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Southwest

The southwestern region of the United States is a land of extremes and contrasts. Elevations vary from below sea level in the Imperial Valley of California to mountain peaks approaching 4,000 meters. Landscapes are striking and variable and include mountains, foothills, canyons, deserts, plains, and rivers. The area is arid or semiarid and, depending on the location, may have mild winters and summers, periods of bitter cold, or intervals of intense heat. Climate is inextricably tied to water and its availability. Historically, water varied from abundant to sparse over the span of a year, and adaptations of native plants and animals reflect those extremes. Annual precipitation, usually in the form of rain, varies from 30 to 40 millimeters in the low-elevation Sonoran Desert to more than 1,000 millimeters in the high mountains (Brown 1982a; Bahre and Shelton 1993). This variation in topography and climate has produced great floral and faunal diversity.

The Southwest, as discussed here, includes Texas west of the Pecos River, most of New Mexico, Arizona, the Colorado Desert of southeastern California, and the Colorado Plateau of western Colorado and eastern Utah (Fig. 1). Our review of the status and trends of the biota of this region was aided by several particularly useful sources, especially Brown (1982a) for Arizona, Dick-Peddie (1993) for New Mexico, Harper et al. (1994) for the Colorado Plateau, and MacMahon (1979, 1988a) and West (1988) for North American arid ecosystems in general.

Brown (1982a) discussed the biotic resources of the Southwest within a life-zone context, in which ecosystem expression is strongly tied to gradual changes in elevation and latitude. This general approach was first formulated from visits made by C. Hart Merriam (Merriam and Steineger 1890) to the San Francisco Peaks, just south of the Grand Canyon in Arizona. Merriam's studies allowed him to postulate a relationship among latitude, elevation, and resulting climatic gradients; his conclusions significantly influenced early biological thought about the American West. He used descriptors such as Lower Sonoran to refer to desert, Upper Sonoran to refer to grasslands and woodlands, Transition to refer to pine forests, and Canadian to refer to higher-elevation forests. Although later work has refined, if not supplanted, most of Merriam's work, his basic approach to life zones in the West is still useful in understanding biological diversity.

Plants and animals in the Southwest respond to a multitude of gradients, and the interactions of gradients such as aspect, elevation, and latitude increase the complexity of biological interactions as well as our ability to understand them. Merriam was especially interested in elevation gradients of vegetation and how such gradients reflected similar north–south latitudinal gradients. The presence of northern conifer forests dominated by fir and spruce on the mountaintops of the Southwest, well to the south of the main concentration of such forests, is an example of this phenomenon (Fig. 2).

In the Southwest, plant and animal distributions are affected by general climatic zones such as significant north–south gradients in temperature and precipitation. To the north, the Colorado Plateau region tends to have extremely cold winters, with winter precipitation predominantly occurring as snow. In contrast, summers in the Colorado Plateau can be quite hot and dry. To the south of the plateau in central and western Arizona, winters are milder and precipitation occurs as rain. Summers are



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Ecologist

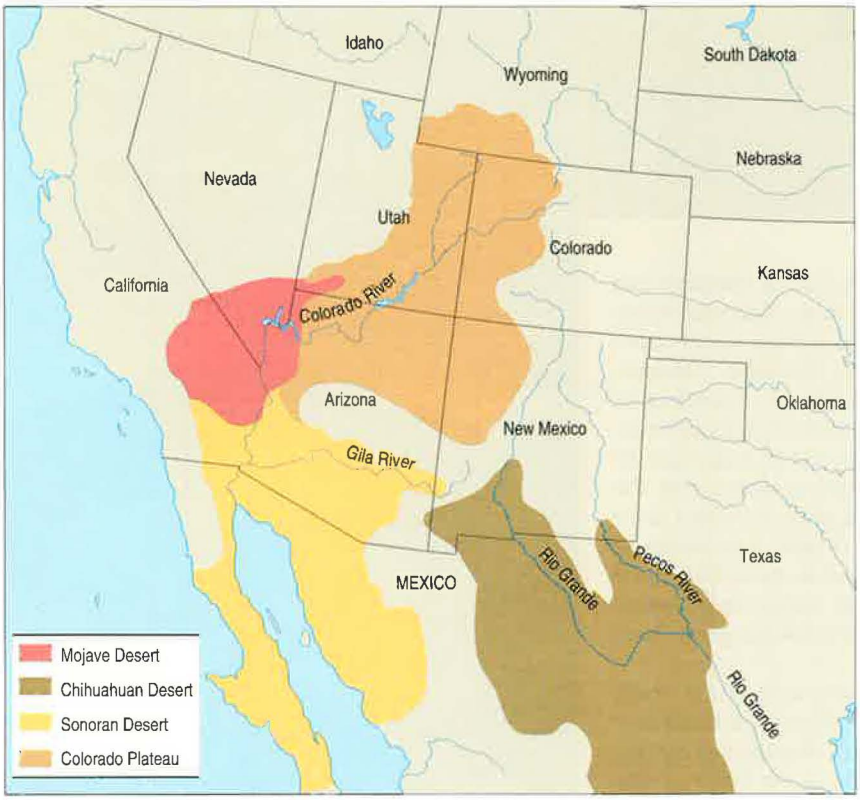


Fig. 1. The southwestern region of North America.

still relatively hot and dry, particularly at the eastern edge of the Mojave Desert. Farther south and eastward, in the Sonoran and Chihuahuan deserts, winters are also less severe, and precipitation shifts, occurring predominantly in late summer as monsoonlike rains. Late spring and early summer are hot and dry.

Ecosystems are also shaped by changes in temperature and moisture along elevation gradients and aspect (that is, north- and south-facing slopes) of local mountain ranges. For example, as elevation increases in the mountains in southeastern Arizona, the vegetation shifts from grasslands, woodlands, and forests of Mexican Sierra Madrean affinity to forests and meadows of Rocky Mountain affinity (Brown 1982a; Muldavin et al. 1996).

People and Processes of the Southwest

Ecosystems in the Southwest have been extensively shaped by their histories of climatic variability and by disturbances such as fires and floods. Superimposed on these natural sources of variation are the prehistoric and recent activities of humans in the Southwest. Most human-induced change has occurred since about 1870, after the Southwest was settled primarily by Anglo-Americans and market forces were developed, as represented by the arrival of the railroad (Hastings and Turner 1965; Bahre 1991; Bahre and Shelton 1993). Recent, rapid population growth (Fig. 3), continued economic transformation, and ongoing resource use in the Southwest have meant that humans have greatly influenced the region's natural systems—and still do.

Climatic Variability

Reconstructions of southwestern climate from studies of tree growth rings have been especially useful in understanding long-term environmental variation (Fritts and Swetnam 1989). Such tree-ring reconstructions reveal that high variability in precipitation occurred at annual, decadal, and centennial time scales extending back for the last 2,000 years (Grissino-Mayer 1995; Fig. 4). Variability in precipitation amounts and timing is related in part to El Niño events in the Pacific Ocean, which bring wetter winters and springs to portions of the Southwest about every 3 to 5 years (Ropelewski and Halpert 1986). Precipitation variability affects biotic productivity and diversity on local to regional scales (Pieper 1994) and also affects disturbance processes such as fires (Swetnam and Betancourt 1990), floods (Molles and Dahm 1990; Webb and Betancourt 1992), and insect population outbreaks (Betancourt et al. 1993; Swetnam and Lynch 1993).



Courtesy C. D. Allen, USGS

Fig. 2. Forests of Engelmann spruce, corkbark fir, aspen, and Douglas-fir in New Mexico.

Human Settlement

People have inhabited the Southwest for more than 10,000 years, from Clovis Paleo-Indians to sedentary farmers (for example, Anasazi, Mogollon, and Hohokam peoples) and nomadic peoples ancestral to the modern Navajos, Apaches, and Utes (Stewart and Gauthier 1986). Prehistoric peoples possibly contributed to the extinction of the Pleistocene megafauna (Martin 1967) and to localized deforestation of woodlands and depletion of wildlife and soils (Betancourt and Van Devender 1981; Samuels and Betancourt 1982; Kohler 1992). At the time of Spanish incursions in the 1500's, about 100,000 Native Americans lived in about 100 communities (pueblos) in northern and central New Mexico (Schroeder 1979), but colonial disruptions of their cultures and diseases introduced by Hispanic colonists drastically reduced their numbers. Today, the Southwest is home to more than 330,000 Native Americans, who live on millions of hectares of tribal lands. For example, in Arizona, about 8 million hectares (27%) are tribal lands, and in New Mexico, about 3 million hectares (9.4%) are tribal lands (Williams 1986; Utter 1993).

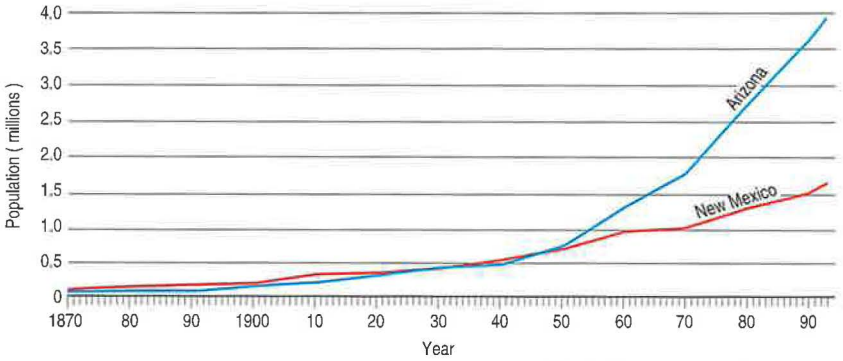


Fig. 3. Human population growth in Arizona and New Mexico, 1870–1993 (data from U.S. Bureau of the Census 1975, 1994).

