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## Diversity of animal communities on southwestern rangelands: Species patterns, habitat relationships, and land management

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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

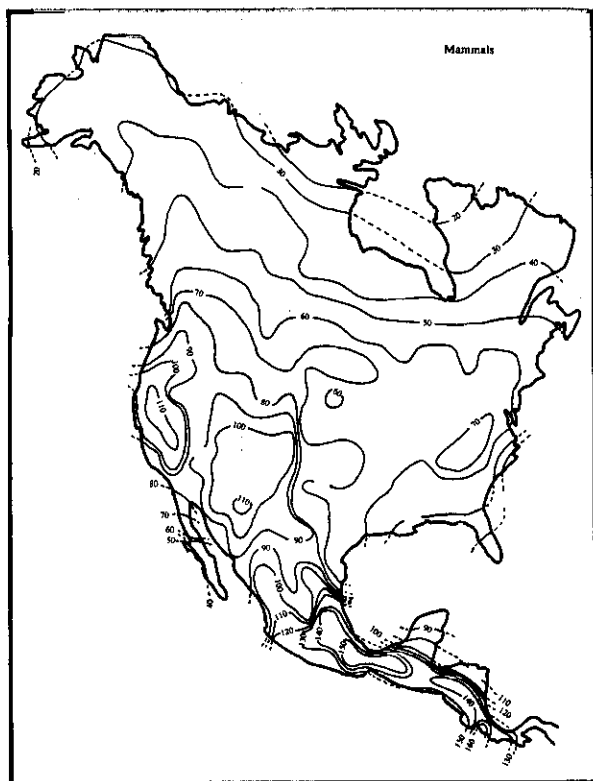


Figure 1. Contour map of mammal species richness in North America (from Simpson 1964, with permission).

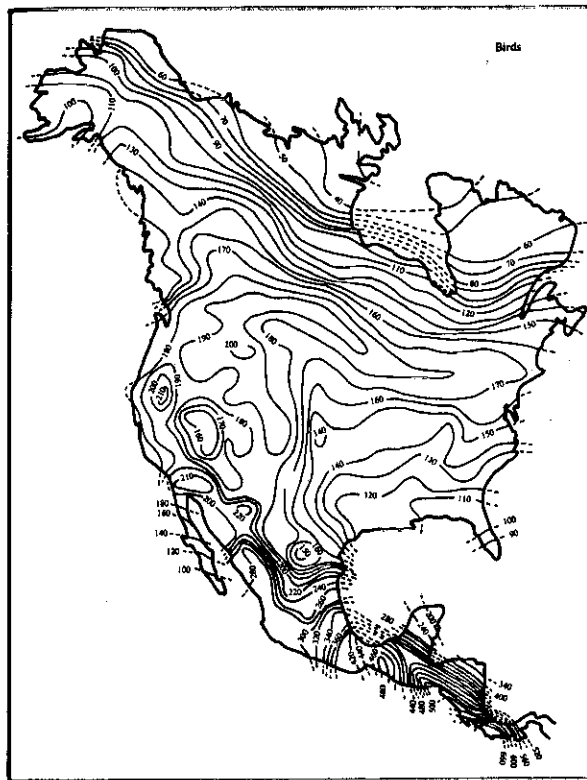


Figure 2. Contour map of bird species richness in North America (from Cook 1969, with permission).

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.

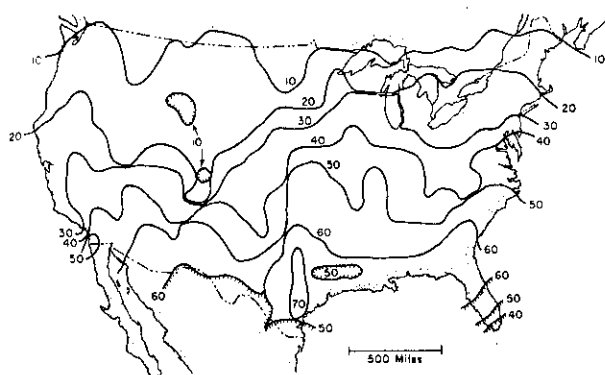


Figure 3. Contour map of reptile species richness in North America (from Kiestler 1971, with permission).

