	
		Undisturbed habitat (successional status: early, mid, late)	Disturbed habitat
Flanigan:		sagebrush (late)	Indian ricegrass/shrub (mid)
	<i>Dipodomys merriami</i>	89	54
	<i>Dipodomys ordii</i>	2	27
	<i>Dipodomys panamintinus</i>	1	12
	<i>Dipodomys deserti</i>	0	3
	<i>Perognathus longimembris</i>	1	3
	<i>Ammospermophilus leucurus</i>	7	1
Red Rock:		Agropyron/shrub (mid)	Agropyron (early)
	<i>Dipodomys panamintinus</i>	2	16
	<i>Perognathus parvus</i>	55	67
	<i>Peromyscus maniculatus</i>	14	17
	<i>Reithrodontomys megalotis</i>	29	0
Noble:		sagebrush/grass (mid)	medusahead (early)
	<i>Perognathus parvus</i>	23	2
	<i>Peromyscus maniculatus</i>	50	95
	<i>Reithrodontomys megalotis</i>	23	2
	<i>Spermophilus lateralis</i>	4	0

reestablished in the postfire habitat five years following fire, perhaps because plant litter, which appears to be an important habitat requirement of harvest mice (Clark and Kaufman 1991), is sparse in the latter habitat.

These empirical and theoretical examples serve to illustrate that the diversity of animals across a landscape is a function of spatial habitat heterogeneity at different scales. The greater the patchiness of habitats at small scales, the more ecological opportunities for specialized species to occupy different patches, and the more possible distinct higher-level patches that arise from combining smaller patches. For terrestrial animals, habitat patches are generally defined by structural features of the environment, especially vegetation. It may be plant genotypes, species, or physiognomy that particular animal species use to distinguish good from poor habitat patches. Thus, the greater the patchiness of plant communities across a landscape, the greater the animal diversity. The remainder of our discussion will therefore focus on temporal and spatial aspects of plant patchiness of western Great Basin landscapes.

PLANT DIVERSITY OF GREAT BASIN LANDSCAPES

Plant diversity at the landscape level is a function of three interacting factors: physiography, genetic heterogeneity, and successional status. Physiography may have little effect on diversity in the case of a vast expanse of a dominant landform with a very similar set of soils. Such a landscape is likely to contain a single, uniform community type, although depending on spatial and temporal scales of stand renewal this uniform appearance may mask considerable demographic diversity among different patches. The basin and range topography of the Great Basin produces the opposite effect: distinct communities occur among physiographically distinct units of the landscape. Not only does heterogeneity induced by physiographic discontinuities affect plant species diversity, but for physiographically widespread species such discontinuities may enhance genetic diversity through local adaptation. Moreover, at the genetic level, a landscape that appears perfectly uniform may, in fact, harbor a diversity of genotypes of the dominant vegetation. The opposite extreme may also occur; the most efficient assemblage of plants to occupy a uniform landscape may be the least diverse that is capable of producing stable duplicates of itself through self-pollination. Finally, the diversity of any plant assemblage is likely to be affected by changes in the frequency and/or extent of disturbance and stand renewal, and it is examples of this last influence on plant diversity of Great Basin landscapes—stand renewal—which we will discuss in detail.

STAND RENEWAL PROCESSES

To those familiar with contemporary Great Basin environments, the mention of stand renewal invokes images of catastrophic renewal of big sagebrush (*Artemisia tridentata*) by wildfires. Certainly the frequency and seasonality of wildfires has much to do with landscape diversity in the Great Basin, and this theme will be developed later in relation to the role of *Bromus tectorum*. Despite the importance of wildfires

in changing diversity, it is important to realize that (1) even in big-sagebrush-dominated communities, other mechanisms of stand renewal exist, and (2) for vast areas of salt desert vegetation, wildfire has a limited role in stand renewal.

Herbivory of Dominant Woody Species

Superficially, the low preference exhibited by most vertebrate herbivores for the dominant species of sagebrush appears to suggest that herbivory is not a major proximate factor in directly shaping the diversity of landscape vegetation in the Great Basin. While this lack of herbivory is generally taken as evidence that herbivores have been important selective agents in the evolution of defensive chemicals among nonpreferred, dominant sagebrush species, one should not overlook the more subtle effects of herbivores on sagebrush communities. For example, herbivory has been credited as an indirect influence on woody vegetation through suppression of preferred herbaceous vegetation that consequently releases woody species from competition. Such selective herbivory decreases biodiversity by enhancing the biomass of woody plants at the expense of herbaceous species. Moreover, even dominant woody species that are generally protected may not be completely immune to herbivory; big sagebrush ecotypes exist that are preferred by large herbivores (e.g., Welch et al. 1981).

Differential herbivory by mule deer (*Odocoileus hemionus*) is known to reduce seed production by preferred ecotypes of mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) (Rodriguez and Welch 1989). In reciprocal transplant garden studies we have noted that introduction of subspecies of big sagebrush to habitats where they are not native resulted in early mortality due to selective herbivory by mule deer (Evans and Young 1990). In native stands it would be very difficult to identify differential herbivory of big sagebrush seedlings. While selective herbivory can influence diversity on a gross scale by restricting representation of preferred genotypes, such influences are probably largely unnoticed at the landscape level.

Perhaps even less appreciated than potential effects of large vertebrate herbivores on woody plant biodiversity in Great Basin landscapes are the effects of smaller vertebrate herbivores and invertebrates. In our experience most collections of basin big sagebrush (*A. tridentata* ssp. *tridentata*) can be transplanted as seedlings to prepared areas in big sagebrush potential sites without damage from blacktail jackrabbits (*Lepus californicus*). However, most transplanted collections of mountain big sagebrush perish without protection from jackrabbits, unless the jackrabbit population in the area is at an extremely low density. Basin big sagebrush is the only woody plant we know of with seedlings that are not routinely consumed by jackrabbits when transplanted in small numbers to a site with big sagebrush potential.

In transplant gardens, we have found that shadscale (*Atriplex confertifolia*) seedlings are more susceptible to predation by small mammals than seedlings of fourwing saltbush (*A. canescens*) (Young and Young 1992a). Seedling recruitment in antelope bitterbrush (*Purshia tridentata*) is strongly affected by collection and scatterhoard caching of

seeds and subsequent predation on emerging seedlings by small mammals (Young and Evans 1981a, Vander Wall 1990).

Voies (*Microtus* spp.), by girdling the trunk of big sagebrush plants, have caused severe damage to the shrubs on a localized basis (e.g., Frischknecht and Baker 1972). A potentially greater effect on stand renewal and plant diversity in big sagebrush communities is attributable to selective seed predation and caching by vertebrate granivores. The woody species of sagebrush have very small seeds (achenes) with deciduous pappus. With 3,000 to 4,000 seeds per gram (Young and Young 1992b), an individual big sagebrush seed is not a very significant component of granivore diets. Harvester ants may utilize such small seeds, but there is no evidence that small mammals consume or cache seeds of big sagebrush. The seeds may approach a lower limit of acceptable size for small mammals (Price 1983) or may be protected from predation by their volatile chemical content. By contrast, substantial fractions of seeds produced by larger-seeded plant species are often utilized by rodents, which may ameliorate seedling competition for small-seeded species such as sagebrush (Brown et al. 1979, Henderson 1990). Thus, although granivores are typically the most abundant and diverse group of herbivores in North American deserts, the diminutive seeds of sagebrush escape predation by an important group of desert granivores (rodents), while the potential big sagebrush seed production is staggering (Young et al. 1989).

Nonvertebrate herbivory of the dominant big sagebrush has been well documented for larvae of the sagebrush defoliator moth (*Aroga websteri*) (e.g., Hsiao 1986). One year after a prescribed burning experiment on the Likely Table in northeastern California in the 1960s the sagebrush defoliator largely killed the big sagebrush in an unburned control treatment (B. L. Kay, personal communication). In this case the stand was apparently very even-aged and the insect infestation was as effective as fire as a stand renewal process. More typically, the sagebrush defoliator kills the oldest or largest big sagebrush plants, releasing the younger, more vigorous plants. In such cases there is no break in sagebrush dominance of the site, but insect herbivory affects the age and size structure of the local sagebrush population. The sagebrush defoliator moth can have a significant interaction with wildfires. If cheatgrass is present in the understory when big sagebrush plants are partially or totally defoliated, an extreme fire hazard develops. Such was the case in 1974 when the Hallelujah Junction wildfire burned 18,000 hectares in the western Great Basin.

Leaf feeding beetles of the genus *Trirhabda* have been reported to destroy 50 percent of big sagebrush stands in British Columbia (Pringle 1960). There are probably many other examples of insects influencing the relative abundance of particular plant species in such a patchy fashion without overtly killing whole stands. This generalization is supported for big sagebrush by experimental results indicating that patchy predation by insectivorous birds produces significant variation among individual plants in abundance of phytophagous insects (Wiens et al. 1991).

Lee Sharp of the University of Idaho recognized in the 1950s that the key stand-renewal process in shadscale communities was insect related. He founded the short-lived "Salt Desert Shrub" research group that was the first to focus research interest on range plants other than perennial grasses in the Intermountain area. Dr. Sharp's concern was halogeton (*Halogeton glomeratus*) invasion of shadscale communities killed by insects. During the 1980s several large-scale die-offs of shadscale in the Intermountain area were associated with large infestations of mealybugs (Hemiptera) (Nelson et al. 1990) and root boring beetles (Coleoptera) (Haws et al. 1990). Insect herbivory appears to contribute to salt desert shrub mortality in conjunction with osmotic, matric, and/or extreme cold-induced stress.

Infestations of root crowns with grubs has been linked with population dynamics of Great Basin shrub species as diverse as winterfat (*Ceratoides lanata*) (Strickler 1956), and green rabbitbrush (*Chrysothamnus viscidiflorus*) (Young and Evans 1974a). Even the extreme halophyte *Allenrolfea occidentalis* is a host for root grubs. Root grubs may play a major role in ending the low-seral dominance of green rabbitbrush in disturbed big sagebrush communities, and the successional transition from rabbitbrush to sagebrush in these communities which, in turn, is a major temporal determinant of plant community diversity in Great Basin landscapes.

Phytophagous insects that are not specialized on particular host plant taxa, and therefore feed relatively indiscriminately on available vegetation, can also affect diversity at the landscape level. Perhaps the best-known example of such generalized insects inducing stand renewal in Great Basin plant communities comes from extensive, irregular outbreaks of Mormon crickets (*Anabrus simplex*) that may be decades apart (Young 1978).

With experience gained from observing known infestations of sagebrush defoliator moths or Mormon crickets, we suspect that skilled interpreters of remotely sensed data could recognize the lasting impacts that such infestations have had on Great Basin landscape diversity. The limited information available in the literature seems to suggest that both vertebrate and invertebrate herbivores may be important players in determining Great Basin plant diversity, that their influences may be subtle or profound and operate on a micro- or macrosite scale, and that much additional study will be necessary to interpret fully these influences. At the very least herbivory has influenced genetic expression in Great Basin plant communities on an evolutionary time scale, but based on our admittedly limited understanding of plant/herbivore interactions in these communities, it also seems to have very profound effects in ecological time on biodiversity in Great Basin landscapes. Considering all the forms of herbivory that apparently influence Great Basin vegetation, its effects on landscape diversity literally whiff through the air in the form of aromatic compounds produced by the native shrubs in response to predation by various suites of herbivores, past and present.

Stand Renewal in Wildfires

The sudden catastrophic destruction of Great Basin plant communities by large-scale wildfires is the most highly visible means of stand renewal. As with most landscape-scale processes it is a temporally and spatially heterogeneous process. Young et al. (1972) previously suggested that within a century, the sagebrush communities of the Great Basin have known wildfires at some pristine level, promiscuous burning after the advent of European man, and attempted complete suppression of wildfires. Since this latter period we have observed the advent of prescribed burning, let-burn policies (de facto more than official), and enhanced safety concerns in fire suppression significantly contributing to changing stand renewal by burning on a landscape level in the Great Basin. Probably few big sagebrush communities now exist on alluvial fans that were last renewed by wildfire under pristine conditions. The estimate by the Soil Conservation Service, USDA, that less than 1 percent of the big sagebrush plant communities in the Lahontan Basin were in good condition supports this conclusion (Young et al. 1976).