European settlers also introduced new plants, animals, technologies, and land-use patterns to the Southwest. Over the past century, these factors, along with the rapidly increasing human populations and their accompanying resource consumption, have resulted in unprecedented effects on southwestern ecosystems. Agents of change that have significantly affected the status of southwestern ecosystems and are largely responsible for ecosystem trends

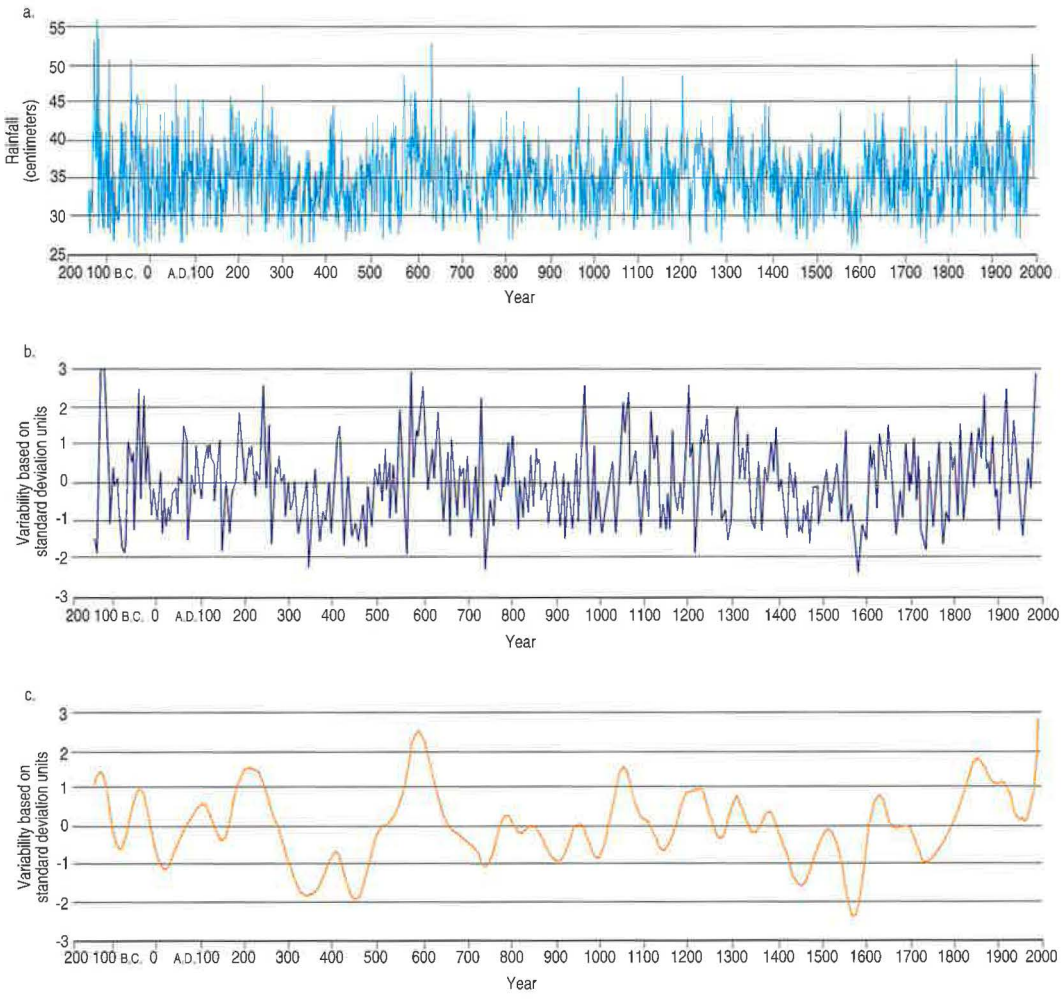


Fig. 4. a) Reconstruction of annual rainfall from El Malpais National Monument, New Mexico, based on tree-ring analysis; b) 10-year smoothing line of the reconstruction, using standard deviation units to highlight short-term (fewer than 25 years) climatic episodes; c) 100-year smoothing line showing long-term (more than 50 years) climatic trends (Grissino-Mayer 1995).

that we can identify today include grazing, fire suppression, logging, dams and water diversion, biocides, agriculture, fragmentation of wildlands by roads and other construction, introduction of nonindigenous plants and animals, and urbanization.

Grazing

Widespread grazing of domestic livestock has caused major cumulative effects on the ecology of the arid Southwest (see Fleischner 1994 for a comprehensive review). Even before this area became part of the United States, livestock production was an important activity (Denevan 1967). Sheep were the primary stock favored by the Spanish, with at least several hundred thousand sheep inhabiting New Mexico from about 1788 onward (Denevan 1967). After Native Americans were confined to reservations and railroads were linked to external markets, an immense boom in the livestock industry, particularly cattle, occurred in the early 1880's (Wooton 1908; Stewart 1936; Denevan 1967). In Arizona, livestock increased from about 142,000 in 1880 (Stewart 1936) to 650,000 in 1885 (Hastings and Turner 1965), and roughly 1,500,000 in 1891 (Cameron 1896; Morrisey 1950; Bahre 1991). In New Mexico, cattle numbered about 137,000 in 1880 and reached 1,380,000 by 1889 (Wooton 1908; Williams 1986), while numbers of sheep in New Mexico increased from 619,000 in 1870 (Denevan 1967) to roughly 2,000,000 in 1880 and 5,400,000 in 1884 (Wooton 1908). In general, livestock numbers peaked between the 1880's and 1920's and have declined since (Schickedanz 1980; Branson 1985).

Overall stocking rates have decreased primarily because of a transition from sheep grazing to cattle grazing. In 1906 in New Mexico there were a little more than a million cattle and almost 6 million sheep; by 1979, the number of cattle had increased to 1.5 million and the number of sheep had declined 90% to 604,000. Reductions in livestock numbers are associated with the end of open ranges, the Taylor Grazing Act of 1934, and some increasing control asserted by federal land management agencies over public lands (deBuys 1985; Bahre and Shelton 1993). In New Mexico, about 44% of total lands are privately held; the remainder belong to federal, state, and tribal governments (Williams 1986). Figures for private land in Arizona are similar. Most southwestern lands continue to be grazed, including even apparent reserves (for example, wilderness areas and some national and state parks). Even relatively secure areas (for example, Department of Defense lands) have experienced some level of grazing pressure in recent years that is mostly undocumented (E. Muldavin, New Mexico Natural Heritage Program, Albuquerque, personal observation).

The extremely high historical stocking rates and concomitant overgrazing and livestock preferences for certain more palatable plants (for example, grasses) led to significant alterations in the species composition of vegetation across the Southwest (Leopold 1924; Cottam and Stewart 1940; Cooper 1960; Buffington and Herbel 1965; Humphrey 1987; Grover and Musick 1990; Archer 1994; Fleischner 1994; Pieper 1994). Cool-season grasses and other preferred forage species declined (Bohrer 1975), while unpalatable and weedy species, such as broom snakeweed, and shrubs, such as creosotebush and mesquite, increased (Wooton 1908; Bahre and Shelton 1993). Cole (1995) has shown that over the last 5,450 years vegetation in one area of the southern Colorado Plateau remained fairly stable up to the last few hundred years. Since settlement, plants preferred by sheep and cattle, such as winterfat and ricegrass, have disappeared entirely from pollen profiles, whereas plants associated with overgrazing (such as whitebark rabbitbrush, snakeweed, and greasewood), which were not recorded in pollen profiles before settlement, are now present. Livestock also altered vegetation composition by serving as an agent for the spread of weedy and nonindigenous plant species such as Lehmann lovegrass (Warshall 1995). Concentrated livestock use of riparian zones has had particularly significant negative ecological effects (General Accounting Office 1988; Szaro 1989; Bahre and Shelton 1993; Fleischner 1994).

The year-round, high-intensity grazing of open ranges that occurred in the past also led to marked reductions in herbaceous plant and litter ground cover (Fleischner 1994). Because the productivity (and thus grazing capacity) of many southwestern rangelands varies markedly in response to annual variability in precipitation (Pieper 1994; Fig. 4), the tendency to stock ranges at the carrying capacity of the wetter years results in severe overgrazing effects during drought conditions (Cameron 1896) unless livestock numbers are rapidly reduced to track actual range conditions. Overgrazing is also widely considered a major trigger of soil erosion, flooding, and arroyo cutting in the Southwest (Wooton 1908; Leopold 1924; Cooperrider and Hendricks 1937; Cottam and Stewart 1940; Smith 1953; Cooke and Reeves 1976; Bahre and Bradbury 1978; Branson 1985; Bahre 1991), although climatic fluctuation has also been considered an important factor by other authors (Leopold 1951; Hastings and

Turner 1965; Denevan 1967; Graf 1986; Humphrey 1987; Webb and Betancourt 1992). Similarly, while Turner (1990) provided evidence of climatic influence on Sonoran Desert vegetation, Bahre and Shelton (1993) generally dismissed the effect of climate change as the primary agent of long-term directional vegetation change in the Southwest; rather, they attributed such change to livestock grazing and fire suppression. Fleischner (1994:637) said, "For now, the best historic evidence seems to support the idea that livestock grazing, interacting with fluctuations in climatic cycles, has been a primary factor in altering ecosystems of the Southwest." However, Brown and McDonald (1995), among others, have questioned the objectivity of Fleischner's presentation. We recognize that significant, ongoing efforts have been made to make livestock grazing more ecologically sensitive and sustainable (for example, rest and rotation systems, better spatial distribution, and immediate stocking reductions when droughts occur). Still, livestock grazing clearly remains a key process affecting southwestern ecosystems, and eliminating livestock entirely may be the only way to allow some systems to recover.