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 <sup>2</sup> )	36	102	21
Chiricahua Mountains, AZ (~ 320 km <sup>2</sup> )	58	221	30
Sevilleta LTER Sites, Socorro Co., NM (~ 12,800 km <sup>2</sup> )	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 km<sup>2</sup> in southeastern Arizona; and (3) within the 12,800 km<sup>2</sup> 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]).

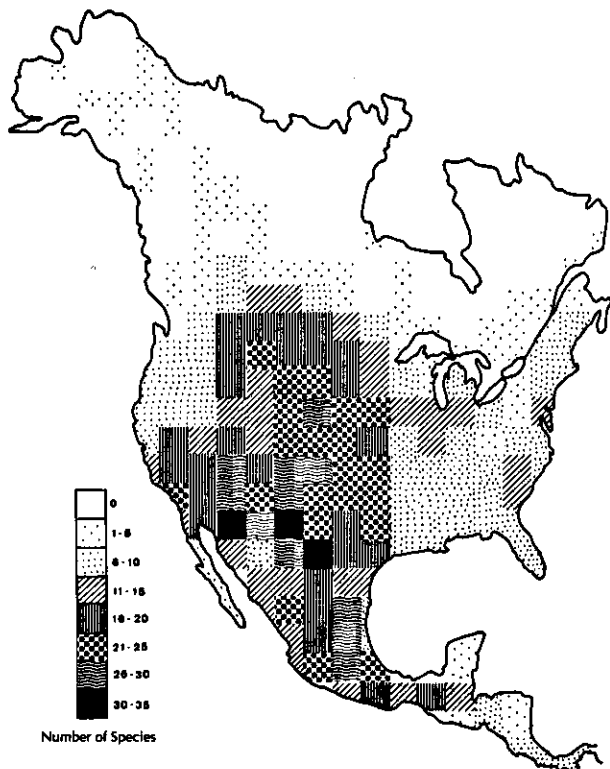


Figure 4. Map of species richness patterns of gomphocerine and acridine grasshoppers in North America (from Otte 1981, with permission).

**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).

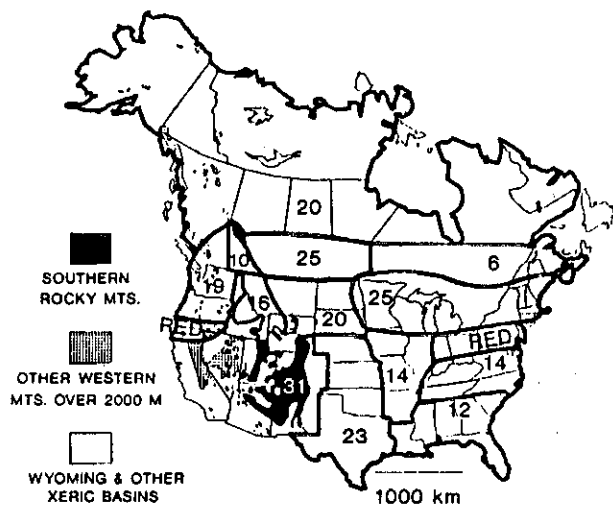


Figure 5. Map of species richness patterns of the ground beetle genus *Harpalus* (Carabidae), in North America (from Noonan 1990, with permission).

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).

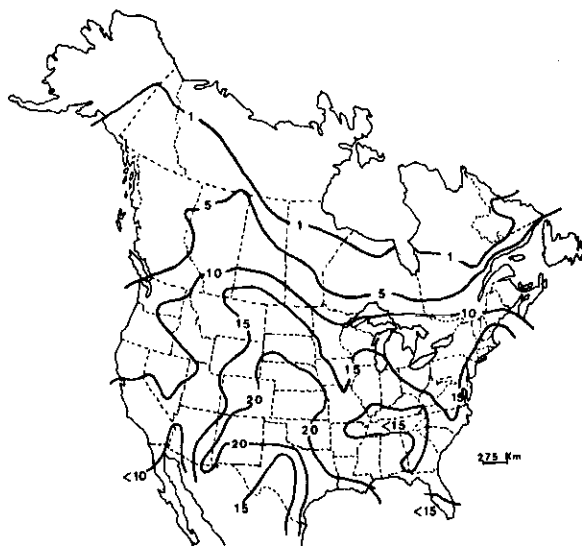


Figure 6. Contour map of tiger beetle (Cicindelidae) species richness in North America (from Pearson and Cassola 1992, with permission).