The role of wildfire in the environment of the Great Basin at the time of European contact has never been clearly defined. Fire scars from coniferous trees have been used most commonly for chronological studies of prehistoric wildfires. The lack of such trees in the bulk of the sagebrush/bunchgrass and salt desert portions of the Great Basin has limited application of this procedure. One estimate of fire frequency in pristine environments in juniper (*Juniperus* spp.) woodlands would have effectively eliminated woody plants from the environment (Burkhardt and Tisdale 1969). Based on data from Young and Evans (1974b) on green rabbitbrush (*Chrysothamnus viscidiflorus*) demography in burned big sagebrush communities, Wright (1978) suggested that if the frequency of wildfires was less than 10 to 15 years apart, the pristine environment would not have been dominated by big sagebrush.

Wildfires and Dwarf Sagebrush Communities

The role of wildfire in low or dwarf sagebrush communities is even less understood than for big sagebrush. Western juniper (*J. occidentalis*) trees with fire scars occur in low sagebrush (*Artemisia arbuscula*) communities in northeastern California, but most of the older trees in these communities either lack scars completely or have century-long gaps between scars (Young and Evans 1981b). Currently, most low sagebrush and black sagebrush (*A. nova*) communities do not have sufficient herbaceous vegetation to allow the spread of wildfires. This exclusion of wildfires as a stand renewal process is apparently a product of domestic animal herbivory that favored the shrubs at the expense of the more highly preferred perennial grasses, because if shrub dominance is reduced such sites become dominated by perennial grass (Eckert et al. 1972). There still are examples of dwarf sagebrush communities where sufficient native perennial grasses exist to carry fires. For example, dwarf sagebrush/bluebunch wheatgrass (*Pseudoroegneria spicata*) communities occurring on Tule Peak northeast of Reno, Nevada, are capable of carrying a wildfire, as evidenced by recent fire scars in co-occurring Utah juniper (*J. osteosperma*) trees.

Black sagebrush communities in west-central Nevada currently have stands with unequal representation of age classes, and renewal occurs in a manner somewhat analogous to an old-growth forest (Young and Palmquist 1992). Essentially, individual shrubs die and the mounds on which they grew then support a flush of herbaceous succession. Eventually the mound blows away without the shrub to stabilize it, and new mounds form around seedling black sagebrush plants.

Promiscuous Burning

Quite probably, plant communities still exist in the Great Basin that are successional results of anthropogenic promiscuous burning. Many of the older stands of pinyon/juniper woodlands almost certainly date from cutting and slash burning for energy harvesting to produce charcoal during the 19th century (Budy and Young 1979). Botanist David Griffiths reported that during an early autumn trip from Winnemucca, Nevada, to Burns, Oregon, in 1900, he found that the mountains had numerous fires apparently set by sheep herders (Griffiths 1902). In the 1970s it was difficult to find sagebrush plants more than 80 years old in most big sagebrush plant communities in the Lahontan Basin (Young and Evans 1974b), apparently reflecting the previously widespread practice of promiscuous burning. The promiscuous burning period was probably brought to an end by the growth of livestock numbers in the early 20th century that reduced herbaceous fuels to a point where fires would not carry. Perhaps more importantly, understories of brush-dominated stands that initially resulted following promiscuous burning were probably purged of sparse herbaceous fuels even by limited grazing.

The sagebrush plant communities that followed promiscuous burning were quite stable and relatively depauperate in diversity. It is not known what would have happened to these communities if they had aged a century or beyond, because the introduction and spread of the annual cheatgrass (*Bromus tectorum*) ended most of these monotypic big sagebrush communities by reintroducing stand renewal by wildfires.

Cheatgrass and Wildfires

The invasion of cheatgrass into the western Great Basin early in the 20th century changed the fuel characteristics of sagebrush plant communities. Cheatgrass matures six weeks earlier than the native perennial grasses. The nearly continuous cover and fine texture of cheatgrass herbage enhance both the chance of ignition and the rate of spread of wildfires. Although this was apparent in the 1930s when C. E. Fleming wrote about livestock grazing on bronco-grass (*Bromus tectorum*) (Fleming et al. 1942), in the 1960s in the Lahontan Basin of northern Nevada only 1 percent of the big sagebrush landscape was dominated by cheatgrass (Young et al. 1976). Currently, however, about 25 percent of the landscape with big sagebrush potential is dominated by cheatgrass (Young, in press).

Aspect, structural, physiological, and genetic diversity in sagebrush/bunchgrass communities invaded by cheatgrass is probably controlled by stand renewal through wildfires.

The frequency and extent of such fires is controlled by the abundance of cheatgrass herbage. Based on experimental plots established over four decades ago, Dwight Billings stated that the greatest threat to biological diversity in the Great Basin was cheatgrass (Billings 1990). There are at least two reasons for this. First, cheatgrass reduces heterogeneity across whole landscapes because it is capable of dominating the herbaceous understory of previously distinct plant communities that would have been occupied under pristine conditions by a variety of different native grasses. Second, cheatgrass causes increasing fire frequencies and catastrophic stand destruction over vast areas, eliminating herbaceous and woody plants simultaneously. Cheatgrass then rapidly dominates these burned areas in a near monoculture.

Why has the spread and dominance of cheatgrass accelerated in the last three decades? Young and Tipton (1990) suggested that grazing management systems that include rest in rotation have contributed to the increase in cheatgrass herbage and therefore wildfires. Grazing management systems designed to favor the growth and reproduction of perennial grasses also favor the growth of cheatgrass.

Perhaps the most interesting aspect of the increase in cheatgrass abundance in the Great Basin has been the spread of this annual grass from sagebrush/bunchgrass potential sites in the 25 to 35 cm precipitation zone to both drier environments on the margin of salt deserts and more mesic conifer woodlands. This adaptive variation has sparked interest in the evolutionary biology of cheatgrass as evidenced by the 1992 symposium "Ecology, Management, and Restoration of Intermountain Annual Ranges" held in Boise, Idaho. It is ironic that while the scientific interest expressed at this symposium was centered on the breeding system and ecotypic variability of cheatgrass populations that are rapidly expanding, cheatgrass populations in the western Great Basin were undergoing their greatest retraction in both extent and density in 50 years. This retraction in the range of cheatgrass was probably the cumulative result of six years of drought.

The retreat of cheatgrass has left thousands of hectares of foothill rangelands either virtually bare or densely populated with halogeton, Russian thistle (*Salsola australis*), or barbwire Russian thistle (*S. paulsenii*), depending on the distribution of summer precipitation. From the air, these denuded areas have the aspect of new landscapes never before apparent on such a scale in the western Great Basin. In effect vast landscapes are open for the recruitment of native perennials for the first time in 50 years (Robertson and Pearse 1945), but these bare areas are also open for the return of cheatgrass dominance from dormant seeds in the seed bank (Young et al. 1969) or for the rapid spread of new colonizing species. A significant issue in the evolutionary biology of cheatgrass during its present retraction in range and density is its persistence in small refuge populations that may allow rapid reexpansion when conditions permit.

Cheatgrass and Landscape Heterogeneity

Natural early seral plant communities in the big sagebrush environments were dominated by the relatively short-lived perennial grasses squirreltail (*Elymus hystrix*) and Sandberg bluegrass (*Poa sandbergii*) (Franklin and Dyrness

1973). Both of these species exhibit a great deal of morphologic and genetic variability as compared to the late seral native perennial grasses (Stebbins 1957, Dewey 1964). This diversity was enhanced by the number of broadleaf herbaceous species that have maximum expression in seral communities the first season following wildfires (Young and Evans 1978). Therefore, under pristine conditions herbaceous plant diversity was probably greatest in Great Basin landscapes with the greatest proportions of patches consisting of early seral plant communities.

The woody portion of native early seral plant communities in the big sagebrush zone is also quite diverse. Rabbitbrush species crown-sprout after fires and produce abundant seeds with excellent wind dispersal abilities (Young and Evans 1974b). Rabbitbrush species are extremely diverse with many recognized subspecies, varieties, and forms (Anderson 1975). By contrast, there are only a handful of recognized big sagebrush subspecies and rarely would two subspecies co-occur in a late seral community. As in the case of herbaceous species, this suggests that in natural succession in the big sagebrush zone of the Great Basin, shrub diversity decreased as succession proceeded to late seral conditions.

The present-day competitive dominance of cheatgrass in many areas of the big sagebrush zone may have changed this pattern; early seral communities are nearly cheatgrass monocultures, while late seral communities include shrubs, cheatgrass, and remnant native grasses. Certainly, the diversity of both early and late seral contemporary communities dominated by cheatgrass is reduced relative to that of pristine communities.

In the context of nested patch hierarchies, the recent cheatgrass-induced increase in temporal frequency and spatial extent of wildfires can affect biodiversity in both the burned and unburned portions of Great Basin landscapes. In burned portions, rapid recovery of early seral plant species homogenizes previously heterogeneous patches and thus leads to decreased patchiness and biodiversity. This increased homogeneity at the landscape level may cascade to lower levels as well; obviously, if landscapes become more homogeneous, the communities within these landscapes are likewise homogenized and species diversity is reduced. For those species that do persist in a burned area, mixing of previously disjunct populations occurs, stands are more evenly aged, and certain genotypes may respond most favorably to the disturbance. In plant communities that were renewed historically by herbivory, but are now renewed by fire, genetic diversity within species may be reduced because some genotypes are resistant to herbivory but none are resistant to burning. Therefore, diversity at the community, species, population, and genetic levels can be reduced by large-scale catastrophic disturbances at the landscape level.

Possible effects of large-scale wildfires in the unburned portions of a landscape are more complex. Fire creates fragmented islands of unburned habitat among a sea of burned habitat, creating numerous subpopulations in these unburned islands from a previously composite population. If migration between these subpopulations is possible and frequent enough a metapopulation results, which can maintain a species over a landscape even though it may tempo-

rarily go extinct in particular unburned patches. Differential extinction probabilities are likely among unburned postfire patches because of demographic stochasticity and because these patches probably differ in species composition. Thus, some patches may have relaxed competitive environments, fewer predators, or other situations that allow a species to persist where it previously could not in a panmictic community.

For species that cannot migrate between unburned patches of a fire-fragmented landscape, there is no metapopulation structure, so the decrease in patch sizes and population densities after fire increases extinction probabilities, resulting in reduced biodiversity. The probability that a metapopulation results from such habitat fragmentation depends on the dispersal ability of a particular species over unfavorable habitat, which depends on distances between unburned patches and on the vagility of the species. Thus, birds should be more likely to persist than many small mammals, reptiles, or nonflying insects, and plant species with small wind-dispersed seeds may persist better than those dispersed by animals. Additionally, even a highly mobile species may not persist if its grain size exceeds the size of unburned patches left behind, because the patches are too small to support individuals. Thus, large species may be more vulnerable to extinction following fire than smaller species that utilize smaller grain patches. The net effect of fire on diversity within unburned patches will depend on relative numbers of species that can migrate between different patches and persist within individual patches.

These points concerning fragmentation, size, and distribution of unburned habitat patches are clearly applicable to two current issues in the field of conservation biology. First, for situations in which unburned patches are distributed too widely to permit a metapopulation structure, creation of appropriate dispersal corridors or intermediately spaced patches that permit "island hopping" may unite otherwise disjunct populations in a metapopulation. Second, fragmentation of Great Basin shrub-steppe landscapes serves as a model for studies of the "SLOSS" issue; that is, the question of whether conservation of biodiversity would be best served by establishing a single large reserve or several small reserves. The unprecedented loss of shrublands in these landscapes makes it imperative that we investigate empirical effects of habitat fragmentation on biodiversity, preferably with controlled experiments, which have heretofore been conducted only in more mesic environments (e.g., Robinson et al. 1992).

Stand Renewal Under Pristine vs. Contemporary Conditions

Based on the anthropogenic increases in the temporal and spatial extent of disturbance and subsequent stand renewal detailed above, it is clear that contemporary Great Basin landscapes are considerably less heterogeneous than they were under pristine conditions.

Although our emphasis on western Great Basin landscapes has led us to center our discussion on the increased frequency of disturbance that has come with human encroachment in these environments, it should be noted that a

reduction in disturbance frequency can also result in reduced heterogeneity and biodiversity. Such effects can be seen on a localized scale in senescent big sagebrush stands lacking a herbaceous understory in parts of the Great Basin. This lack of herbaceous fuel together with human fire suppression has decreased the frequency of stand renewal and the homogeneity of associated big sagebrush stands. That homogeneity induced by such reductions of disturbance can reduce biodiversity in a manner similar to increased disturbance frequency is illustrated by the low levels of bird species diversity found in decadent big sagebrush habitats (McAdoo et al. 1989). Denslow (1985) suggests that either an increase or decrease in the pristine disturbance and stand renewal regimes can result in reduced landscape biodiversity. Based on such effects of deviation from historical disturbance regimes in a variety of ecosystems, the "intermediate disturbance hypothesis" (Connell 1978, Huston 1979) proposes that unnaturally high or low levels of disturbance in time and/or space result in reduced species diversity.