Fire

Fire is an integral process in many southwestern ecosystems, and fire scars on trees demonstrate that past fires were frequent and widespread in forested landscapes (Swetnam and Baisan 1996). Even desert grasslands apparently sustained significant fires (Bahre 1991). Fires affect ecosystems at scales ranging from site-level nutrient cycling (White 1994) to formation of landscape-scale vegetation patterns (Allen 1989).

The cessation of frequent natural surface fires all across the Southwest in the late 1800's apparently was due to reduced vegetation caused by intense grazing by livestock (Savage and Swetnam 1990; Swetnam 1990; Swetnam and Baisan 1996). Except in a few isolated localities protected from grazing, this region-wide reduction in fires began several decades before people began to actively initiate fire suppression (Madany and West 1983; Touchan et al. 1995) and testifies to the ubiquity and intensity of regional livestock grazing effects during the late 1800's. The initial suppression of natural surface fires by livestock grazing graded into the period of active suppression of all fires by land management agency personnel after about 1910 (Swetnam 1990). Fire suppression over the past century pervasively affected many southwestern ecosystems (Covington and Moore 1994).

Forest Logging and Forest Health Issues

Forestry practices on large land grants and public lands in the Southwest have gone through several phases in the past century. Relatively indiscriminate cutting practices characterized the late 1800's and early 1900's (deBuys 1985), selective logging the mid-1900's, and even-aged management the 1960's through 1980's; now we are back to more selective, uneven-aged silvicultural practices. Until recently, forest harvest practices tended to remove all old-growth trees to bring forest stands under "control," and extensive road networks proliferated to aid forestry activities (Allen 1989). More recently, new management plans support the maintenance of at least some old-growth forests and roadless areas as important for ecological and social reasons (see compilation in Kaufmann et al. 1992).

Fire suppression, commercial forestry practices, and overgrazing have pervasively altered the structure and species composition of most southwestern forests (U.S. Forest Service 1993; Covington and Moore 1994). Old-growth forests have been greatly reduced by high-grading and even-aged management practices that targeted the most valuable old trees, especially ponderosa pine. In addition, until 20 years ago, snags (dead trees) were systematically removed as fire and forest health hazards, while extensive road networks aided those who poached fuelwood (poachers often focused on snags). Hence, most managed forests now lack desired numbers of large-diameter snags, which serve important ecological roles such as cavity-nesting sites for many breeding birds (Thomas et al. 1979; Hejl 1994) and probably for many bats as well (H. Green, U.S. Forest Service, Arizona, personal communication; M. Bogan, U.S. Geological Survey, Albuquerque, New Mexico, unpublished data). Today's forests are characterized by unnaturally dense stands of young trees, a variety of forest health concerns, increasing potential for widespread insect population outbreaks (Swetnam and Lynch 1993), and unnatural crown fires (Covington and Moore 1994; Sackett et al. 1994; Samson et al. 1994).

Southwestern forests, while limited in areal distribution and regional importance for timber production, do provide a multitude of essential market and nonmarket benefits, ranging from human recreation to protection of watersheds and biodiversity. Increased forest densities lead to decreases in total streamflow, peak flow, and base flow (Troendle and Kaufmann 1987; Ffolliott et al. 1989), important concerns in the water-limited Southwest. Timber harvests from

public forests have declined markedly in recent years because of the depletion of large, high-value trees and increased attention to environmental constraints (for example, sensitive species, water quality, old-growth set-asides). Forest health issues drive current efforts directed at thinning understory trees mechanically and with prescribed fires to restore more natural, sustainable forest structures and processes.

Biocides

Extensive applications of biocides such as DDT on forests and agricultural lands during the 1950's and 1960's have left persistent concentrations of these compounds in southwestern ecosystems (also see Environmental Contaminants chapter). Our knowledge of biocide use in the Southwest is largely anecdotal. For example, U.S. Forest Service operations against western spruce budworm included spraying 514,664 kilograms of DDT on 478,055 hectares of the Santa Fe National Forest and adjacent Carson National Forest (both in New Mexico) between 1955 and 1963 (Brown et al. 1986). Likewise, over the past decade, about 40,000 hectares of Bureau of Land Management lands in southeastern New Mexico have been aerially treated with tebuthiuron to enhance livestock range values by converting Havard's oak sandhills to grass-dominated systems (C. Painter, New Mexico Department of Game and Fish, Santa Fe, personal communication). Schmitt and Bunck (1995) and Glaser (1995) reviewed persistent environmental contaminants and their recent effects on fish and wildlife. The magnitude and full effects of past and potential biocide use in the Southwest remain unassessed.

Dams, Water Diversions, and Roads

Most declines and extirpations of aquatic organisms in the Southwest can be traced to the construction of dams, either for water storage or flood control, and to other development on or near waterways, such as diversion structures and drainage of wetlands. Dam building and water diversions have significantly degraded most major river systems (Szaro 1989; Crawford et al. 1993), causing dire consequences for native fishes. In addition, such structures often contribute to habitat fragmentation (Crawford et al. 1993), with plant and animal distributions often reduced to increasingly small areas. Similarly, landscapes have been fragmented by proliferating road networks (Fig. 5), with numerous negative ecological implications (Allen 1989).

Southwestern Ecosystems

The biotic communities of the Southwest have responded in different ways to the prehistoric and recent effects of human activities on the natural southwestern environment. We focus on several important ecosystem types, which are defined primarily by dominant vegetation and are arranged along an elevation gradient. We consider the status and trends of each in the context of specific biotic composition, climate considerations, and human uses.

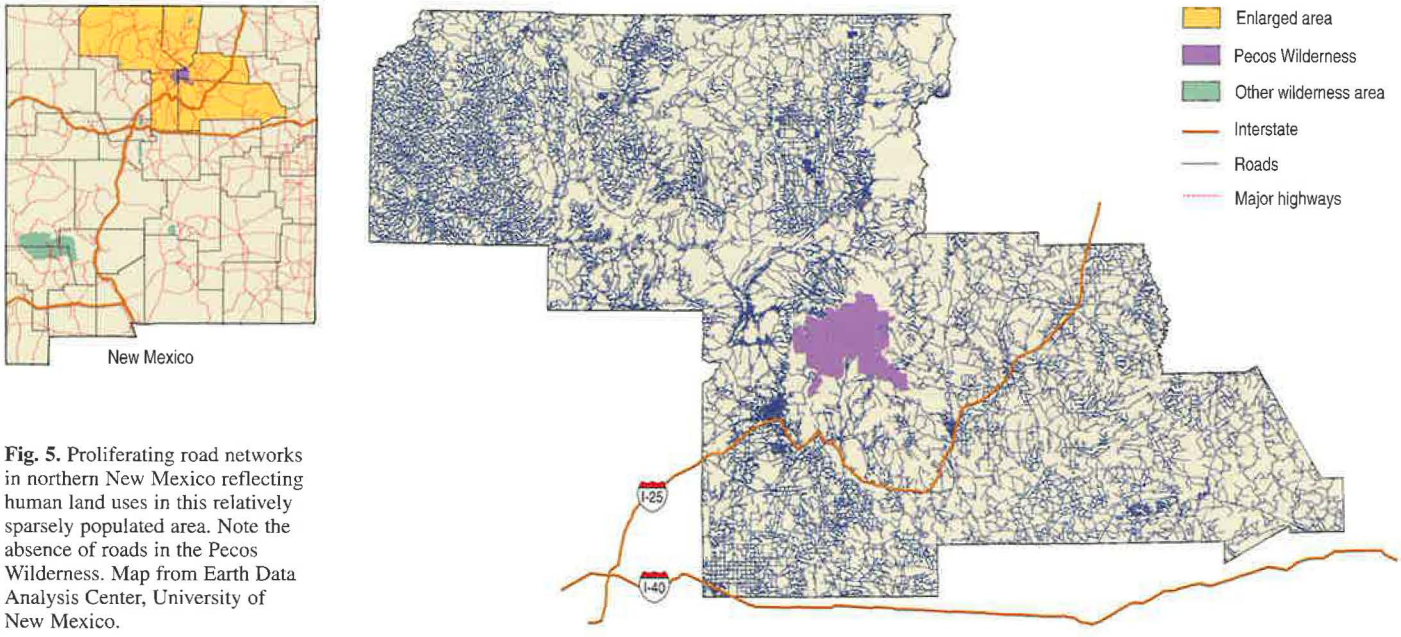


Fig. 5. Proliferating road networks in northern New Mexico reflecting human land uses in this relatively sparsely populated area. Note the absence of roads in the Pecos Wilderness. Map from Earth Data Analysis Center, University of New Mexico.

Alpine Tundra, Subalpine and Montane Grasslands, and Meadows

Alpine tundra occurs above treeline atop the highest mountain peaks and covers relatively little area in the Southwest; it occurs principally in northern Arizona, northern New Mexico, and western Utah (see summaries by Pase 1982; Baker 1983; Moir 1993). Alpine tundra is characterized by prostrate woody shrubs (commonly willows), herbs, lichens, and mosses growing in cool, usually wet, conditions within a relatively short growing season. The status and trends of tundra and its associated organisms in the Southwest are little known. Most southwestern tundra ecosystems occur within national forests, commonly within wilderness areas, but they are still subject to grazing by cattle, sheep, and horses during the growing season (Dick-Peddie 1993). Effects of grazing on alpine tundra, such as changes in plant species composition and soil compaction, need to be assessed. Researchers are also concerned about the effects of localized recreational use, warming climates, and acid deposition in the alpine tundras (Moir 1993). In the highlands of the Southwest, extensive grasslands (on uplands) and meadows (in drainages) occur above and below treeline (Brown 1982b). These grasslands are dominated by perennial bunchgrasses such as fescues, oatgrasses, and wheatgrasses; the meadows are characterized by herbaceous plants, grasses, sedges, and rushes.