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).

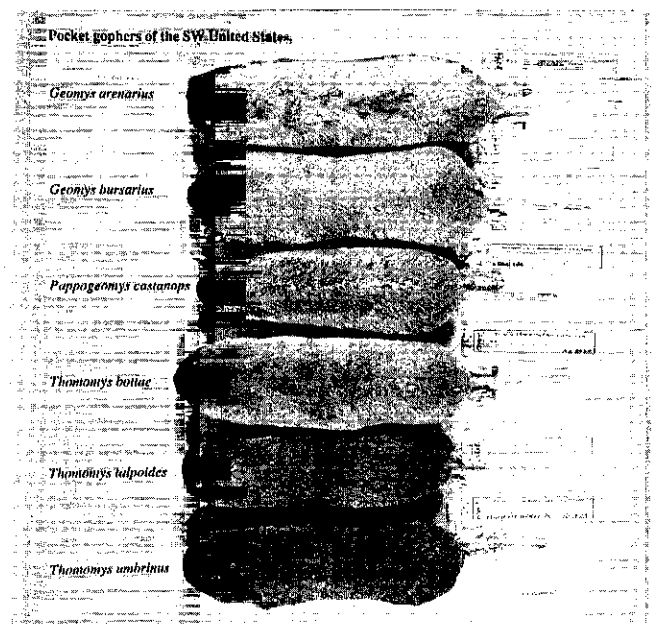


Figure 7. Museum specimens of pocket gophers (Geomyidae) of the Southwest (not shown: *Geomys atwateri*).

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

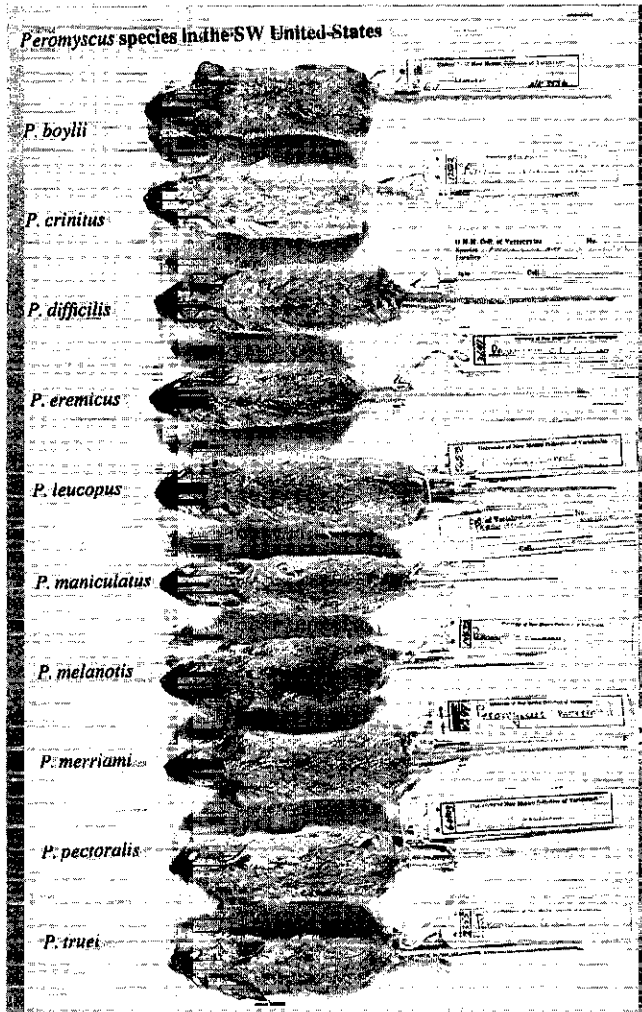


Figure 8. Museum specimens of mice in the genus *Peromyscus* from the Southwest (not shown: *P. gairdneri*).