Grazing and Landscape Heterogeneity

To this point we have emphasized renewal of woody plant populations in Great Basin landscapes. When one considers renewal of herbaceous plants in contemporary landscapes, domestic animal grazing is certainly an important determinant of biodiversity.

From one perspective, rest-rotation grazing and the subdivision of range landscapes into separate grazing allotments and pastures create patches that differ in grazing intensity and in the time elapsed between episodes of grazing. Superficially, this would seem to have the potential of increasing biodiversity by establishing grazing-differentiated patches across a relatively uniform landscape. However, as we have discussed, patchiness at small scales is essential to maintaining biodiversity at larger landscape scales. With typical stocking rates, livestock grazing will often have the effect of homogenizing this small-scale patchiness over whole pastures or allotments, reducing biodiversity. Moreover, domestic animal grazing of a specific site is often too frequent to permit reestablishment of late seral herbaceous plant species, and thus leads to dominance of early seral species. Such problems may be ameliorated by lower stocking rates relative to the size of pastures and/or longer rest periods between grazing.

Although the historical importance of grazing by native vertebrate herbivores in Great Basin landscapes is uncertain and thus debatable, it is nearly certain that current patterns of herbivory by domestic ungulates, like the increased frequency and extent of wildfire discussed above, represent a more chronic disturbance of herbaceous plant populations than pristine disturbance patterns. The more acute nature of disturbance in pristine Great Basin plant communities promoted environmental heterogeneity and associated biodiversity. If grazing is to be compatible with biodiversity concerns, grazing management practices should strive to simulate such acute disturbance patterns. With the newfound public emphasis on maintenance and enhancement of biodiversity, perhaps future grazing management practices will involve a trade-off between sustained livestock produc-

tion and maximizing biodiversity rather than the current trade-off between maximizing livestock production and sustained range productivity.

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Managing Wildlands for Biodiversity: Paradigms and Spatial Tools

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Abstract

The increasing concern for the conservation of biodiversity arises from a fundamental and ongoing shift in the perception of natural resource systems and the role of humans within nature. The new management paradigm emerging from this shift emphasizes intergenerational time scales, nonequilibrium dynamics, and the information content of nature. The information content of nature manifests itself in variation in patterns at multiple spatial scales. Conservation of the information content of nature requires consideration of the entire landscape, rather than just small fragments, and must specify how anthropogenic disturbances can maintain patterns at multiple spatial scales. New geographic information system tools provide a vocabulary for analysis of pattern and specification of desired future conditions. Lacking a profound functional understanding of ecosystems, managers can use the range of variation in pattern over recent evolutionary time as an interim guide for the development of desired future conditions.

INTRODUCTION

The conservation of biodiversity has become a major concern for both public and private land managers. As with many issues, the definition, scope, and implications of biodiversity remain unclear. Various actors in the play—scientists, advocates for industry and environmental groups, land owners and managers, court justices, legislators—struggle to define the issue in terms at least comprehensible and frequently beneficial to their interests. The very complexity of the intellectual and political stew—the Endangered Species Act, Gap Analysis, the Agreement on Biodiversity, environmental mapping analysis program, among others—indicates that the issue of biodiversity is just one tip of a multi-tipped iceberg. This conceptual iceberg embodies a fundamental and continuing shift in our perception of natural resource systems and of the role of humans within nature.

The success of managers, which is measured as much in social and political as in biological terms, will depend largely on how well they appreciate the nature of this change. This paper explores the nature of this shift and formulates the resource-management problem in terms of the heterogeneity of ecological systems. It then illustrates the relationship among heterogeneity, scale, and management and follows with an examination of the types of strategies that might be used to conserve heterogeneity. Finally, I demonstrate through several case studies a range of geographic information system (GIS) tools that can be used to assess management strategies.

THE CHANGING RESOURCE-MANAGEMENT PARADIGM

What is the shift in resource-management paradigms? Simply put, we are now called upon to manage complex and still poorly understood systems in the light of an unknown future in ways that do not reduce the ability of future generations to do the same thing. Biodiversity may be used as a measure of the options open to future generations.

Many other policy concerns that apparently compete with biodiversity for attention are complementary and can be reconciled under this new paradigm. The issue of global climate change emphasizes the uncertain future. Ecosystem management expresses the notion that nature is not a static collection of commodities but rather a system whose function perpetuates its components and, therefore, provides multiple byproducts—not just to our generation but to all generations to come.

To understand this emerging imperative, we can compare it to our historical mode of management (Table 1). Under historical management, the governing time frame has been short term: we satisfy the desires of this generation and discount the desires of future generations. Perhaps because of this discounting of the future, we viewed natural resource systems in coarse-grained terms: we perceive only those aspects of the system that are important to us now. Histori-

TABLE 1. A COMPARISON OF HISTORIC TO EMERGING MANAGEMENT MODE IN TERMS OF SELECTED CHARACTERISTICS.

CHARACTERISTIC	HISTORIC	EMERGING
Time frame	1–10 years	1–200 years
Categorical grain	coarse: “biomass”	fine: “information”
Dynamics	equilibrium-centered: noise irrelevant to system trajectory	non-linear, directional, chaotic: small differences are important
Imperative	maximize production of biomass subject to constraint set	ensure at a given probability the persistence of all system components
Tool	linear programming	dynamic stochastic programming

cally, biomass—forage, timber—or just mass—minerals, water—has been the principal interest. The discounting of the future may also have implied a perception of the system as equilibrium centered, wherein noise did not affect the dynamics of the system, at least not at the time scale we used. Within this set of perceptions, the management imperative has been to maximize the production of the major product subject to a host of constraints. Resource management looked to industrial management and developed its preferred tool: linear programming.

In the emerging mode of management, the governing time frame is far longer because it begins to value the desires of the future. The expanding time frame forces us to consider the structure of the system in far more detail because no one generation can tell what aspect of nature future generations may value. Three centuries ago, the inhabitants of California placed enormous value on acorns. Given our current resource-inventory technology, they might have classified their ecosystems with respect to that particular resource. They may have considered the oozy tar pits of the Los Angeles basin as an interesting but economically trivial phenomenon. Had we used only their perspective in labeling nature, we would have missed the preeminent resource of the industrial world—petroleum—and been left with maps of acorn production, now an interesting but economically trivial phenomenon.

We cannot know now what people three centuries hence will value. What we can recognize now is the underlying heterogeneity within nature that supports the shifting desires of generations. The vocabulary of mass is simply incapable of expressing this heterogeneity. It will be supplanted by other vocabularies that stress the information content of nature, from the DNA that governs individuals to the structure of landscapes that provide habitat to individuals. This information content of nature is succinctly captured in the concept of biodiversity: “the variety and variability among living organisms and the ecological complexes in which they occur” (Office of Technology Assessment 1992). Biomass will certainly remain important—livestock do eat grass and houses are built of wood—but it will become more what it really is: residue left as living systems perpetuate themselves.

Just as our simple perceptions of resource systems give way to ones of increasing complexity, our equilibrium-centered perception of their dynamics is quickly yielding to one that accepts directional change, multiple states, and perhaps even chaos. This expanding understanding of dynamics increases our uncertainty in two ways.

First, we know that small differences, what we used to consider noise, can be extremely important to long-term dynamics. When seeds of exotic annuals sprouted in California in the late 1700s (Burcham 1981), not even modern plant-community-inventory methods would have noticed the weed patch. Yet that virtually undetectable original blip on California’s vegetational history led to a nearly complete replacement of native grassland species (Burcham 1981). Over time, small differences and individual species can be very important (Vitousek 1990).

Even if we could detect all the differences that might be important, our uncertainty regarding the values of future-driving variables, such as climate, fire, disease, and their interaction with ecological systems, makes prediction of the future very difficult.

As our perception of the environment has changed, so has the management imperative. In this new world of dizzying biological diversity and unpredictable dynamics, resource managers are now called upon to manage in ways that increase the probability that the system will persist into the future. No new tool has yet emerged that quantifies this risk-aversion problem. However, just as the description of the problem resembles that of fitness, resource management may look to ecology, particularly foraging theory and dynamic stochastic programming (Mangel and Clark 1988), to find new quantitative methods. In the context of dynamic stochastic programming, the resource-management question will become, “Given an uncertain future, what actions can I take in the next time period that will not reduce below some minimum the probability of maintaining the biological diversity of the system many time periods into the future?”

An important aspect of foraging theory and by extension natural resource management is learning and the incorporation of knowledge gained in the current time period into decisions in succeeding time periods. Monitoring and ex-

PLICIT protocols for updating management decisions based on new knowledge are essential elements of any serious response to uncertainty.

FALLING INTO CALIFORNIA: THE PATTERNS OF LIFE AT MANY SCALES

If the general resource-management problem deals with biological diversity, we need a means to analyze biological diversity. The definition of biological diversity given by the Office of Technology Assessment starts in the middle of life ("organisms") but then looks both up ("ecological complexes") and down ("variability among") the spatial scale. This paper proposes no new definition but simply a single trajectory through the same conceptual space—from the larger to the smaller spatial scale. This way of approaching biodiversity derives its power in part from hierarchy theory, i.e., larger processes set the stage for smaller processes (O'Neill et al. 1986), and in part from landscape ecology (Urban et al. 1987), in which those hierarchical patterns play out in space.

The great virtue of this approach for managers resides in the assumption that by conserving the system at one scale one has a high probability of conserving the smaller component parts as well, even though the manager may never know the true extent or nature of those parts. This approach allows managers to move ahead in promising directions without waiting for those ultimate systematic inventory and ecological studies that, while desirable, may never happen.

Figure 1 portrays how northern California appears from high in space. Much of the spectral and textural variety in the scene derives from the response of life to climate and geology. By means that remain obscure, our eyes and brains can classify the scene into a pattern of subregions. Figure 1 shows one way of drawing this pattern, a way that corresponds to landscapes Californians identify as the Sierra, the Central Valley, the North Interior Coast Range, the Delta, and so on.

Does this classification capture all the diversity and information within the scene? Put another way, is it possible to distinguish other patterns at a smaller scale within each polygon outlined in Figure 1, or are the components within each polygon randomly distributed? To answer this question, we zoom in to the box outlined in Figure 1, the contents of which are portrayed in more detail in Figure 2.

At this lower altitude, we see not only the pattern distinguished at the higher altitude but a great deal more detail as well. Patterns emerge within those larger polygons, with some of these drawn as additional polygons in Figure 2. Once again, these patterns correspond to landscape elements Californians recognize on the ground. Some of these landscape elements relate to human use of the environment. For instance, the metropolitan area of Sacramento clearly differs from less developed adjacent areas. Thus, certain types of disturbance—urban and irrigated agriculture—are detectable at this scale. Questions regarding such development may be most economically answered with data from this scale alone.

Again we may ask if this yet finer characterization of life has captured all the important information. Are there issues that require yet finer-grained perception? We must once again zoom in further, this time into the area near Lake Berryessa shown in Figure 2 and reproduced in more detail in Figure 3. New patterns emerge—east-facing slopes emerge from the mass of the Coast Ranges—but these new patterns do not clearly relate to a particular process or issue. They may exemplify the notion of a measured heterogeneity that has little evident relationship to our current understanding of how the system operates (Kolasa and Rollo 1991).

The iterative nature of this analysis should now be clear. As we examine more closely in Figure 4 the outlined area in Figure 3, we find again patterns that relate to our understanding of the landscape. At this scale, we can see particular habitat types, such as oak woodland, annual grassland, and riparian areas. Thus, at this scale we detect conversion of oak woodland to grassland or riparian habitat to agriculture. While coarser-grained changes (wildland to urban areas) could be analyzed with coarser-grained data, conversions within wildland require finer categorical and spatial grain.

In Figure 5 we see the area outlined in blue in Figure 4. Now we see variation within the habitat types: areas with different canopy closure in oak woodland and areas of bare soil within the grassland. Because we can detect these changes, this scale would be appropriate for monitoring management of the oak woodland and the grassland.

This trajectory could, of course, continue. In Figure 6 we see vertical variation in the structure of oak woodland patches with the consequent creation of special habitat elements—perching branches and cavities in oak trees, seasonal wet spots, and so on. This scale is appropriate for monitoring management activities that operate within habitat stages but nonetheless affect habitat suitability, e.g., water spreading, pruning, hazard-tree removal.

Closer to the ground in Figure 7, we see patterns of species distribution within the grassland. This scale is a favorite for plant demographers and by extension for foraging ecologists and range-livestock scientists interested in how grassland floristics and structure alter feeding behavior.