By the late 1800's, the species composition and vegetation structure of these high-elevation herbaceous ecosystems were being altered by intense grazing by livestock, especially sheep. For example, moist meadows in the Jemez Mountains of New Mexico are often dominated now by nonindigenous plants such as Kentucky bluegrass, white clover, and dandelion (Allen 1989; Wolters 1996). Additionally, increased tree densities in surrounding forests may be transpiring water that previously kept many meadows moist. Channel incision, caused by elimination of beavers and continued livestock grazing, also has caused many meadow sites to become drier, allowing trees (often blue spruce) to invade their margins. Reduced competition from grasses, fire suppression, and climatic warming also have enabled widespread tree invasion of montane and subalpine grasslands (Allen 1989; Moir and Huckaby 1994; J. Elson, W. deBuys, W. Moir, and C. Allen, Santa Fe, New Mexico, unpublished data); parks and grasslands throughout the region are being diminished by tree invasion (Fig. 6). Better management practices and reduced livestock numbers, especially far fewer sheep, have allowed improvements in grassland conditions in many areas from their low point in the early twentieth century (Branson 1985), for example in the Pecos Wilderness (J. Elson, W. deBuys, W. Moir, and C. Allen, unpublished data). Many moist meadows, though, are still heavily grazed by domestic livestock and burgeoning elk populations (Allen 1996a; Wolters 1996).



Courtesy C. D. Allen, USGS

Fig. 6. Conifer tree invasion of a montane grassland in northern New Mexico.

Subalpine Forests

Forests cover about 6.5% of Utah, 6.8% of Arizona, and 8.4% of New Mexico (Powell et al. 1993), although Van Hooser et al. (1993) reported that only 6.2% of New Mexico has more than 10% forest canopy cover. The highest-elevation forests in the Southwest are subalpine forests, characterized by stands of conifers such as Engelmann spruce and subalpine fir. These forests most often occur in relatively small, isolated mountaintop stands (Pase and Brown 1982a; Moir 1993). Spruce–fir forests grade into bristlecone pine stands on some treeline sites and into mixed conifer forests at lower elevations. Large stands of quaking aspen commonly occur in subalpine forests, particularly after fires. In closed-canopy conifer forests few herbaceous plants grow amidst the blankets of needle and wood litter, whereas aspen stands may have luxuriant herbaceous plant-dominated understories. Spruce–fir forests cover about 0.2% of Arizona and 0.5% of New Mexico (Alexander 1987).

Major natural disturbances in the subalpine forest are the uprooting and blowdown of trees by wind (windthrow), spruce beetle outbreaks, and fire. Windthrow of remnant trees is a problem because partial cutting of spruce–fir forest stands exposes remaining old trees to new wind stresses (Alexander 1987). Because spruce beetles prefer downed trees, major outbreaks usually originate in material from blowdowns or logging operations (Schmid and Frye 1977).

Fire histories of southwestern subalpine forests have been little studied, but recent work indicates that some spruce–fir stands experienced mixed fire regimes, with patchy crown fires occurring about every several hundred years and more frequent surface fires occurring every 15 to 30 years (Grissino-Mayer et al. 1995; Touchan et al. 1996). Because of these longer fire intervals, subalpine forests have probably been altered less by modern fire suppression than have other southwestern forest types. Also, because of the natural paucity of herbage in these forests, they have been spared much livestock grazing.

The greatest human effects on spruce–fir forests have resulted from silvicultural practices, especially clear-cuts of old-growth forests. Windthrow, spruce beetle infestation, and tree regeneration problems have occurred in the process (Alexander 1987). Projected climate changes might eliminate some subalpine forests from isolated mountain ranges in the Southwest (Gosz 1992).

Many aspen forests in the Southwest are now composed of trees more than 100 years old; these trees are subject to increased insect and disease problems as they decline in vigor. Modern fire suppression has prevented aspen regeneration, and conifer understories are now widely overtopping aspen stands; for example, between 1962 and 1986, the area of aspen stands declined by 46% in Arizona and New Mexico (U.S. Forest Service 1993). Elk herbivory on aspen sprouts now retards regeneration on small burns or clear-cuts (Moir 1993; Allen 1996a). Without major fires, aspen stands will continue to decline, although aspen clones are able to persist in a suppressed state in the understories of conifer forests for many years. The high probability of intense fires in southwestern conifer forests in the coming decades suggests that new aspen stands will develop again soon, changing their status from declining to increasing.

Mixed-Conifer Forests

Diverse forests of mixed-conifer species blanket many southwestern mountains. Dominant species include Douglas-fir, white fir, limber pine (in the north), southwestern white pine (in the south), ponderosa pine, and blue spruce (Pase and Brown 1982b; Moir 1993; Muldavin et al. 1996). Aspen, along with Gambel oak, is prominent in these forests following disturbances (DeByle and Winokur 1985; Moir 1993). Numerous herbaceous plant species may occur in these forests, and understory conditions vary widely, from dry, open-canopy forests with grassy undergrowth on open slopes and ridges to moist, closed-canopied stands dominated by herbaceous plants in the canyons and ravines.

Fire histories vary with forest composition and landscape characteristics, from frequent surface fires to infrequent, patchy crown fires (Grissino-Mayer et al. 1995; Swetnam and Baisan 1996; Touchan et al. 1996). Mean fire return intervals were about 10 years at many sampled sites until the late 1800's, when widespread fires stopped. As a result of fire cessation and suppression, southwestern mixed-conifer forests have undergone major changes in structure and species composition in the past century, as they have elsewhere in the interior West (Samson et al. 1994). Ponderosa pine was once codominant in many mixed-conifer forests with relatively open stand structures, but fire suppression has allowed the development of dense sapling understories, with regeneration dominated by the more fire-sensitive Douglas-fir and white fir. Forest stand inventory data from Arizona and New Mexico show an 81% increase in the area of mixed-conifer forests between 1962 and 1986 (U.S. Forest Service 1993). Because white fir and Douglas-fir are the preferred host species for spruce budworms, the increases in fir abundance and distribution have led to increasingly intense and synchronous spruce budworm outbreaks throughout mixed-conifer forests in the southern Rocky Mountains (Swetnam and Lynch 1993). Herbaceous understories have been reduced by denser canopies and needle litter, and nutrient cycles have been disrupted. Heavy surface fuels and a vertically continuous ladder of dead branches have developed, resulting in increased risks of crown fires (U.S. Forest Service 1993). When droughts such as the drought of the 1950's recur, such conditions could lead to catastrophic widespread fires, which could significantly reduce, or even eliminate, mixed-conifer forests from the smaller sky island mountains along the United States–Mexico border. As these forests become reduced or fragmented, local endemic plants could become threatened or endangered (Warshall 1995).

Ponderosa Pine Forests

Forests dominated by ponderosa pine cover extensive portions of the Southwest (Pase and Brown 1982b; Moir 1993; but see Betancourt 1990 for the Holocene nature of the phenomenon) and grade into mixed-conifer forests at higher elevations and into woodlands below. On rugged mountain slopes and in canyons, these forests can form closed-canopy stands with a complex undergrowth structure of shrubs—particularly oaks (for example, Gambel oak, gray oak, wavyleaf oak, Arizona white oak)—and a high diversity of herbs. On more gentle terrain,

such as on plateaus and mesas or in wide valley bottoms, the forests tend to form more open parklike stands with grassy ground cover and scattered clumps of shrubs (Fig. 7). An array of herbaceous plant species occurs across the range of these forests, and understory conditions vary widely.

Before European settlement, ponderosa pine forests were generally open stands with well-developed herbaceous understories (Cooper 1960). Widespread surface fires that occurred every 2 to 15 years favored grasses and kept pine densities in check (Swetnam and Baisan 1996). Fire suppression since the late 1800's has had pervasive effects on ponderosa pine forests (Covington and Moore 1994) similar to those described for many mixed-conifer forests. The most obvious result has been great increases in the density of young pine trees, with associated buildups of thick blankets of needle litter; these buildups have markedly reduced the



Courtesy C. D. Allen, USGS

Fig. 7. Open-stand structure of ponderosa pine forest characteristic of presettlement conditions.

A Ponderosa Pine Natural Area Reveals Its Secrets

Monument Canyon Research Natural Area preserves an unlogged 259-hectare stand of old-growth ponderosa pine in the Jemez Mountains of New Mexico. This preserve, established in 1932, is the oldest research natural area in the state. This two-tiered forest displays an old-growth density of 100 stems per hectare (Muldavin et al. 1995), with an understory thicket of stagnant saplings and poles that raises the total stand density to an average of 5,954 stems per hectare, with concentrations as high as 21,617 stems per hectare (Fig. 1).

The old overstory trees in the research area are declining and dying, possibly from altered nutrient and water availabilities and competition with the dense understory saplings (Sackett et al. 1994). A thick layer of ponderosa pine needles blankets the forest floor, and herbaceous plant diversity is low. Although 34 herbaceous species have been found on the 259-hectare site (Deichmann 1980), as many as 60 might be expected in more open stands that have regularly experienced fire and which lack the dense sapling layer. Further, those herbs that do occur are usually found only as isolated individuals across the landscape.