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

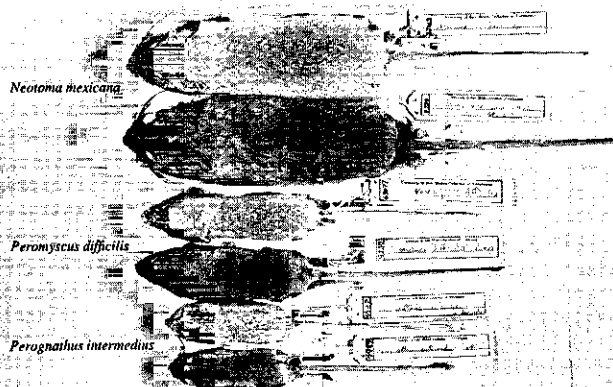


Figure 9. Examples of melanism in rodents from the Southwest.

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.<sup>1</sup>

#### 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-<sup>1</sup>See 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

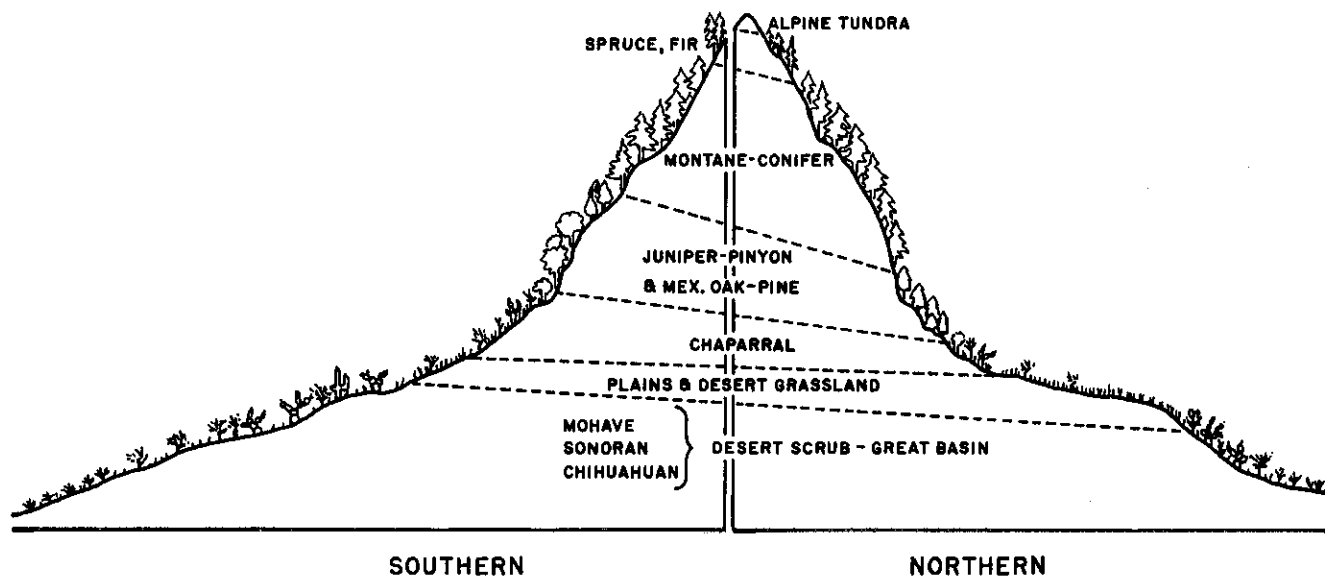


Figure 10. Diagram of the distribution of plant communities across a typical elevation gradient in the Southwest (from Hoffmeister 1986, with permission).

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 (Scoggan 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>Boettettix 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 samalayuca</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