We will halt our trajectory in Figure 8 at a scale appropriate to anatomy. The patterns apparent at this scale derive from development processes operating on genetic material. Few human activities consciously operate at this scale. Many management activities have inadvertent and unexpected repercussions at this level.

This trajectory across spatial scales is of course an incomplete portrayal of the heterogeneity of life. Nature changes over time as well as over space. Different temporal patterns emerge at different temporal scales: vegetation types shift in response to long-term climatic changes, seral stages succeed each other after disturbances such as fire or floods, nutrient reserves are translocated within plants in response to seasonal changes. To display accurately the heterogeneity of life at different spatial and temporal scales simultaneously requires a medium more like video than photography.

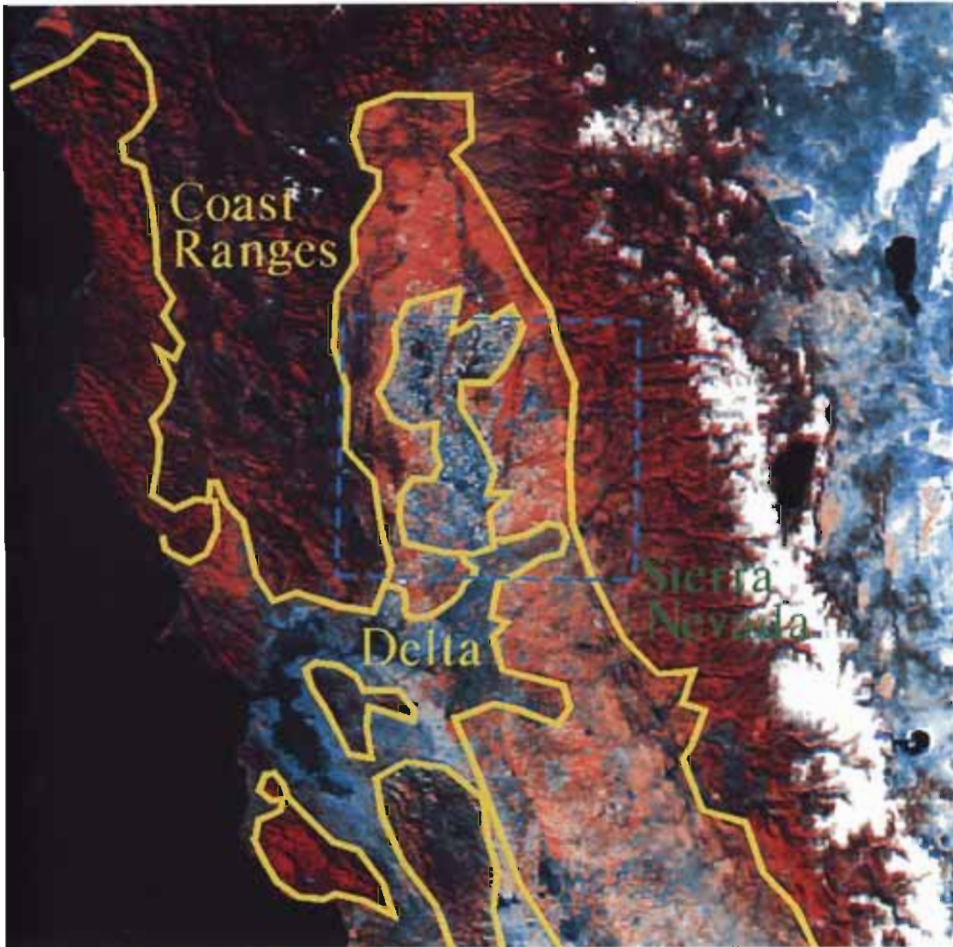


Figure 1. AVHRR scene of northern California on November 1, 1989, with selected regions outlined in yellow. Area in Figure 2 outlined in green. (Imagery: NASA Ames Aircraft Data Facility.)

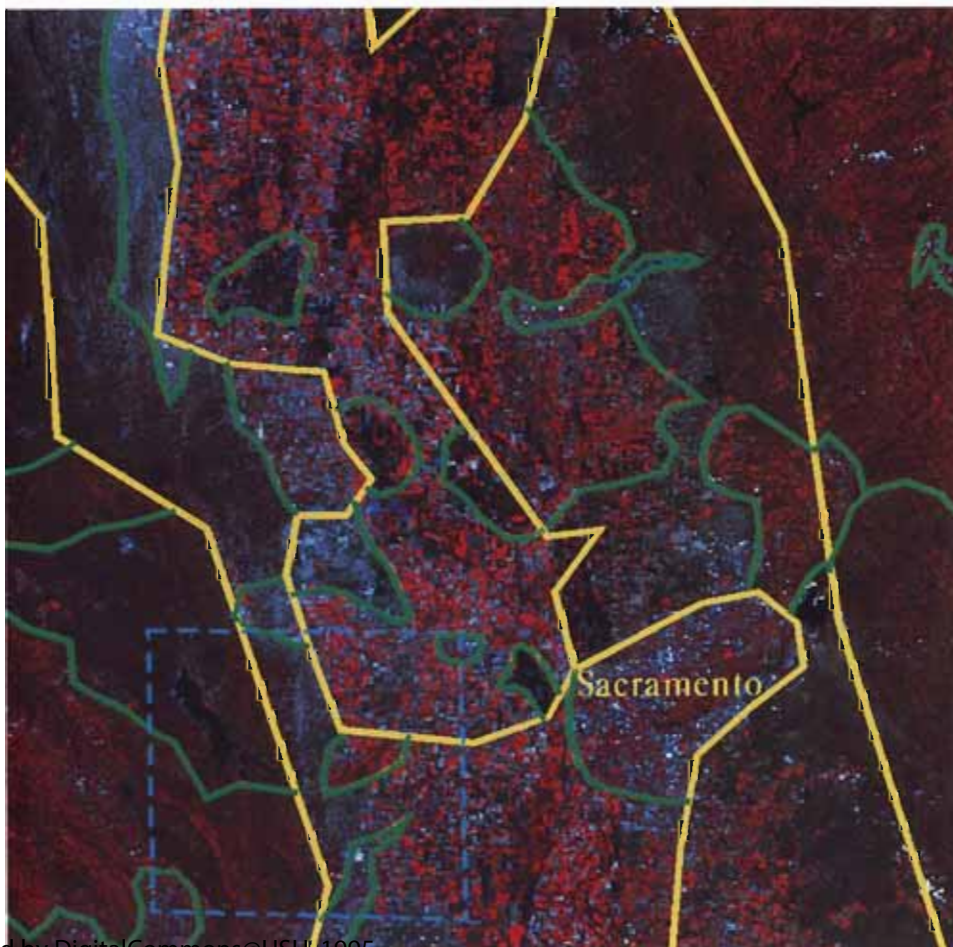


Figure 2. TM scene (bands 4, 3, and 2) of Lower Sacramento Valley on June 20, 1990, with previously selected regions in yellow, newly distinguished regions in magenta. Metropolitan Sacramento denoted by "SAC." Area covered in Figure 3 outlined in green. (Imagery: NASA Ames Aircraft Data Facility.)



Figure 3. NS001 Airborne Thematic Mapper Simulator scene of western Yolo and Solano Counties on May 31, 1991, with previously selected regions in yellow, newly distinguished regions in magenta. Area covered in Figure 4 outlined in green. (Imagery: NASA Ames Aircraft Data Facility.)

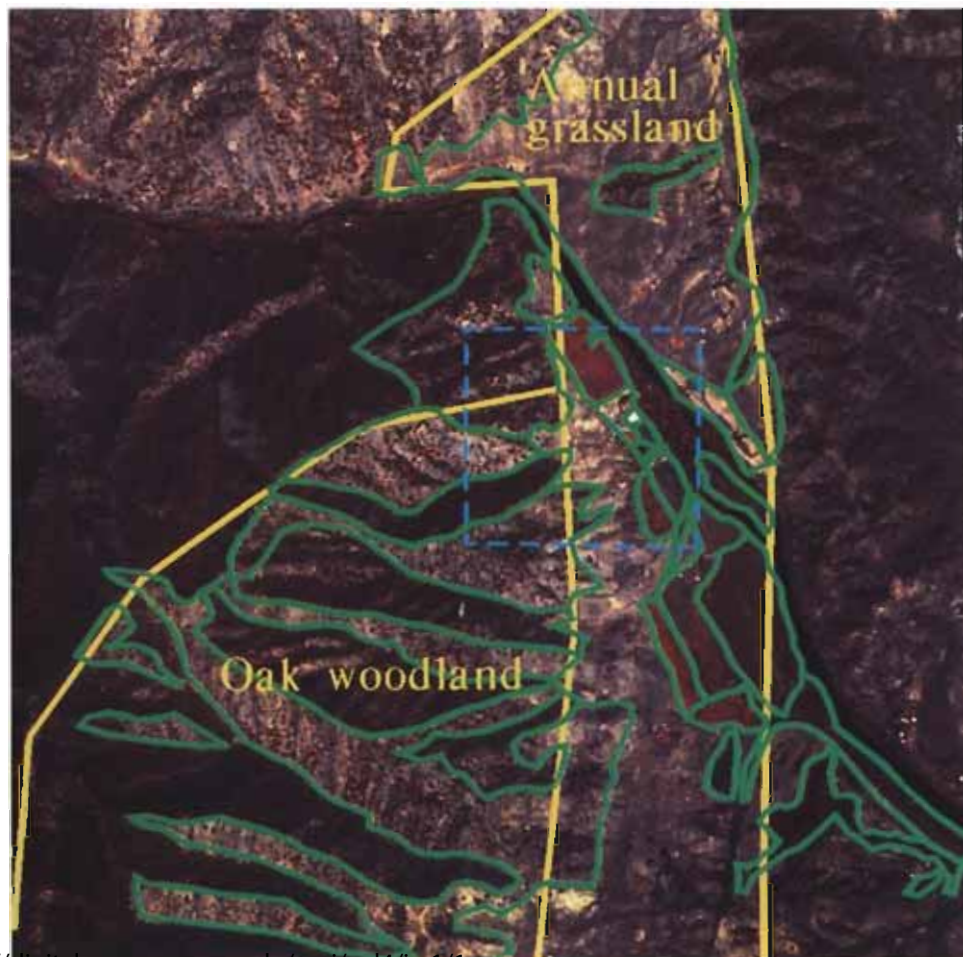


Figure 4. Scanned high-resolution IR photograph of lower Putah Creek Canyon on May 31, 1991, with previously selected regions in yellow, newly distinguished regions in magenta. Area covered in Figure 5 outlined in green. Different habitat types are readily distinguishable: oak woodland, annual grassland, irrigated agriculture. (Imagery: NASA Ames Aircraft Data Facility.)

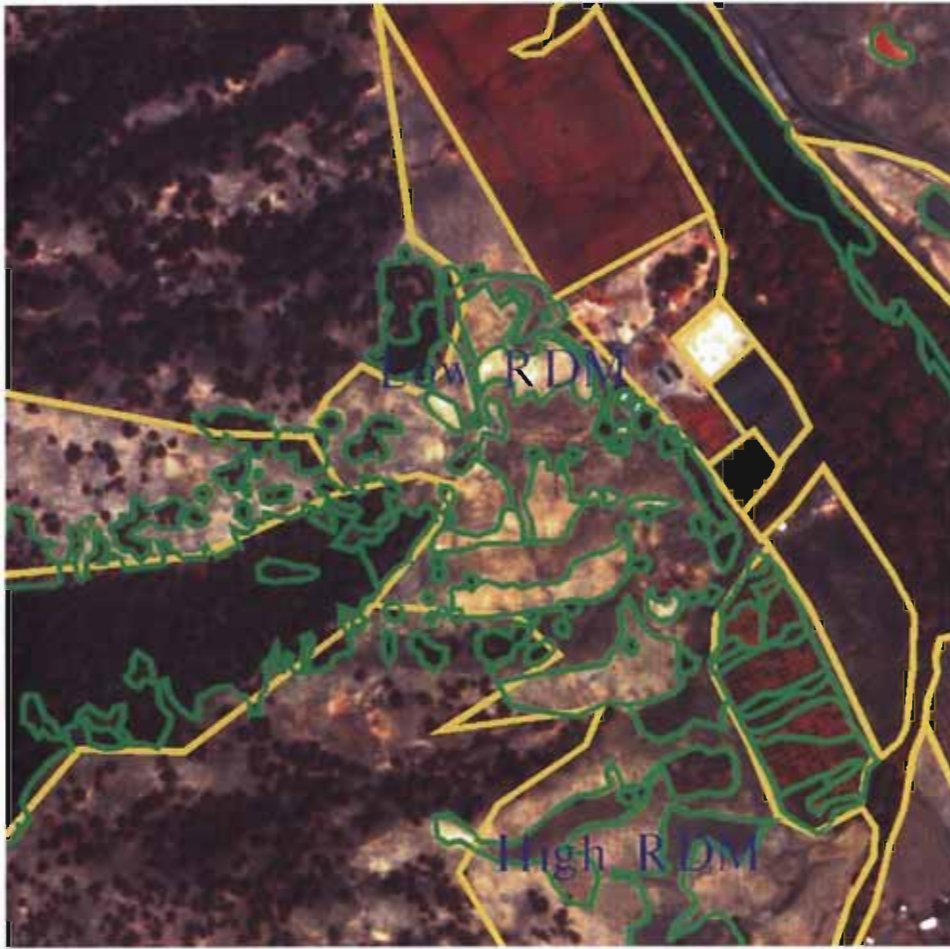


Figure 5. Scanned high-resolution IR photography of ranchlands adjacent to Putah Creek with previously selected regions in yellow, newly distinguished regions in magenta. Different habitat conditions are readily distinguishable: open vs. dense oak woodland, low residue vs. high residue annual grassland. (Imagery: NASA Ames Aircraft Data Facility.)