Fire scars show that surface fires burned through this forest about every 6 years for at least 300 years until 1892, when the last significant fire occurred (Fig. 2). Understory saplings that have been dated reveal that tree establishment greatly increased in the early 1900's (Muldavin et al. 1995; Fig. 3) after grass competition was reduced because of



Courtesy C. D. Allen, USGS

Fig. 1. Dense doghair thicket of young ponderosa pine in the Monument Canyon Research Natural Area.

livestock grazing and after the fires that once inhibited pine regeneration were suppressed. As a result, a highly unnatural stand structure has developed, with the doghair thickets representing extreme density conditions, although similar conditions are found in many southwestern ponderosa pine stands (Covington and Moore 1994).

Analogous stand structures and high fuel loads prevailed in the nearby area burned by the 1977 La Mesa fire (Foxx and Potter 1984), when an intense crown fire converted 4,000 hectares of dense ponderosa pine forest into largely treeless grasslands. It is clear that fire is a keystone process in ponderosa pine forests—without it the whole ecosystem changes markedly. From this perspective the admonition emblazoned on the Monument Canyon Research Natural Area boundary sign acquires ironic overtones: "This area must be preserved in a natural state as near as possible."

A number of small archaeological sites from ancestral Pueblo people are found within this research natural area; these sites are typified by a two-room field house dated to between 1330 and 1630. This house was probably used while the people tended adjoining farm plots. The ponderosa pine thicket that shrouds these sites today would render even small-plot farming impossible without wholesale forest clearance. Fire suppression is the primary reason for the profound transformation this forest has experienced in the past century.

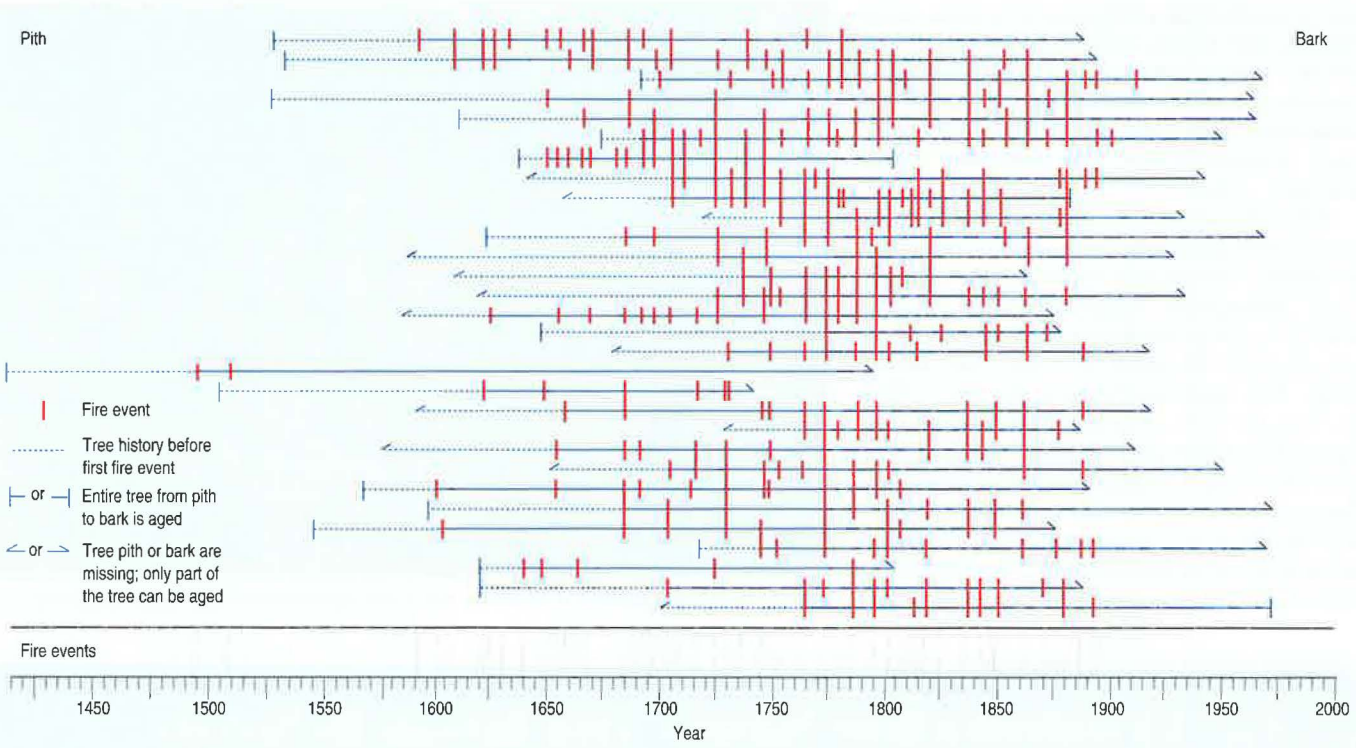


Fig. 2. Fire-scar chronology for Monument Canyon Research Natural Area. The horizontal lines represent the life spans of individual trees, while fire-scar events are shown by short vertical bars. The longer vertical lines at the bottom indicate the dates of fire events in which at least 10% of the sampled trees recorded a fire. Note the cessation of spreading fires after 1892. For additional information on the fire history of ponderosa pine forests and on the use of fire scars to date fires, see the U.S. Geological Survey Biological Resources Division LUHNA (Land Use History of North America) website at http://biology. usgs.gov/luhna/southwest/southwest.html.

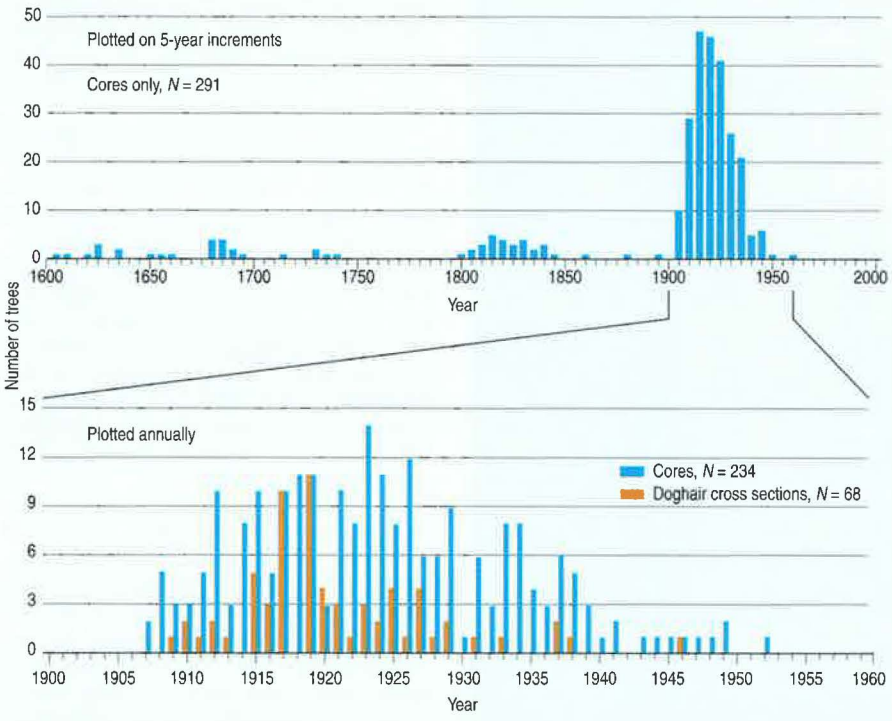


Fig. 3. Ponderosa pine recruitment dates from Monument Canyon Research Natural Area (Muldavin et al. 1995). Dates are estimated from increment cores taken from living trees over 10 cm diameter at breast height and from cross sections taken at root crown from poles in doghair thickets. Because increment cores were taken near ground level but often did not intersect the pith, dates from cores are considered less accurate than dates from cross sections.

See end of chapter for references

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quantity and diversity of herbaceous understory plants. Fire suppression has also changed ponderosa pine forests in more subtle but important ways. For example, the buildup of flammable aromatic, monoterpenoid compounds in the needle litter caused by fire suppression inhibits nitrification in ponderosa pine ecosystems (Covington and Sackett 1992; White 1994), which in turn disrupts nitrogen cycling and contributes to poor tree growth.

Although crown fires in ponderosa are unknown from regional fire histories (Swetnam 1990), by the 1950's crown fires had begun to occur as ponderosa pine forest structures changed. Today, the potential for crown fire is widespread in southwestern pine forests. Thus, fire suppression has led us into a "catch-22" situation, where the more we suppress fires, the more hazardous the fuels become, leading to further suppression efforts. Yet, despite these efforts, more fires are occurring that cannot be suppressed, as crown fires develop during extreme weather conditions in the extreme fuel conditions that active fire suppression helped create. Increasing urbanization in and near forests further complicates the fire suppression picture.

The dramatic ecological results of unnatural crown fires on ponderosa pine forests are illustrated by the relatively well-studied 1977 La Mesa fire in the Jemez Mountains (Foxx 1984; Allen 1996b). By trying to "protect" ponderosa pine forests from fire we have actually fostered conditions that can destroy these forests (Moir and Dieterich 1988). Historically, these forests have been the focus of timber harvest in the Southwest. As a result, relatively little old-growth ponderosa pine forest remains. On marginal low-elevation sites the harvest of ponderosa pine can cause site conversion to pinyon–juniper woodland.

Almost all of these forests are grazed by livestock in the Southwest; there are few ponderosa pine forests left that are protected from grazing and from which we can assess the effects of grazing on biological diversity. Livestock grazing undoubtedly affects species composition by reducing or removing palatable species and replacing them with thorny, less palatable, or even poisonous species and nonindigenous species. We suspect a significant trend in the reduction of biodiversity in these forest ecosystems is a function of fire suppression and grazing, but further research is needed.