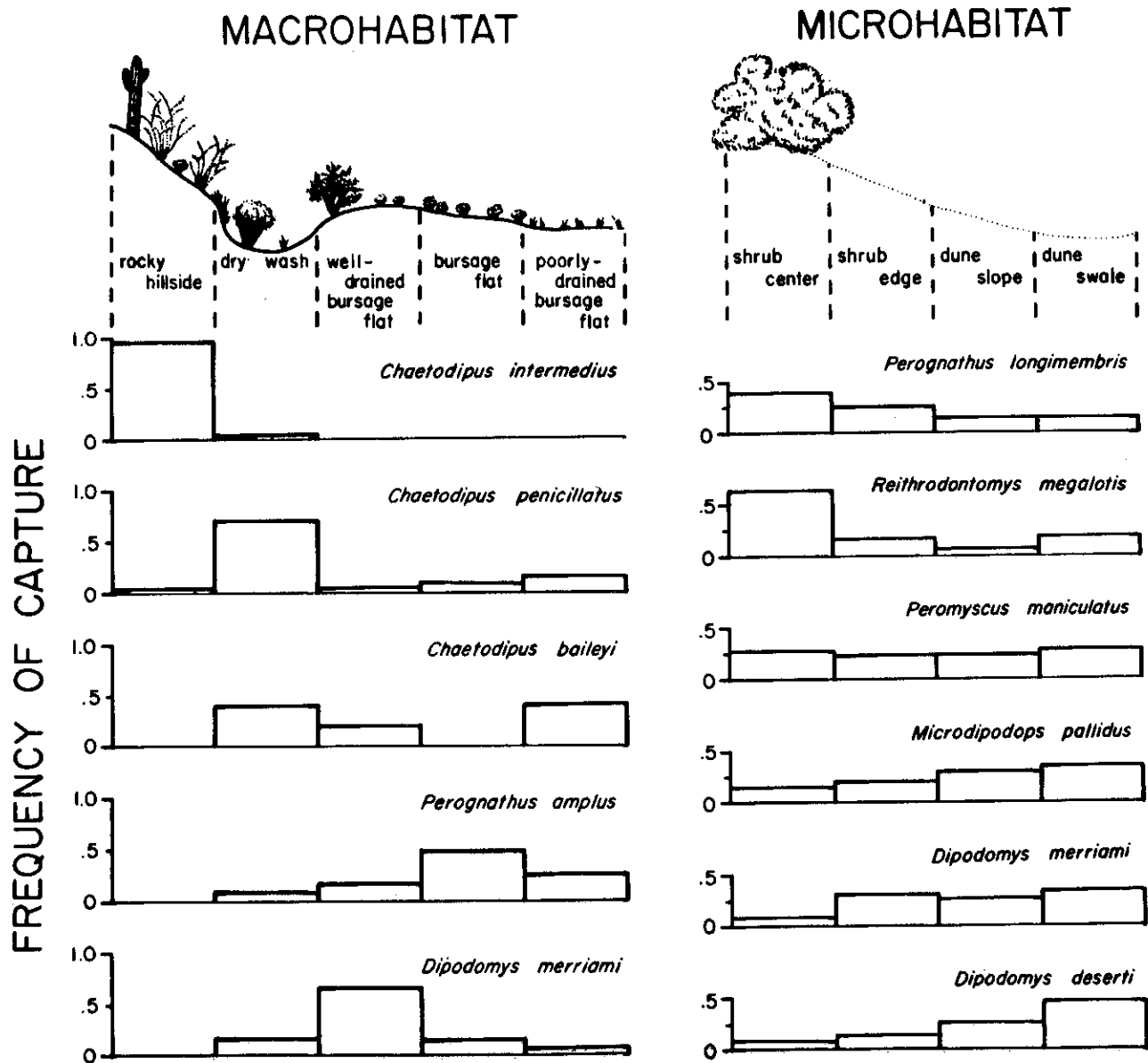


Figure 11. Distribution of desert rodent species among different macrohabitats and microhabitats based on trap capture frequency data. Data from J. H. Brown.