Figure 6. Typical valley-foothill oak woodland showing different microhabitats and special habitat elements. Photo by author.



Figure 7. Herbaceous layer within valley-foothill oak woodland showing variable species composition. Photo by author.



Figure 8. Anatomical features of a single organism within the herbaceous layer. Photo: Endangered Plant Program, California Department of Fish and Game.



Figure 9.

Captions for Figures 9-18 follow the illustration section.



Figure 10.



Figure 11.

Captions for Figures 9-18 follow the illustration section.



Figure 12.

Figure 13.



Captions for Figures 9-18 follow the illustration section.

Figure 14.





Figure 15.

Captions for Figures 9-18 follow the illustration section.

WHR HABITATS: HUMBOLDT COUNTY PILOT SITE

1990



2040: EXISTING RULES

0 10 MILES

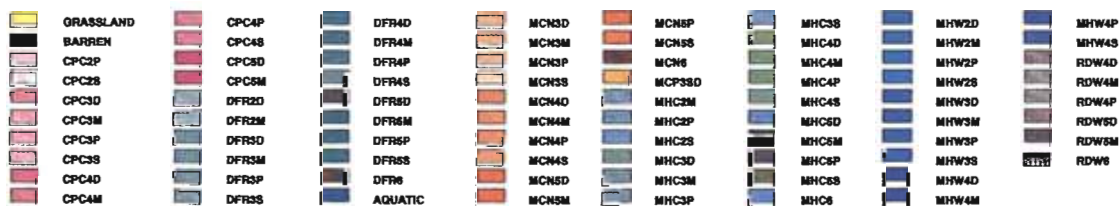
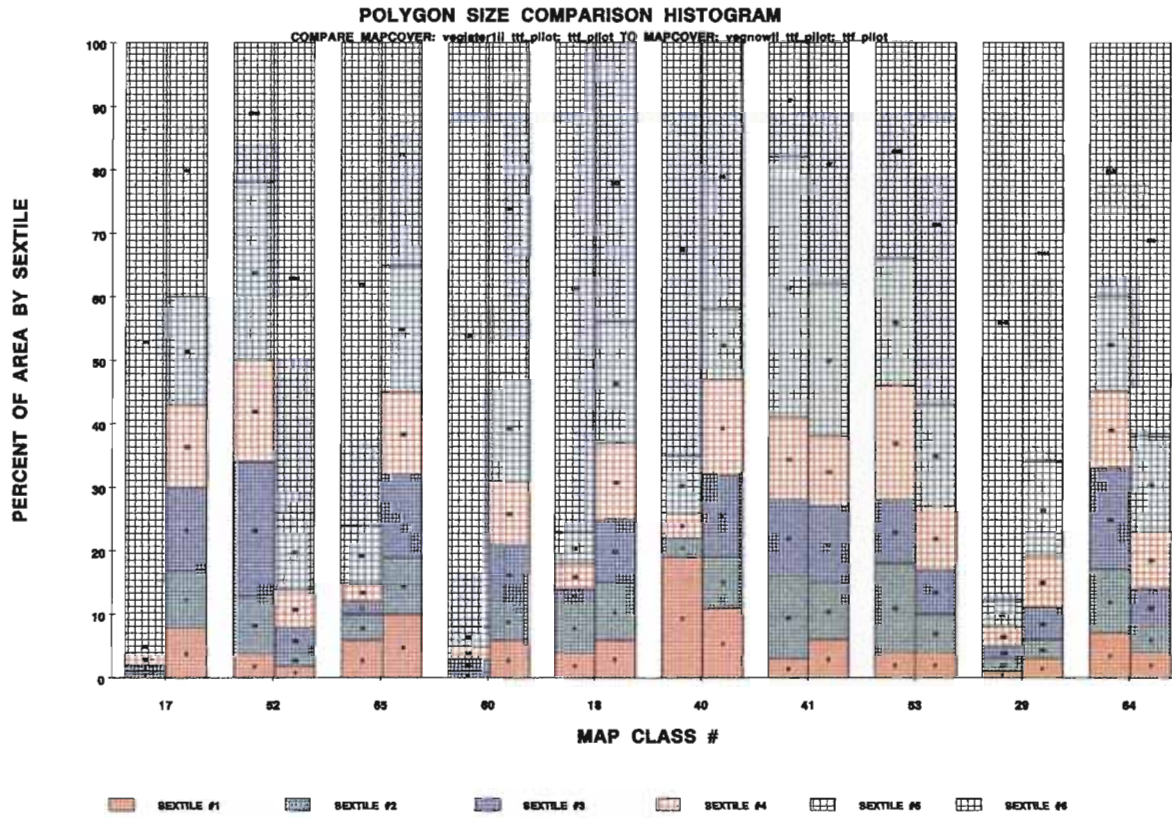


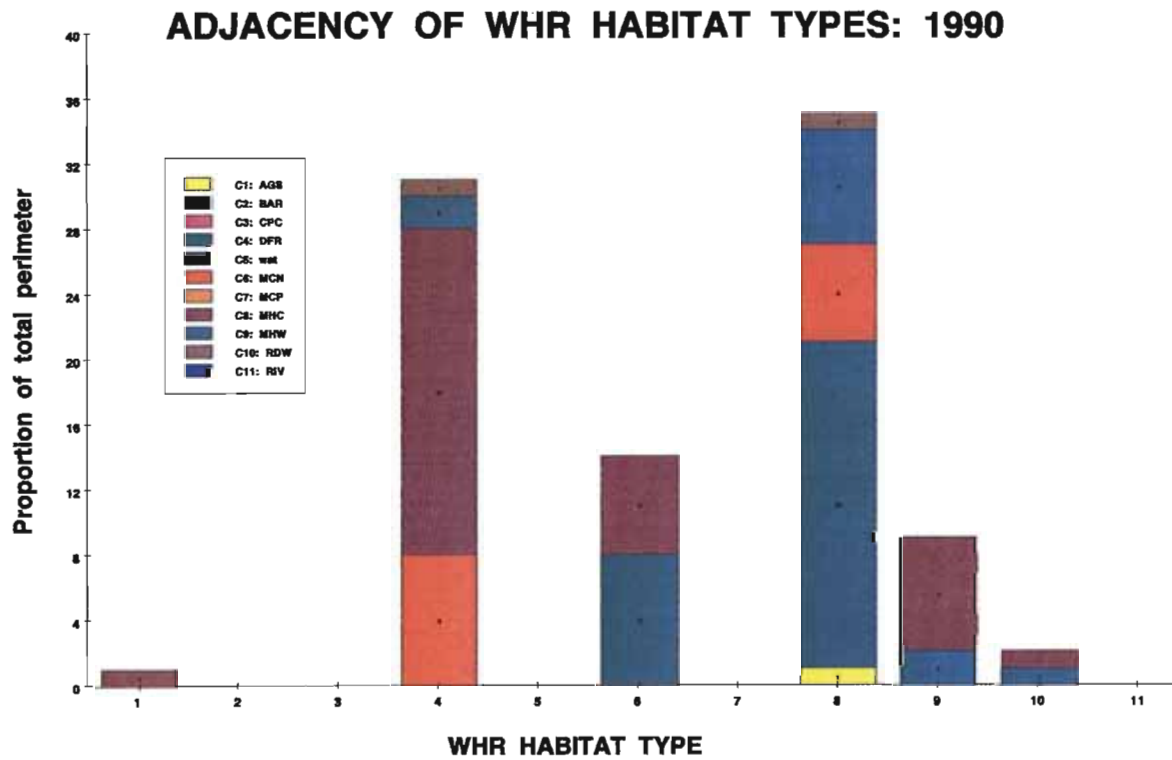
Figure 16.

Figure 17.



Captions for Figures 9-18 follow the illustration section.

Figure 18.



Captions for Figures 9–18, shown on previous pages.

- Figure 9. *Starry Night* by Vincent van Gogh, a visual metaphor for the environment.
- Figure 10. Red and orange pixels are analogous to rare species and are located through inventory.
- Figure 11. The rare pixels, now shown as magenta, can be placed within a landscape context.
- Figure 12. The overall result of creating a conservation strategy that relies entirely on reserves for rare species: the species may be temporarily saved but the environment as a system is lost.
- Figure 13. Removing a single color everywhere throughout the image is analogous to intense single-use management.
- Figure 14. Removing some of every color everywhere throughout the image dims the image but conserves most of the information within it.
- Figure 15. Reserve, light use, and intense use can be combined over the entire image to conserve the image while using it.
- Figure 16. Current habitat and that projected for 2040 under current forest practice rules for a 170,000-acre pilot site in northern Humboldt County, California.
- Figure 17. Comparisons of patch size histograms in 1990 and 2040 for selected habitats in the pilot site. Each pair of stacked bar graphs refers to a particular habitat stage, with the right bar referring to current conditions, the left to projected conditions. Segments within each bar contain the same number of polygons. Only those habitats with the greatest shifts in patch size are shown. Map class 17 = Douglas fir, pole size, dense canopy closure (DFR3D), map class 52 = montane hardwood conifer, small tree, dense canopy closure (MHC4D).
- Figure 18. Adjacency histogram for habitat types within the pilot site in 1990. Each stacked bar represents the proportion of total edge within the map constituted by the total perimeter of a given habitat; the segments within each bar represent the proportion of the total edge that a particular habitat type shared within another habitat type.

The principal lessons of this descent into California are these:

1. The variation at all spatial scales is indeed biodiversity. Single measures of biodiversity, such as species richness (Figure 7) are only indices abstracted from this continuum after one decides on a specific grain and a single scale of observation.
2. The patterns are the structural evidence of processes and disturbances that characterize a place. Human use of the environment—urbanization, conversion, management—is just another, albeit important, class of disturbance, operating at many spatial scales as well and altering the pattern of life at those scales.

STARRY NIGHT: THE CONSERVATION OF PATTERN AT ALL SCALES

If the management imperative is to maintain biodiversity over the long term, and if biodiversity is manifested in a hierarchy of patterns, what sorts of management strategies are needed to conserve these patterns?

The painting *Starry Night* by Vincent van Gogh provides a metaphor (Figure 9). It is similar to life as described in the previous section: it consists of millions of entities (brush strokes) that, when taken together, form patterns at several scales. Metaphors are always tricky coding devices, and this one deserves some examination.

The ecological analogue to the brush stroke is an individual organism. Of course, any brush stroke contains smaller elements of color and, therefore, the classification of a brush stroke is not unambiguous. It is convenient to classify organisms into species or demes. Since there are many species or demes, these classifications might be characterized as using “16-bit color.” The larger elements of the painting—the trees, the village, the sky—are characteristic aggregations of species communities or habitats.

The classification of brush strokes into species is, however, not the only possible way of coping with variation at that level. Ecologists might perceive not species but guilds or functional groups. Since these constructs reduce the amount of variation, the functional ecology perspective might be using “8-bit color.” Philosophers and ethicists might perceive each individual, each brush stroke, as unique (24- or 32-bit color), while molecular biologists might see not brush strokes but individual pigment molecules within each stroke (by using a higher-resolution screen). Since there is as yet no “general theory of life,” we must be content with a certain open-endedness to the biological correlate of a brush stroke. Nonetheless a painting clearly emerges and exists, even if its ultimate building block remains unclear.