Noss et al. (1995) reported that old-growth ponderosa pine forests in the intermountain west, including Arizona and New Mexico, are endangered, having suffered 85%–98% areal declines due to destruction, conversion to other uses, and significant degradation in structure, function, or composition since settlement.

Madrean Forests

Along the border with Mexico in southeastern Arizona and southwestern New Mexico occur highly diverse forests dominated by species that are characteristic of the mountains of the Sierra Madre Occidental of northern Mexico (Whittaker and Niering 1965). Within the United States, these forest ecosystems are very restricted and occur among the various sky island mountain ranges that rise from the desert floor (Warshall 1995). The sky islands are the only areas in the United States where trees such as Apache pine, Chihuahua pine, Arizona pine, Mexican pinyon, and Arizona cypress dominate the forests (Brown 1982c; McPherson 1992; Moir 1993; Barton 1994; Muldavin et al. 1996). Associated with these conifers are several evergreen oaks that are extensions of populations in northern Mexico (for example, netleaf oak, silverleaf oak, Emory oak, Arizona white oak, Mexican blue oak, and gray oak). Plant and animal biodiversity levels are high in Madrean forests; in fact, some groups of animals, such as certain insects and hummingbirds, reach their highest diversity levels in these forests (Marshall 1957; Whittaker and Niering 1965; Niering and Lowe 1984; Opler 1995). Herbaceous ground cover is also highly diverse, with as many as 50 different species occurring within a given forest stand (Muldavin et al. 1996).

Like most forests of the Southwest, grazing is ubiquitous, with only a few areas currently protected (for example, Saguaro National Monument in the Rincon Mountains, Ramsey Canyon [The Nature Conservancy] and Garden Canyon [U.S. Army] in the Huachuca Mountains, and Chiricahua National Monument in the Chiricahua Mountains). Historically, these forests were logged for mining timbers (Bahre and Hutchinson 1985), but little commercial forestry is practiced now (U.S. Forest Service, Coronado National Forest Management Plan).

Historically, Madrean forests had high-frequency fire regimes similar to those of other southwestern forest types (Caprio and Zwolinski 1992; Swetnam and Baisan 1996); frequent fires still persist in some Mexican forests. Fire suppression increases potential for crown fires in these forests just as it does in other forest types. Although commercial forest exploitation occurred historically (Bahre 1991), Madrean forests in the United States are now used primarily for recreation, fuelwood, and livestock grazing (U.S. Forest Service, Coronado National Forest Management Plan).

Pinyon–Juniper Woodlands and Juniper Savannas

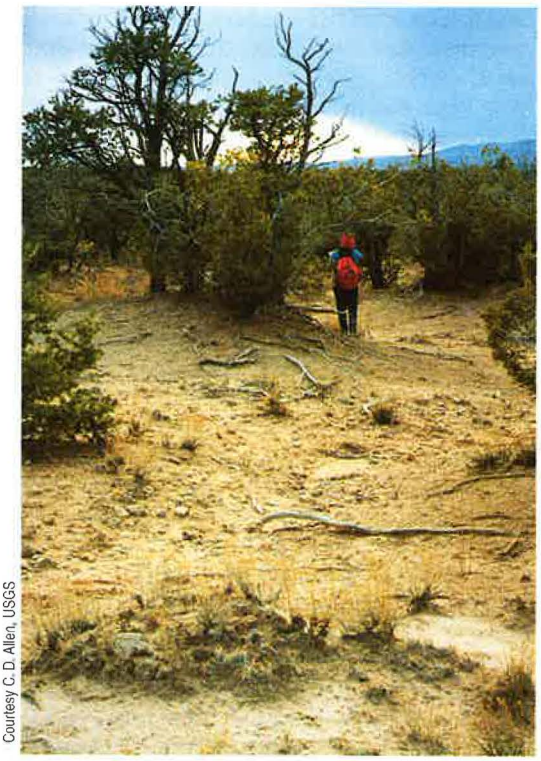
Pinyon–juniper woodlands cover about 15 million hectares in the Southwest, including about 11.4% of New Mexico (Van Hooser et al. 1993). These woodlands are diverse; in Arizona and New Mexico the U.S. Forest Service distinguishes 32 pinyon and 23 juniper plant community types (Bassett et al. 1987; Larson and Moir 1987). Dominant woody plants include several species of pinyon and juniper, along with many kinds of shrubs (for example, oaks, sagebrush, mountain-mahoganies, and rabbitbrush).

Pinyon–juniper woodlands harbor relatively few endemic vertebrate animals (for example, see Brown 1982d) but contain significant levels of biodiversity in less prominent organisms within the ecosystem, particularly herbaceous vegetation and soil organisms (Gottfried et al. 1995). Recent compilations of information on southwestern pinyon–juniper woodlands include Everett (1987), Evans (1988), Aldon and Shaw (1993), Gottfried et al. (1995), and Shaw et al. (1995).

At higher elevations the woodlands are dominated by pinyons and tend to form more closed-canopied stands that exhibit forest-like dynamics and species composition, commonly including a significant shrub component of oaks and alderleaf mountain-mahogany and limited grasses. In contrast, at lower elevations the woodlands are dominated by junipers in open savannas of scattered trees without a significant shrub component, except in areas where big sagebrush has become dominant in the grasslands. These savannas are a broad ecotone between true woodlands and grasslands or sagebrush shrublands (Dick-Peddie 1993).

The long history of livestock grazing has markedly diminished and altered herbaceous vegetation in most of these semiarid woodlands (Branson 1985; West and Van Pelt 1987; Miller and Wigand 1994), leading to widespread desertification of understory conditions (Gottfried et al. 1995). Major changes occurred in understory herbaceous species composition, density, vigor, and productivity (Wooton 1908; Bahre and Bradbury 1978), including decreases in cool-season grasses and increases in grazing-resistant plants such as snakeweed (Archer 1994). Researchers believe that across the landscape, year-round grazing suppressed former fire regimes in the late 1800's (Branson 1985), because surface fires could no longer spread through the bare interspaces between the trees; however, there is little firm documentation of woodland fire histories in the Southwest (Allen 1989; Despain and Mosley 1990; Gottfried et al. 1995). Fire suppression and reduced herbaceous competition allowed tree densities to increase within these woodlands, and pinyon–juniper ecosystems expanded upslope into ponderosa pine forests and downslope into grass and shrub communities (Leopold 1924; Bradley et al. 1992; Dick-Peddie 1993; Miller 1994; Miller and Wigand 1994). Van Hooser et al. (1993) estimated that 2.6 billion trees occur on 3.6 million hectares of pinyon–juniper woodland in New Mexico, mostly in young age classes. Tree densities have increased to the point that larger proportions of pinyon–juniper woodland can now support crown fires.

Accelerated precipitation runoff and soil erosion (Fig. 8) commonly occur in the often barren, desertlike interspaces between woodland trees. Ongoing soil erosion is causing significant, permanent losses of site productivity in many southwestern woodlands; Van Hooser et al. (1993) reported evidence of soil erosion on 78% of 1,014 woodland plots in New Mexico. Sampling of more than 3 kilometers of line transects in Bandelier National Monument (New Mexico) woodlands revealed tree canopy coverage ranges of 12% to 45%, herbaceous plant coverage (basal intercept) of only 0.4% to 9%, and exposed soils covering between 38% and 75% of ground surfaces, with widespread sheet erosion evident (C. D. Allen, U.S. Geological Survey, unpublished data). High erosion rates can be expected wherever such large



Courtesy C. D. Allen, USGS

Fig. 8. An eroding pinyon–juniper site in northern New Mexico. Note the barren interspaces between the clumps of trees.

percentages of exposed soil occur in woodlands. At current erosion rates, one intensively studied watershed at Bandelier National Monument will lose its entire mantle of soil, averaging 35 centimeters, in about 100 years.

Extensive efforts to convert woodlands to grassland, largely to improve forage conditions for livestock, have occurred in the Southwest. For example, about 600,000 hectares of pinyon–juniper woodlands were mechanically treated in Arizona during the 1950's and early 1960's (Cotner 1963), as were about 223,000 hectares of woodland on U.S. National Forests alone between 1950 and 1985 (Dalen and Snyder 1987). Herbicide applications have also been used to control woodland trees in the Southwest (Johnsen 1987). Efforts to convert pinyon–juniper woodlands to open grasslands have been greatly reduced on public lands since the 1970's because of environmental concerns and the questionable economics of such treatments given that trees tend to reestablish dominance rather quickly (Dalen and Snyder 1987). Harvests of fuelwood apparently peaked in the 1970's, when harvest levels proved unsustainable in at least some areas (deBuys 1993). The U.S. Forest Service has attempted to focus more attention on active management of southwestern woodlands to restore less erosive watershed conditions (Shaw et al. 1995); these efforts include harvest of fuelwood and thinning projects (Edwards 1995). Given current concerns over woodland influences on watershed conditions, a thorough review should be conducted of the areal extent and ecological effects of the widespread woodland conversion efforts of the 1950's to 1980's. Gottfried et al. (1995) outlined additional ecological research needs for southwestern pinyon–juniper woodlands.

Encinal Oak Woodlands

In the United States, encinal oak woodlands are limited to southeastern Arizona and southwestern New Mexico. These woodlands form moderately closed to open stands (savannas) dominated by a high diversity of evergreen oaks (for example, gray oak, Mexican blue oak, Arizona white oak, Emory oak, silverleaf oak, and netleaf oak), along with border pinyon and alligator juniper. Ground cover is rich in herbaceous plants and grasses, creating one of the more diverse ecosystems in the United States (McLaughlin 1986, 1989).