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

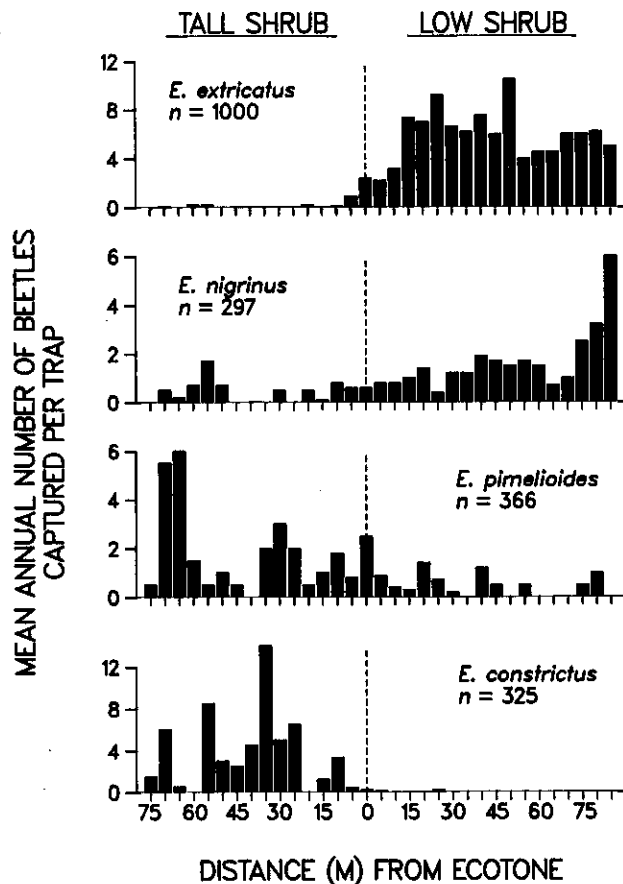


Figure 12. Numbers of darkling beetles (*Tenebrionidae*: *Eleodes* spp.) captured in pitfall traps in low and tall shrub microhabitats in sagebrush-steppe rangelands near Kemmerer, Wyoming (from Parmenter et al. 1989a, with permission).

(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 (km<sup>2</sup>) through stands (m<sup>2</sup>) to individual plants (cm<sup>2</sup>).

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.)<sup>2</sup> 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

<sup>2</sup>However, 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 <sup>1</sup>	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 <sup>2</sup>	56 (29%)	46 (15%)	102 (20%)
Totals:	193	307	500

<sup>1</sup> Excluding Alaska, Hawaii, and Pacific Islands.

<sup>2</sup> 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 <sup>1</sup>	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 <sup>2</sup>	2 (6%)	99 (24%)	101 (22%)
Totals:	36	416	452

<sup>1</sup> Excluding Alaska, Hawaii, and Pacific Islands.

<sup>2</sup> Excluding Caribbean Islands.

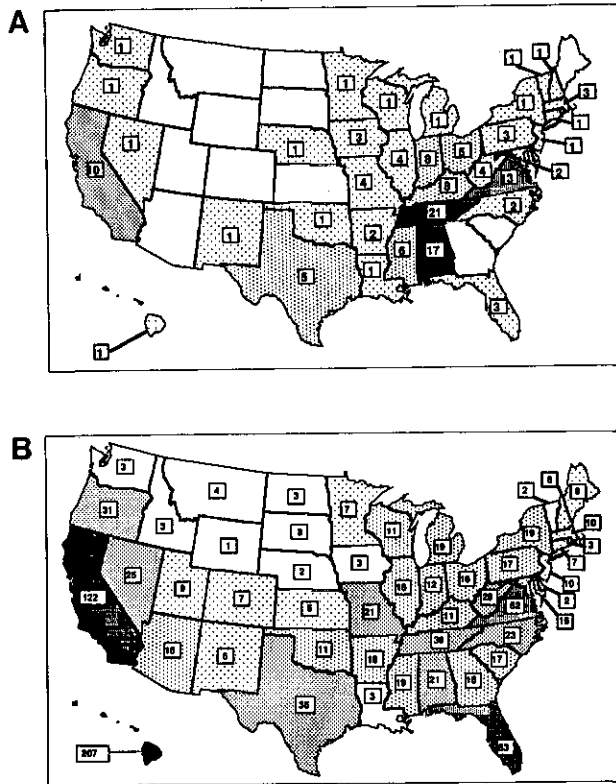


Figure 13. Numbers of invertebrate species in each state that are listed as (A) Federal threatened or endangered species, and (B) category 1 and 2 candidate species for Federal listing (from Hafernik 1992, with permission).

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.

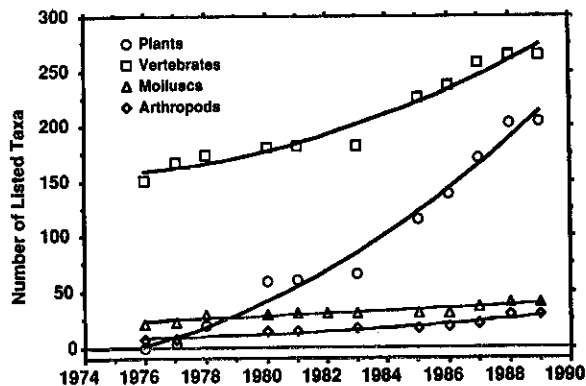


Figure 14. Rate at which taxa have been listed as Federal threatened or endangered species since 1976 (from Hafernik 1992, with permission).

### 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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