The painting is also not dynamic and, therefore, falls short of accurately portraying life. However, one can imagine a painting that wavers and flickers over time but that nonetheless remains identifiable as *Starry Night*.

Our metaphorical problem, as resource managers, is to use the painting while at the same time maintaining the painting’s integrity. In the light of the previous sections, integrity is maintained if the painting remains identifiable as *Starry Night*. Like the metaphor itself, this imperative requires closer examination.

First, maintaining integrity does not mean maintaining some transcendental quality such as “beauty” in the landscape. It means maintaining the patterns at many scales that make a landscape identifiable as a place. Patterns at many scales provide a structural vocabulary for defining desired future conditions of the ecological system.

Second, maintaining integrity does not mean “freezing” the landscape. The patterns that give a place identity are frequently the result of disturbance and other ecological processes. Therefore, the continued existence of those patterns—realization of the desired future condition—can be assured only through the maintenance of the processes—natural or human—that generate those patterns.

Third, the target level of integrity is as open-ended as is the meaning of the brush stroke. For the functional ecologist who sees life as the transfer of energy and nutrients over a short time horizon, the integrity of the painting is carried by coarse patterns of guilds or trophic levels within habitats. The nature of individual brush strokes can vary a great deal before

the coarse-grained picture loses its identity (Johnson and Mayeux 1992). However, for the evolutionary biologist who perceives life as the transfer of genetic information through time (with the transfer of energy and nutrients as supporting acts), even slight changes in species composition are noticeable. Many system configurations that would still be identifiable as *Starry Night* to the functional ecologist would not be identifiable to the evolutionary biologist.

In a fundamental sense, neither of these perspectives is more "correct" than the other. The relevance of each species to ecological function remains an open question,¹ depending largely on the temporal scale of the analysis and the fineness with which one defines ecological function (Chapin et al. 1992, Solbrig 1992). The use of ecological function as a surrogate for human welfare may itself be a generationally centered perception that understates the value of genetic diversity to future generations.

None of these considerations drastically changes the metaphorical challenge: to determine strategies that we might employ to "have our painting and use it too."

Many of our current conservation strategies are oriented around rare and endangered species (e.g., Thomas et al. 1990). *Starry Night* is generally bluish, with red and orange being relatively rare colors and, therefore, candidates for our metaphorical rare species. With a good inventory we can locate sites with high densities of these rare colors (Figure 10).

We can then locate these rare colors, now shaded magenta, within a landscape context (Figure 11). We can then design a reserve system that encloses high densities ("viable populations") of rare colors throughout the range of their occurrence. However, if we do not concern ourselves with the land between the reserves, we may save the colors/species but lose the painting/wildland (Figure 12). This scenario corresponds to a California that consists of either urban sprawl, irrigated agriculture, or national park. While such a scenario may seem far-fetched now, a simple glance at a map of Western Europe should convince one that over the long term such a scenario is quite possible.

The main point of Figure 12 is that reserves alone do not constitute a sufficient strategy to maintain the integrity of the painting. To conserve the diversity within *Starry Night*, we must also consider the fate of the nonreserved areas that we now see, since they contain most of the information within the painting (the biological analogue—that considerable biodiversity is maintained within managed ecosystems—is discussed by Pimental et al. 1992). Simply enlarging the size of reserves would be technically effective; but in any populated region, putting more land in nature reserves is very difficult and in any event is not likely to encompass more than a small fraction of the land surface.

What strategies might we employ on nonreserved areas? Historically, we have frequently managed landscapes for particular resource values, such as water, large saw logs, or particular forage plants. Within our metaphor, such single-use management appears as the complete extraction of a single color, such as green, from throughout the painting (Figure 13). When we do this, we get a cartoon of the original

painting—something that reminds us of what once was but is really quite different from the original.

Another alternative is to take out some of all colors throughout the scene (Figure 14). This strategy corresponds to a selective harvest scheme that removes a small proportion of all species and age classes. This strategy certainly dims the painting but results in a scene that when compared to those left by other strategies is closest to the original.

These strategies could be combined over the entire landscape (Figure 15). Reserves would maintain all the information in nature as clearly as possible, while management of most of the remaining landscape maintains enough information to assure the integrity of the entire system. Finally, certain areas are reserved for intensive culture and urban development. While virtually no information remains in those areas, the information they formerly contained appears in other areas and is not lost to the entire system. The resulting scene is not identical to the original; but the strategy allows the current generation to use the scene, as it must for its survival, while maintaining the integrity of the scene, as must be done for the survival of future generations.

The metaphoric strategy works—the painting remains apparent—principally because the strategy maintains the pattern of color over the whole scene. The take-home lessons are two:

1. If management is to succeed, it must consider the entire landscape, not simply small pieces of it.
2. In addition, the management prescriptions related to biodiversity must get beyond the no-use recommendation and must begin to describe how use can be tailored to maintain the patterns characteristic of the place at all scales.

LANDSCAPE EVALUATION: THE DESCRIPTION OF PATTERNS AT MANY SCALES

Assessing how well a strategy maintains the pattern of life at many scales requires a means to quantify those patterns. The California Department of Forestry and Fire Protection has developed a vocabulary of pattern analysis and implemented that vocabulary in its Landscape Evaluation Module or LEM.

Figures 1 through 8 illustrate the problem. In each figure, different units each have a distinct gestalt. Areas within each unit are not identical, yet the image analyst sees them as similar enough to lump together as different from another area. How can this gestalt be quantified?

For a given landscape mapped to a given level of detail, LEM calculates three classes of measures that taken together portray the gestalt of the landscape mosaic:

1. How much of each map class we have (e.g., aggregate acres within each habitat type).
2. How total area in each map class is broken into pieces (e.g., the proportion of each habitat type in six different class sizes).
3. What map classes are next to what other map classes (e.g., edge between two habitat types as a proportion of the total edge within the map).

¹See West and Whitford, this volume.

The premise that underlies these measures is that two different areas that are similar in all three of these dimensions are ecologically equivalent at least for organisms and processes that correspond to the grain of the data.

This software has been used for a variety of issues at a variety of scales but generally within forested landscapes. Its use to analyze changes in forested habitats resulting from silvicultural prescriptions comes closest to how the software might be used in rangeland.

Problem definition establishes certain perceptual parameters that differ from those appropriate to other problems. Table 2 compares these parameters to those involving urbanization impacts in a six-county area of the Central Sierra Nevada (Greenwood and Marose 1993). It also contains some guesses regarding the parameter values that might be obtained in rangelands for certain management issues.

In the silvicultural case, the management disturbance alters habitat characteristics. To detect those changes, the analysis requires data of fine categorical and spatial grains. Specifically the analysis uses a map of WHR habitat stages (Mayer and Laudenslayer 1988) that portrays habitat in terms of species mix, mean diameter breast height of trees, and average canopy closure. The spatial grain, or minimum mapping unit, is five acres. To date, the study has been limited to 170,000 acres (Barrett et al. 1993).

In contrast, the management disturbance of development eliminates rather than alters habitat characteristics. The categorical grain of the data need not be very fine to capture these changes. In the case of the Central Sierra, the analysis used a map of WHR habitat types, i.e., habitats defined by species mix alone. The problem definition also establishes an upper and lower limit on what we can see, with the entire region covering 10^5 acres and the minimum mapping unit 100 to 1,000 acres.

Table 2 also includes some estimates of parameters relevant to more traditional rangeland management issues. If prescribed fire generally renews shrublands, then a finer-grained description, perhaps using seral stages or maturity classes, is necessary to understand impacts. If, however, prescribed fire results in type conversions, a coarser-grained description utilizing life-form classes may be sufficient. The spatial scale will depend on the spatial scale of factors that drives fire intensity and the resulting effects of fire. The extent of analysis might be defined by management concerns or by larger ecological factors that set the nature of the fire regime.

The categorical and spatial grains associated with grazing management depend, as do those associated with prescribed fire, on how grazing affects the entire system. If the effects must be characterized in terms of species composition, a very fine categorical grain may be necessary. The corresponding spatial grain will depend on the scale of factors that interacts with grazing intensity to determine species composition and may not be fine at all. Similar arguments can be engaged where soil erosion rather than species composition is the primary characteristic affected by grazing.

Figure 16 shows fine-grained habitat data for a 170,000-acre swath through northern Humboldt County, California. The habitat data for 1990 were obtained under contract as part of the Timberland Taskforce established by the California Legislature in 1990 (California Timberland Taskforce, in press). The habitat data for the year 2040 represent a projection based on existing California Board of Forestry timber harvest rules (Barrett et al. 1993)

LEM provides a means of quantifying the differences between the current and future scenarios in Figure 16. The first output of LEM captures changes in the aggregate acres of habitat stages (Table 3). The future scenarios affect differ-

TABLE 2. PERCEPTUAL PARAMETERS OF DIFFERENT MANAGEMENT PROBLEMS, (WHR HABITAT TYPES, AND STAGES DESCRIBED BY MAYER AND LAUDENSLAYER 1988)

DISTURBANCE	CATEGORICAL GRAIN	SPATIAL GRAIN	EXTENT
Silvicultural treatments in commercial timberland	fine (WHR habitat stages)	$10^0 - 10^2$ acres	10^5 acres
Residential and commercial development in wildlands	coarse (WHR habitat types)	$10^2 - 10^3$ acres	$10^6 - 10^7$ acres
Prescribed fire in shrublands	fine (seral stages if shrubs remain)	?scale of factors driving fire intensity	?
	coarse (life-forms if type conversion occurs)		
Grazing management in grasslands	very fine (in areas where grazing shifts competitive advantage among plant species)	?scale of factors driving species mix	?
	fine (in areas where grazing changes erosional processes)	?scale of topography	

TABLE 3. EXTENT OF DOUGLAS FIR (DFR) AND MONTANE HARDWOOD CONIFER (MHC) HABITAT STAGES IN 1990 AND PROJECTED FOR 2040 UNDER CURRENT RULES, IN TERMS OF ACRES AND PERCENT OF STUDY AREA, WITH PERCENT CHANGE (COMPARATOR ACRES * 100/REFERENCE ACRES). [AVERAGE TREE SIZE: 1=SEEDLING, 2=SAPLING, 3=POLE, 4=SMALL TREE, 5=LARGE TREE, 6= MULTI-LAYER; CANOPY CLOSURE: S= SPARSE, P= PARTIAL, M= MODERATE, D= DENSE]. CHANGES IN OTHER HABITATS NOT SHOWN.

	COMPARATOR ACRES	REFERENCE ACRES	COMPARATOR %	REFERENCE %	PERCENT CHANGE(%)
DFR1	2406	0	1	0	999999
DFR2D	1715	15	1	0	11433
DFR2M	3217	22	2	0	14623
DFR2P	320	0	0	0	999999
DFR2S	3303	0	2	0	999999
DFR3D	7694	356	5	0	2161
DFR3M	939	1284	1	1	73
DFR3P	6	139	0	0	4
DFR3S	9	74	0	0	12
DFR4D	17997	24636	11	15	73
DFR4M	2767	5634	2	3	49
DFR4P	74	932	0	1	8
DFR4S	152	404	0	0	38
DFR5D	4777	9776	3	6	49
DFR5M	22	162	0	0	14
DFR5P	171	13	0	0	1315
DFR5S	601	47	0	0	1279
DFR6	46411	24934	28	15	186
MHC2M	0	15	0	0	0
MHC2P	0	112	0	0	0
MHC2S	0	185	0	0	0
MHC3D	152	1865	0	1	8
MHC3M	64	2955	0	2	2
MHC3P	0	1023	0	1	0
MHC3S	0	1365	0	1	0
MHC4D	3951	36712	2	22	11
MHC4M	1470	5105	1	3	29
MHC4P	1252	1226	1	1	102
MHC4S	869	866	1	1	100
MHC5D	2788	5801	2	3	48
MHC5M	138	108	0	0	128
MHC5P	691	74	0	0	934
MHC5S	3	49	0	0	6
MHC6	7511	770	4	0	975

ent habitat types in different ways. In Douglas fir habitats, the area in both early and late seral stages increases, while intermediate habitat stages decline. In montane hardwood-conifer habitats, only late seral stages increase as all other habitat stages decrease. The origin of these changes can be understood in terms of the aging of all habitat types on national parkland, harvesting of dense intermediate habitat types, and replanting of montane hardwood-conifer as Douglas fir plantations. One might expect, therefore, that different watersheds within this swath might vary considerably from this average change over the whole area.

The second type of output (Figure 17) refers to change in patch-size distribution within a habitat type. Each pair of columns refers to a habitat stage, with the right column

capturing its patch-size distribution in 1990 and the left the distribution expected in 2040. To create each column, LEM ranks all polygons within each habitat type according to their area and then divides that list into six groups with equal numbers of polygons. Each segment of a column shows the area encompassed by polygons in each sextile.