Because this ecosystem is distributed mostly within forest reserves established between 1902 and 1910, it has not been subjected to extensive settlement or agricultural conversion, and its overall distribution remains comparatively stable when compared with grasslands and shrublands. Before 1902, these woodlands were extensively used for fuelwood for homes and in copper smelters (Bahre and Hutchinson 1985). After the turn of the century, use of fuelwood declined until the energy crisis of the 1970's (Bennett 1992).

Although grazing may have been more concentrated in adjacent lowlands, grazing in oak woodlands exceeded carrying capacity up until the 1960's (Allen 1992; McClaran et al. 1992) and had significant effects. Grazing continues today but at much lower stocking rates (McPherson 1992). As seen elsewhere in the Southwest, grazing by large livestock herds of the late 1800's reduced fuels, which subsequently lowered fire frequencies. Reduced fire frequency has increased the overall density of trees and may be leading to limited expansion of woodlands into semidesert grassland and to juniper encroachment into short-grass prairie. This expansion, though, may be counterbalanced by increased oak seedling mortality due to grazing (McPherson 1992). Grazing may also adversely affect several rare species through changes in species composition and vegetation structure (McClaran et al. 1992). Long-term trends are difficult to ascertain, and we need much more research on the effects of livestock use, lower fire frequency, and consumption of fuelwood on overall diversity and ecosystem dynamics of encinal woodlands.

Desert Shrublands and Semidesert Grasslands

In the Southwest, desert shrublands and semidesert grasslands form a highly diverse and complex mosaic of vegetation across arid landscapes. They extend from the "cold" desert of the elevated Colorado Plateau region of southern Utah, south into the "warm" Sonoran and Chihuahuan deserts of southeastern California, Arizona, New Mexico, and west Texas. We discuss desert shrublands and grasslands together because they occur near one another and are commonly related to one another through time by desertification processes (Schlesinger et al. 1990). The coming of the railroad and the cattle industry to these arid lands in the late 1800's extensively changed ecosystems that, unlike the grasslands of the Great Plains, previously lacked large grazing animals (except for pronghorn). The current mosaic of shrublands and grasslands in the Southwest is in large part a reflection of continuing desertification (Grover and Musick 1990) in concert with urbanization and conversion to agriculture.

In the cool-temperate Colorado Plateau region of southern Utah, northern Arizona, and northwestern New Mexico, most precipitation falls in the winter as snow. In response, much of

the native vegetation was at one time a mosaic of deep-rooted shrubs and grassland dominated by cold-tolerant, cool-season bunchgrasses (for example, western wheatgrass, Indian ricegrass, galleta), which are most productive during spring and early summer. The extent of these grasslands has been greatly reduced, and what remains may represent one of the rarest ecosystems in the Southwest (Cottam 1947; Hull and Hull 1974). The decline can be attributed to several causes: native cool-season bunchgrasses sustain high mortality when grazed heavily in spring (Stoddard 1946) and are generally not tolerant of grazing (Branson 1985); fire suppression has favored shrub species; accelerated soil erosion has permanently altered site conditions; and bare ground is aggressively colonized by nonindigenous Eurasian annual grass species such as cheatgrass. The loss of perennial grasses occurred in only 10–15 years of overgrazing by cattle near the end of the last century (Hull 1976).

Much of what was grassland in the early nineteenth century has been converted to shrublands dominated by saltbush, greasewood, and big sagebrush, a hardy, cold-tolerant shrub that shapes the ecosystems it dominates. The expansion of big sagebrush on the Colorado Plateau has been remarkable (Gross and Dick-Peddie 1979; Dick-Peddie 1993); the shrubs are commonly widely spaced with herbaceous plants and grasses living beneath them and with intershrub spaces that are barren or contain microphytic crusts composed of lichens and algae. The shrubs form islands of fertility that concentrate water and nutrients and that are not easily altered (West 1983). There are sites where these shrublands have always existed as natural soil- and climate-determined communities, but only a few are protected enough to give us a sense of what presettlement conditions were like (Edwards 1995).

Grazing on these ranges continues today, and extensive amounts of land also are being converted to agricultural production, particularly in the Four Corners area, where Arizona, Colorado, New Mexico, and Utah meet. Conversion of dominant plant cover to annual nonindigenous species such as cheatgrass is expected to continue (Rogers 1982). Many of these nonindigenous plants are flammable (Fig. 9). Once these shrublands—with or without nonindigenous annuals—become established, there is only limited potential for conversion to native grasslands, either mechanically or by removal of grazing (Potter and Krenetsky 1967; Rice and Westoby 1978; West et al. 1984).

To the south of the Colorado Plateau, the Sonoran Desert covers much of southeastern California, south-central and southwestern Arizona, and northwestern Mexico; summers there are very warm and winters are mild. In the northern and western parts of the desert, precipitation falls mostly in winter but as rain rather than as the snow that occurs in the northern plateau region. In the southern and eastern portions of the desert, the rainfall pattern shifts to a predominantly summer regime (McClaran 1995). The Sonoran Desert is characterized by great floral richness, including large columnar cacti, such as saguaro, cardon, and organpipe, as well as many shrub species and an undergrowth of grasses and herbaceous plants with subtropical affinities (Brown 1982a).

The western lowland basins (lower Colorado River valley of Brown 1982a) are dominated by creosotebush, white bursage, and saltbushes. In uplands and to the east, saguaro, yellow paloverde, and ocotillo become more prominent and form the classical Arizona desert. This area has an extremely high diversity of spiny shrubs and subtrees, cacti, yuccas, agaves, herbaceous plants, and grasses (MacMahon 1979), which make this ecosystem one of the most diverse in the Southwest or perhaps in the entire United States.

To the east across the Continental Divide lies the Chihuahuan Desert, which has colder winters and summer-dominated precipitation (monsoons). The Chihuahuan Desert extends from south-central New Mexico southward into western Texas and Mexico. Creosotebush and saltbushes are still common dominants but share

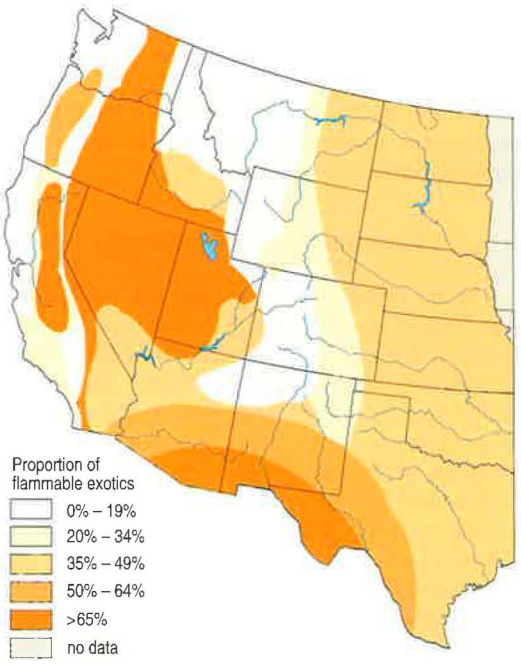


Fig. 9. Geographic distribution of flammable nonindigenous plants in the western United States (U.S. Environmental Protection Agency, Environmental Systems Monitoring Laboratory, Las Vegas, Nevada).

the landscape with honey mesquite, cat-claw acacia, tarbush, and a variety of noncolumnar cacti.

Semidesert grasslands are intermixed with the desert shrubs and extend farther northward or to higher elevations, where they meet encinal and pinyon–juniper woodlands or the short-grass prairie of the Great Plains (McClaran and Van Devender 1995). These desert grasslands are dominated by warm-season grasses, including black grama and other "southern" gramas, tobosa grass, and sacatons. These grasslands, with distinctive shrubby components of sotols, joint-firs or Mormon teas, and yuccas, are especially productive after the summer rains arrive in late summer.

At present, Sonoran and Chihuahuan desert shrubs are expanding their ranges at the expense of semidesert grasslands through a widespread desertification process brought on by livestock grazing in climatically marginal ecosystems of low production and resilience (Grover and Musick 1990; Bahre and Shelton 1993); these grasslands have been declining for more than a century. Grazing pressure was severe across the range in the last half of the nineteenth century; in Arizona alone livestock numbers rose from 5,000 in 1870 to 1,500,000 in 1891 (Hastings and Turner 1965). As a result, these grasslands were greatly altered by 1900 in the United States and by 1940 in Mexico (Brown 1982a); most areas were converted to degraded forms of Sonoran Desert shrubland (Humphrey 1987), and this trend is continuing. A recent satellite imagery study in southern Arizona (Fig. 10) revealed a 35% decrease in overall grassland cover, a 60% decrease in the size of grassland patches, and an increase in the number of patches over time. Only a few relict areas in southern Arizona (for example, the Muleshoe Preserve and around Sonoita) continue to support semidesert grasslands in the Sonoran Desert.

Similarly, in New Mexico and western (Trans-Pecos) Texas, researchers have documented extensive conversions of Chihuahuan semidesert grasslands to Chihuahuan Desert shrubland (Buffington and Herbel 1965; York and Dick-Peddie 1969; Branson 1985; Grover and Musick 1990). Even though livestock numbers in these areas have stabilized well below historical levels, these are marginal grazing habitats, and the combination of reduced fire frequency (Moir 1980) and continued topsoil erosion is likely sustaining an irreversible decline in which much of the remaining grassland is being converted to desert shrubland (Dick-Peddie 1993). The introduced species, honey mesquite, in particular is greatly expanding its range and now dominates extensive areas that once were grasslands. More than 28 million hectares are now dominated by mesquite, an increase of 100% or more over a 100-year period (Parker and Martin 1952). Once this aggressive invader controls a site, significant changes in ecosystem functions occur: water and nutrients become nonuniformly distributed in space and time and are confined to zones beneath shrubs (Schlesinger et al. 1990). This creates a new, relatively heterogenous and stable soil environment when compared with the original grasslands. Such changes may be irreversible, although Robinett (1995) has documented the effective use of fire to reduce mesquite and increase grass cover in the Sonoran Desert.