The proportion of each habitat in larger blocks shifts in different directions. Figure 17 shows that the proportion of Douglas fir, pole-size dense canopy habitat in polygons greater than 15 acres increases greatly (from 40 percent to 96 percent) while the proportion of montane hardwood conifer, 12 to 24 inches dbh, dense canopy closure habitat in polygons greater than 61 acres declines precipitously from 73 percent to 21 percent.

The third type of output captures the spatial relationships between habitat stages. The spatial relationships in any given map are expressed in an adjacency histogram (Figure 18). LEM sets the total length of "edge" within the map to 100 percent. Each column in the histogram corresponds to a habitat type. The total length of each bar represents its perimeter as a proportion of the total edge, while each segment portrays the edge that habitat shares with other habitats.

Table 4 portrays the change in adjacency. Certain pairings of habitats are greatly diminished or eliminated entirely;

others are greatly increased and some new adjacencies are created.

LANDSCAPE STANDARDS

LEM provides GIS tools that quantify patterns of life at any scale. Given different management alternatives, it can quantify differences in resulting landscapes. It stops short, however, of providing standards or criteria by which to judge landscapes; it provides only a vocabulary with which such standards can be expressed.

TABLE 4. PERCENT OF CURRENT TOTAL PERIMETER AND CHANGE IN ADJACENCY OF SELECTED PAIRS OF WHR HABITAT STAGES BETWEEN 1990 MOSAIC AND MOSAIC PROJECTED FOR 2040 UNDER EXISTING RULES. HABITAT TYPES: MHC = MONTANE HARDWOOD CONIFER, DFR = DOUGLAS FIR, MCN = MIXED CONIFER, MHW = MONTANE HARDWOOD, RDW = REDWOOD. AVERAGE TREE SIZE AND CANOPY CLOSURE CODES AS IN TABLE 3.

HABITAT TYPE	HABITAT TYPE	REFERENCE%	%CHANGE
ADJACENCY ELIMINATED			
GRASSLAND	MHC3M	0.13	0
DFR3M	MCN5D	0.10	0
DFR4D	MHC3M	0.12	0
DFR4M	MHC3M	0.25	0
DFR4M	MHC3P	0.11	0
DFR4P	MHC4D	0.15	0
MHC3D	MHW4D	0.47	0
MHC3M	MHC4M	0.12	0
MHC3S	MHC4D	0.16	0
MHC4D	MHW3D	0.80	0
MHC4M	MHC5D	0.10	0
MHC5D	MHW4D	0.27	0
MHW3D	MHW4D	0.27	0
ADJACENCY DECREASED AT LEAST 50%			
GRASSLAND	MHC4M	0.16	6
DFR4D	MHC4D	3.91	10
DFR5D	MHC4D	1.18	2
MCN4D	MHC4D	0.45	2
MCN5D	MHC4D	1.73	1
MCN6	MHC4D	0.39	5
MHC3D	MHC4D	0.52	6
MHC3M	MHC4D	0.46	2
MHC3M	MHW4D	0.24	4
MHC4D	MHC4M	0.69	10
MHC4D	MHC4S	0.11	9
MHC4D	MHC5D	0.54	2
MHC4D	MHW4D	2.37	7
MHC4D	RDW6	0.24	4
ADJACENCY INCREASED MORE THAN 150%			
DFR3M	DFR6	0.10	150
DFR4D	MCN4D	0.18	333
DFR4D	MCN5D	0.60	365
DFR4D	RDW6	0.11	218
DFR5D	RDW6	0.12	242
DFR6	MHC6	0.13	1100
DFR6	RDW6	0.52	502

How might standards be developed? Recall that the goal is to maintain the patterns of life at many scales, with the assumption that patterns at scales smaller than those used will be maintained as well. Since all the species present today survived the recent evolutionary past, an initial working hypothesis is that the highest probability of maintaining all parts to the system is achieved by keeping the system within the parameter space of aggregate area, patch-size distribution, and adjacency of that past. As the managed system diverges from the parameter space, the probability of losing some species or processes increases. Defining the trade-offs between system state and probability of loss is a task for scientists. Deciding the acceptable risk of loss is a task for policy makers.

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Managing Livestock Grazing for Biodiversity

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Abstract

Hatfield's High Desert Ranch is a 400-cow operation on about 35,000 acres of private and federally leased juniper and sagebrush rangeland in central Oregon. The major economic output is breeding stock and value-added beef marketed through a cooperative to health-food stores in the Pacific Northwest and to Japan. Our cows are viewed as tools to enhance the quality of the grass—the main crop we manage. Prescribed burning is used to reduce sagebrush and juniper and simultaneously to improve watersheds as well as cattle forage. Biodiversity in our eyes is different age classes of trees and brush, different species of plants and native animals, as well as lots of grass on the hills. We realize others see other things on the land as desirable or undesirable. Letting ranchland become "ranchettes" following the hands-off type of management in national parks and wildlife refuges is as disastrous to biodiversity as are poorly managed private and federal grazing lands. Proper grazing management can enhance biodiversity both in terms of the variety of species as well as in the mix of age and vigor classes within species of plants. We spend much of our time at meetings getting other ranchers as well as bureaucrats and city folks to see these possibilities. This is part of our job so that our children might have a future making a living based on livestock at our ranch.

While not uncomfortable, I feel very much out of place as a contributor to this volume. The rest of the writers are either academics or governmental scientists. I was trained as a veterinarian but am now a rancher in central Oregon. I guess this puts my contribution in the category of "indigenous knowledge" of biodiversity, as introduced in the first paper in this volume.¹ I think that means it is opinion backed up by more opinion.

My wife, Connie, and I have made our living on the desert for the last seventeen years. Last year, we ran about 400 mother cows on about 35,000 acres of desert rangeland. Normally this should be done on about 20,000 acres, but we have been in an extended drought until this year. Our headquarters and our home are located between our spring/fall and summer rangeland. We are involved in enhancing and growing grass and then converting it into the salable product beef. We sell both breeding stock and carcass beef and process it into further value-added beef.

About half of our beef is sent to Japan and half of it to health-food stores in the Pacific Northwest, along with that from fourteen other ranches organized into a marketing cooperative. We view ourselves not simply as commodity producers; we want to be a part of the ecosystem and kind of nestle down into it. We use the cow as a tool to enhance and promote the vigor and the quality of the grass through our grazing. We also use prescribed burning to reduce sagebrush and juniper and to enhance the herbs that provide most of the forage for cattle. Getting rid of the evergreens has also increased the stream flow and reduced soil erosion.

We think hard about the business of preserving our options for future generations. In many areas, future generations are going to have a man-induced juniper forest with

¹See West, this volume.

little understory unless we do something about it. In order to preserve our options, we better get started to prevent that from happening. I understand that in the absence of fire our juniper will lead to a different system than was naturally meant to be.

With prescribed burning, about 80 percent of our country can be standing grass, predominantly Idaho fescue. These grasslands act like a giant sponge that catches the water, and we want the water to go in the ground where it falls. That water eventually works its way to lower elevations. Thus, we now have quite a few areas on our ranch where we have drowned sagebrush by reducing the hold that juniper once had above. John Buckhouse, our friend from Oregon State University, hastens to tell us that it is always good to kill a juniper but not always to expect a spring to come up under a rock when we do. We are managing semiarid rangeland and have only two ponderosa pine trees and a few clumps of aspen. When we change the vegetation structure so that too many junipers are no longer sucking water, more of the water gets in the underground system. That really changes the total biodiversity of the area.

How do we see biodiversity? We aim for rangelands where there are several different age classes of brush and different species of brush and lots of grass on the hills. We retain some little snags and big snags and young trees and old trees to maintain the homes for many kinds of organisms. The problem is that everybody looks at biodiversity in different ways. Biodiversity is somewhat like pornography: it is hard to define, but you know it when you see it. There is more truth than humor in that statement.

Let's first consider some different portions of our property. We calve in March in large sagebrush bunchgrass pastures. If you are a range scientist like Tom Bedell, you look

and see that there is some basin wild rye on these pastures. There are also thick-spike wheatgrass and maybe a little alien-crested wheatgrass. There is some bluebunch wheatgrass and Idaho fescue on the hills around these home pastures. Obviously, there has been a fire through there because there should be five-foot-tall brush growing in the area. There are patches with a little brush where the fire didn't burn. If you are a watershed specialist, like our friend John Buckhouse, you say that that looks like good grass cover that can handle quite a bit of water running off and can allow water to get in the ground. Some places in the Intermountain West, however, have gullies six feet deep with cheatgrass and tall sagebrush. If you are a cow person, you look at such land and say, "Come June the cows are going to be bred"; but on such "rawhide" desert outfits, cows ranging there are going to be just barely fat enough to come in heat and breed. If they were any fatter, you would have wasted feed supplementing them because you would have bought all that feed—an expensive input. Those are some different things you might see from our perspective.

What do you suppose you see on our rangelands if you are a big-city environmentalist—besides the dust? I guess that is the perspective some writers of other papers here tried to bring out. When you get down to detail, you really are talking about different things like butterflies and maybe rodents that other people are interested in. If you study them hard and long enough, others will find some fungi in the ground; and this may have something to do with why the grass and the brush grow, but I don't know.

Maybe you are into pocket gophers. They are tough to find, but they are there; so are baby golden eagles, another part of our system. If they don't have those rodents to eat, the eagles won't be there. Maybe you are just a plain, old "hook and bullet" environmentalist, and all you want to do is put a hole in the gophers. Target management is what the fish-and-game departments have thrived on. Possibly all you are interested in is the water that runs off that country and makes ponds so that ducks can survive.

What I want to consider now are some rangelands in other parts of the West that have been managed differently. I want to explore what the management does to biodiversity and see if we can communicate on the same level. Let's consider a ranch in a high-mountain valley of Colorado. The valley is about 7,000 feet, with the mountains going up to 12,000 or 13,000 feet. Connie and I were giving a talk over there, and we drove through this valley. We noticed that ranchers in such areas usually put their cows on the mountains in the summer and grow hay in the privately owned meadows. This style of management leads to thick riparian vegetation, with lots of willow and a few old cottonwoods along the stream courses. You wouldn't expect to see new cottonwood in a stable system such as that. The reason the willows are important is because they allow Manley's equation to work. John Buckhouse will be proud of me if I quote Manley's equation: "If the stream channel is wide and the bottom is rough, it slows the water and the dirt falls out." That is what happens in well-vegetated mountain valleys where there is originally a little narrow creek. When the water or flood comes, it spreads out through the willows and slows the

water and the dirt falls out. That is desirable because the dirt does not need to be in the reservoir. The dirt is going to come from other areas where the riparian vegetation has been reduced. Such systems are starting to fall apart, and whether cows are the cause is immaterial. As long as the cows are on the meadows season long, the willows and new cottonwoods aren't going to grow. Probably baby cottonwoods are trying to establish there, but they are being eaten off. There are gravel bars, and cottonwood could establish. We also noticed that there are five-acre homesites in the valley on which the owners haven't done anything. When a larger fraction of the valley comes under such nonmanagement, there will be more trees that use the water themselves and less will end up in the stream. These examples make up different forms of biodiversity. One of them is probably unacceptable and the other two are acceptable, depending upon what you want.

Connie and I recently visited another area affected by grazing—Yellowstone National Park. Plenty of sediment is getting into the reservoirs below there each time the streams rise. You look at it and say, "Maybe that is natural. The water is sure clear and pretty"; but Connie and I hunted around, and we found one stump—one log—where a willow had survived and had a stub about the size of my arm. I don't know how old it is, but it is one that was protected from the grazing animals. The point of these examples is that you could take a group of ranchers to such areas in Yellowstone and the ranchers would say, "My gosh, any idiot can see what is happening. The buffalo and elk, which aren't wild and free-roaming anymore, are camped in this place. They are stuck here, and in the fall they have grubbed every shrub into the ground." You could take a group of biologists to that ranch in Colorado and they could say, "For Pete's sake, a blind man could see those cows are wrecking that creek," because right next to the overgrazed area is an exclosure and on down the road is different management. The biologist in Yellowstone, however, can't see the disaster in that ecosystem; and the rancher in Colorado who has lived on that creek all his life can't see it either. It is very, very hard to break out of those mindsets.

There is another example that has not been talked about before but that I think is interesting. The area involved is another high-mountain valley, but I'm not going to tell you where it is right away. It has a stable meadow system where you do see a few small willows. If you look closer, you can see they're near a stream; but when the stream hits a big fence, the vegetation changes. The people who know the West know that Jackson High School has its nature exclosure on one side. The treeless place next door is where the elk are fed in the winter. The question is whether there is more biodiversity within the exclosure or in the elk refuge. I don't think either is bad; I just think they are different.

Let's now return to our home rangelands to illustrate how we view biodiversity and to see if you were headed in the right direction or not. Let's picture a new Idaho fescue seedling in a bunch of cheatgrass back at our own ranch. The whole world isn't cheatgrass in our area, but we have a fair amount of it. The point is that with proper management, you can grow Idaho fescue in cheatgrass. If you change grazing management, you can even get perennial plants to grow near watering points for the cattle. We planted an old tilled field

to crested wheat in 1976, yet we have native basin wild rye invading the crested wheat. Thus, grazing management can be done to make the most desirable perennial plants become more abundant.

Another thing that we rarely hear anybody talk about when speaking about biodiversity is the variety of plants within a species population produced by grazing. For instance, a *Stipa* (needlegrass) plant that has not been allowed to be grazed for fifty years loses its vigor. Proper grazing management leads to plants of all size, age, and vigor classes and a kind of biodiversity that makes dollars for us. Ungrazed Idaho fescue plants have only about 2 to 3 percent crude protein in winter, and the cows avoid them. However, if the same species is preconditioned by grazing the March before, the protein levels the next year run up to a high of 6 percent in some winters; and many times it is 4 percent. That is enough for a cow to get a big majority of her nutrition from it.

The last story I have to tell is about how we look at the world and what it is like in a simple rancher's view. This story deals with the Trout Creek Mountains of southeastern Oregon. My wife, Connie, was instrumental in bringing together ranchers, environmentalists, and the BLM to deal with Lahontan cutthroat trout in danger where there had been continuous season-long grazing for about 130 years.

This project was started four years ago when a particular mountain watershed was voluntarily rested from three thousand cows for three years. The cows returned in 1993. That deferment wasn't easy, and it wasn't without friction. After the previous examples, most of you can appreciate what the problem was with the aspen. There was just old aspen along Trout Creek and its tributaries. There wasn't any young aspen coming in. We didn't really get it pointed out to us clearly until Britt Lay, the manager of one of the ranches, asked one of our environmental people, "Just what is it you really want? All you can do is moan and complain. What is it you really

want?" "Britt," she said, "I hope you can understand. Along these streams I want to see baby willow, and I want to see teenaged willow, and I want to see middle-aged willow, and I want to see old willow. I want to see baby aspen and teenaged aspen and middle-aged aspen and old aspen. I want the uplands around to be covered with a thick stand of perennial grasses because I want the water to go in the ground and eventually to feed the creek, and I want the creek to be shaded so that I can have baby fish and teenaged fish and middle-aged fish and old fish." Britt thought a while and he said, "Gosh, why didn't you tell us that that's what you wanted? All I have heard is that you wanted to get our cows off of here. What I want is baby ranchers and teenaged ranchers and middle-aged ranchers and old ranchers."

Now, four years later, we do have baby aspen and we do have old aspen. We don't have teenaged aspen, and we don't have middle-aged aspen. Most of the West doesn't have very many teenaged aspen or middle-aged aspen, teenaged cottonwoods or middle-aged cottonwoods, or teenaged willows or middle-aged willows; but as long as we are headed in the right direction with some babies, we can get the teenagers before the old ones are dead and gone. Whether we will have baby ranchers or not I don't know. I think whether we have baby ranchers depends a lot on how well we do on making baby aspen and teenaged aspen. If the ranchers present today can make that happen, I think the baby ranchers will be there. We feel strongly that the landscape in the West, not just ours but all over, is dependent on ranchers practicing ecologically sound management. I hope our children will be feeding cows in big tough winters for a long time to come. The future is a little fuzzy—it isn't really sharp and clear—but I think the basics of it are quite simple.

Biodiversity as a Facet of Rangeland Research

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Abstract

Biodiversity is only partially a scientific issue. Philosophical and political value systems drive much of the debate and action. Better science would, however, help expose much of what is presently intuitive but may be false. A topic upon which range scientists have much to contribute is how plant diversity relates to successional status of woodlands, grasslands, shrub steppe, and deserts. Correspondence of vegetational change to animal habitats and soil erosion follows. Closer monitoring of large blocks of land under multiple use could lead to a blending of research with management. Definitive understanding of mechanisms will, however, require well-designed manipulated experiments with adequate controls maintained over longer time spans than has been the case in the past.

There are many facets to the concept of biological diversity that relate to range management. These include ethics, aesthetics, economics, values, politics, and ecological science. Managers must deal with both the abstract and unmeasurable facets of biological diversity, such as ethics, at the same time that they make decisions based on measurable ecological effects.

Much of the published information regarding biological diversity is speculative. For example, Paulson (1992) suggests that "the constant diminution of neotropical forest habitats will surely cause declines in populations of eastern migrants if it has not done so already." The purpose of many writings is presumably to support the opinions or value systems of the author. Ecocentric views dominate the literature and place high value on biodiversity as a right unto itself. Conversely, anthropocentric views, though less common in the biodiversity literature, promote biodiversity as a good to serve the interests of mankind. These views contribute to the politics of biodiversity that promote a variety of actions based on philosophy that sometimes masquerades as science. To a large degree, the current biodiversity debate is a political struggle with its basis in philosophy.

Despite the highly politicized atmosphere promoting biodiversity, there is a scientific component; and rangeland research has and should increasingly contribute to understanding the concepts embodied in the scientific portion of the biodiversity debate. West (1993) and the papers in this volume present an excellent review of the biodiversity of rangelands. They point out the varied reasons biodiversity should be of concern from ethical to ecological perspectives. The papers in this volume have added substantially to Cooperrider's (1990) treatise on rangeland biodiversity, which emphasized management, awareness, and governmental programs.

¹See, however, Moir and Bonham, this volume.

The limited research, or interpretation of research, in the context of current theories of biological diversity results in a conservative view of ecological robustness in terms of diversity. As research continues, and even as old data sets are reevaluated, the importance of various components of diversity will be clarified. At the same time, we will be clarifying ecological theory as the framework within which we understand interaction of organisms and their environment.¹

ASSUMPTIONS

The prevailing view of succession in our discipline is that succession is linear with given end points. To the extent that this is valid, we can show the orderly change in species abundance; and we can relate the changing diversity of increasers, invaders, decreasers, and various biological-diversity indices to what we call range condition. To the extent that linearity is not the principal mode of succession and that rangelands function more like a state and transition model, traditional measures of biological diversity will not necessarily reflect potential change.

We assume that high genetic diversity will lead to highly stable populations. Though the logic is clear, the experimental evidence is lacking.² Species richness is the aspect of diversity most often measured. Is this because it is the most meaningful attribute of diversity or simply because it is easily measured? We assume animal preference for specific sites or ecological structure is a measure of habitat requirements. So many ideas are seductive in their logic that most of us accept them with little question. Yet as we study nature, we discover that natural systems are more complex than we imagined; feedback and compensatory mechanisms add incredible stability to processes, and often our assumptions are invalid.

²See McArthur and Tausch, this volume.

RESEARCH AREAS

THRESHOLDS

Sustainability or stability of ecosystems is often our goal, and research should be conducted to define how ecological structure and processes relate to sustainability. Stability needs to be defined in spatial and temporal terms that may include significant fluctuation. For example, stability of a shrub-steppe ecosystem may require periodic fire and wide fluctuations in density and cover of shrubs. To prevent the fluctuation of shrub density may force the ecosystem across a threshold into a new state because of soil loss due to an excessive shrub component and limited herbaceous layer. Thus, stability of the site and its original soil is lost; similarly, the vegetation is not sustainable.

We need to understand clearly ecological threshold levels where induced or natural stresses cause permanent change in an ecological state and consequently in biodiversity. These processes will most likely be complex with a myriad of interactions as redundancy and compensation act to prevent a change in state.

SPECIES

Much is written about species in the biodiversity literature. Keystone species are those that have a disproportionate influence on ecosystem function or structure in relation to their abundance (Westman 1990). Other species' roles include critical-link species that play a crucial role in ecosystem function. West (1993) gives a thorough discussion of species roles in ecosystem stability, but West and Whitford have revisited that topic again in this volume and point out that much more definitive work remains to be done on this very important topic.

The role of rangeland species needs careful study to determine the extent to which one species can substitute for another. What are the keystone and other critical species, if any? Are species groups more important than individuals? Under what circumstances can alien species substitute for native species and maintain ecological processes?

The literature and especially the files of range scientists are rich with data on species abundance on the same and similar sites as well as under the same or similar management. A new analysis and interpretation of these data could help in understanding many questions about the role and substitutability of species in evaluating biological diversity. This analysis might also help define the data quality needed to make valid inferences about changes in biological diversity.

SPECIES GROUPINGS AND ENVIRONMENT

Communities, ecosystems, landscapes, and regions are increasingly broad groupings of organisms and their environment. Interaction of a multitude of species, soils, weather patterns, aspects, elevations, and land use results in significant spatial and temporal variation. A logical, though largely

assumed, deduction is that biodiversity buffers changes at all levels under great annual variation and decadal, centennial, and millennial extremes.

Management at all scales depends on understanding the nature of ecosystem structure and function under natural and induced stresses and the interrelationships of different ecosystems at landscape and regional scales as they relate to biological diversity. Little work has been done on rangeland systems at landscape and regional scales. Consequently, the current approach is to assume theory developed on isolated and mesic ecosystems is applicable to rangeland systems in drier environs. This assumption is likely to prove incorrect as information is gathered. As West (1993) indicated, the best way to maintain biological diversity at all scales is to maintain ecosystem integrity. Sustaining this integrity especially means maintaining soil characteristics and ecosystem processes.

Determining when a change in ecosystem state is inevitable due to stresses like species invasions, weather changes, pollution, or other factors is important. If we can predict the inevitability of changes, we can learn to manage the new ecosystem, landscape, or region and not expend energy in futile attempts to change natural or irreversible processes.

It may be feasible to maintain a sustainable ecosystem by focusing management on maintenance of ecological processes with little concern for biological diversity. In this case, ecosystem function would be the key to maintaining a healthy and sustainable landscape and region. To the extent species can substitute or compensate for one another, this becomes a feasible option.

These topics require long-term study. In most cases, at least a decade is required to even experience a normal amount of variability in weather. It is unusual for management to be sustained unchanged for this long, and other natural events will also vary. We need to look at ways of objectively measuring factors we believe to be important today in evaluating biological diversity and sustainability. At the same time, we must maintain flexibility in experimental design to add factors as our vision improves and as we change levels or practices of management in response to ecological change. The statistical considerations of work on this scale will require intense scrutiny of assumptions in the analyses. Modeling will be a major tool used to develop theory in these areas. However, some level of empirical validation will be necessary to accept output of theoretical models. State and federal experimental ranges are important sources of long-term databases where treatments have been maintained for long periods. There is no substitute for long-term empirical data sets that incorporate large-scale landscapes and actual responses to environmental variation. The temptation to make sweeping assumptions will be great and needs to be resisted as much as possible. Once we accept an assumption and it becomes a component of our landscape paradigm, it is difficult to accept an alternative explanation of a phenomenon. For example, if we believe protection from all disturbances will yield a climax of a specific type in the sagebrush steppe, we miss the opportunity to understand that the vigor in ecological processes and soil building may *depend* upon disturbance. If we believe maximum species diversity is the

measure of health, we may overlook the possibility that fewer species in specific functional groups may be more important to maintain the functioning of the system than high-species richness.

Because so little is known about sustainability, we need to keep our minds ready to accept results of objective science as it develops. A major part of every landscape or regional-level study should be to recognize and evaluate the assumptions and the quality of the data collected. Once this is accomplished and standards for biological diversity measures are defined, we can develop effective monitoring procedures.

CONCLUSION

Biological diversity has been a central theme in range science since the discipline was first organized. Current ideas and theory in a variety of ecological subdisciplines are emphasizing the need to preserve diversity for many reasons. The importance of preserving diversity is especially applicable in the extreme cases where ecosystems or species are minimized unnecessarily. Also, considering the broad scale, the interrelationships of all levels of ecological organization are intuitively important.

At the operational level, where species, communities, ecosystems, landscapes, and regions interact under normal

circumstances, the predictability of science is limited. The details of ecosystem management from soils to species, guilds, functional groups, and processes are largely based on experience and theory. Using the ideas generated by current understanding of biological diversity, the range research community can add substance by addressing these ecological issues in a new way and at new scales to define procedures that will improve landscape management.

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