Extant Chihuahuan semidesert grasslands in good condition in New Mexico and western

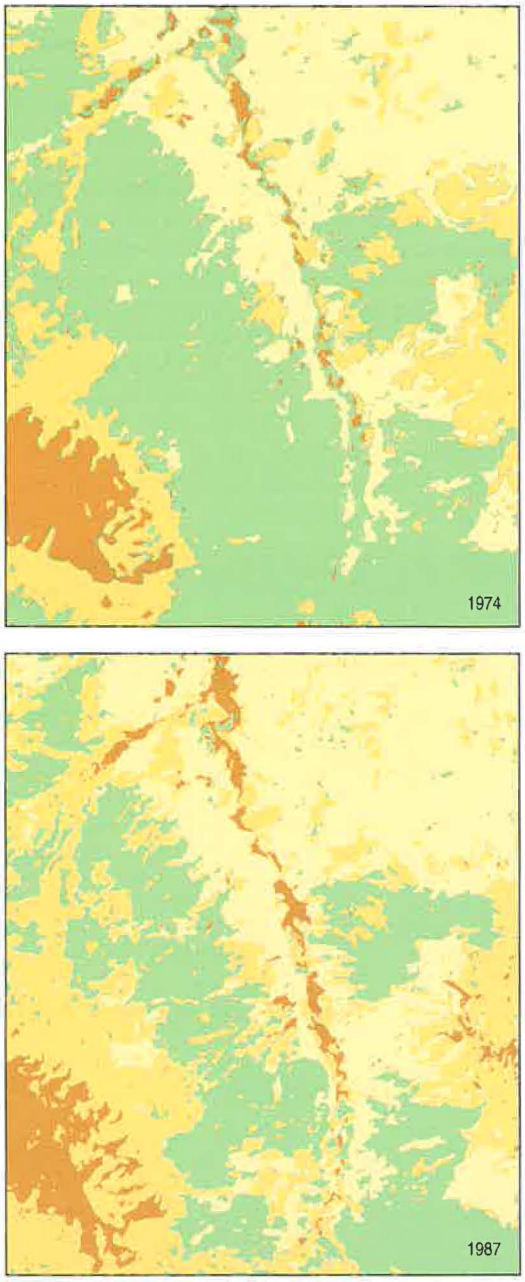


Fig. 10. Grassland cover (green areas) is decreasing in Southern Arizona (drawn from a recent satellite photo [Kepner 1994]).

Texas are rare today. Some limited de facto protection occurs on military reserves such as White Sands Missile Range in New Mexico and Fort Bliss in Texas. Large stands of these grasslands have been protected as an incidental outcome of military activities that preclude livestock use. Increased military activities on these sites, coupled with the presence of nonindigenous grazers (such as gemsbok, feral horses, and cattle that have trespassed) may be significantly affecting the ecosystems and leading to degradation. The only known sites that are truly protected from grazing by nonindigenous species are within national parks and national wildlife refuges (for example, Big Bend National Park in Texas and Bosque del Apache National Wildlife Refuge in New Mexico) and a few small, scattered research natural areas and private preserves. Outside of these sites the actual amount of semidesert grassland that has not been degraded is known imprecisely. To assess and analyze the trends of the remaining extent of functional semidesert grassland ecosystems in the Southwest, researchers need to use high-resolution satellite imagery (for example, Loveland and Hutcheson 1995).

Within the Sonoran Desert, there are significant indications of decline of biodiversity caused by agricultural conversion, nonindigenous species invasion, and urbanization. Much of the saltbush ecosystem has been converted to irrigated agriculture (Brown 1982a). In addition, nonindigenous European grasses and herbaceous plants such as sandburs, Lehmann lovegrass, and weedy mustards are displacing perennial native species (Waser and Price

Soils and Cryptobiotic Crusts in Arid Lands

Cryptobiotic crusts (Fig. 1) are important features of arid and semiarid ecosystems throughout the Southwest, including pinyon–juniper woodlands and deserts. More data on the ecological role played by these crusts in the Southwest are needed, given the widespread (but unsubstantiated) belief among many range managers that the breaking up of such crusts by livestock hoof action may be beneficial (Belnap 1990; Ladyman and Muldavin 1996).

Living soil crusts are found throughout the world, from the hottest deserts to the polar regions. In arid regions, these soil crusts are dominated by blue-green algae and also include soil lichens, mosses, green algae, microfungi, and bacteria (Belnap 1990; Johansen 1993; Ladyman and Muldavin 1996). In the cold deserts of the Colorado Plateau region (parts of Arizona, Colorado, New Mexico, and Utah), these crusts are extraordinarily well developed, often representing more than 70% of the living ground cover (Belnap 1990).

Blue-green algae occur as single cells or filaments; the most common form found in desert soils is the filamentous type. The cells or filaments are surrounded by sheaths that are extremely persistent in these soils. When moistened, the blue-green algal filaments become active, moving through the soils and leaving behind a trail of the sticky, mucilaginous sheath material, which sticks to surfaces such as rock or soil particles, forming an intricate webbing of fibers in the soil. In this way, loose soil particles are joined, and otherwise unstable and highly erosion-prone surfaces become resistant to wind and water erosion. The soil-binding action is not dependent on the presence of living filaments, however—layers of abandoned sheaths, built up over long periods, can still be found clinging tenaciously to soil particles at depths greater than 15 centimeters in sandy soils, thereby providing cohesion and stability in loose sandy soils (Belnap and Gardner 1993).



Courtesy J. Belnap, USGS

Fig. 1. Cryptobiotic crusts on the Colorado Plateau.

The crusts are important in the interception of rainfall. When moistened, the sheaths absorb up to 10 times their volume of water. The roughened surface of the crusts slows precipitation runoff and increases water infiltration into the soil, which is especially important in arid areas with sporadic, heavy rainfall. Vascular plants growing in crusted areas have higher levels of many essential nutrients than plants growing in areas without crusts. Electron micrographs of sheaths (Fig. 2) show that they are covered with fine clay particles upon which essential nutrients cling, thereby keeping the nutrients from being leached out of the upper soil horizons or from being bound in a form unavailable to plants. In addition to stabilizing surfaces and increasing water harvesting, crustal organisms also contribute nitrogen and organic matter to ecosystems, functions that are especially important in desert ecosystems where nitrogen levels are low and often limit productivity.



Fig. 2. Micrograph of filamentous cryptobiotic crust showing sheaths with attached clay particles.

Unfortunately, many human activities are incompatible with maintaining these blue-green algal crusts. The blue-green algal fibers that confer such tensile strength to these crusts are no match for the compressional stress placed on them by machinery or by being stepped on by cows or people, especially when the crusts are dry and brittle. Crushed crusts not only contribute less nitrogen and organic matter to the ecosystem, but the impacted soils are also highly susceptible to wind and water erosion. In addition, raindrop erosion increases and consequent overland water flows carry detached material away, a severe problem when the destruction has occurred in a continuous strip, as it does with vehicular or bicycle tracks. Such tracks are highly susceptible to water erosion and quickly form channels, especially on slopes. After such damage, wind blows away pieces of the pulverized crust and also blows around the underlying loose soil, covering nearby crusts. Since crustal organisms depend on photosynthesis, burial can mean death. When large sandy areas are impacted in dry periods, previously stable areas can become a series of moving sand dunes in only a few years.

Large areas that are disturbed may never recover. Under the best circumstances, a thin veneer may return in 5 to 7 years. When the crust is disturbed, nitrogen fixation stops and underlying sheath material is crushed. Damage done to the abandoned sheath material underneath the surface cannot be repaired because the living organisms occur only on the surface. Instead, sheaths must build up slowly after many years of blue-green algal growth.

See end of chapter for references

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1981; Chew 1982; P. Warren, The Nature Conservancy, Phoenix, Arizona, personal communication). Ongoing urban sprawl, particularly around Phoenix and Tucson, creates air and noise pollution, site conversion to asphalt with its subsequent associated localized increases in air temperatures, and accelerated recreational use. Consequently, desert wildernesses are changing, if not vanishing, even within national parks and monuments.

With respect to grazing, some researchers have suggested that Sonoran shrublands, particularly in lowland areas, naturally lack a significant grass component and historically were less extensively grazed (Hastings and Turner 1965; Branson 1985). In contrast, Bahre and Shelton (1993) presented convincing data that these areas have experienced significant changes, particularly from the increased invasion of mesquite. Niering et al. (1963) concluded that even limited grazing in marginal ecosystems dominated by saguaro has caused long-term, possibly irreversible, declines of that cactus species. Bryant et al. (1990) presented evidence that vegetation conditions deteriorate even more immediately across the United States–Mexico border, apparently because of more severe grazing effects. Assessments of range conditions and trends are badly needed in the border area.

Historically, in the Chihuahuan Desert, most of the range was grazed extensively; it continues to be grazed even though plant and livestock production is low. As a result, desertification resulting in conversion of desert grassland to desert shrubland since the 1850's has been well documented (Buffington and Herbel 1965; York and Dick-Peddie 1969); this process continues today where livestock are not well-managed and stocking levels have not been reduced (Holechek 1991; Dick-Peddie 1993). As with the Sonoran Desert, urbanization and agricultural conversion are increasing as human populations expand. More information is needed to assess the long-term effects of humans on overall biological diversity of desert scrub ecosystems and to assess the specific effects of human activities, including the removal of woody plants that serve as nurse plants to other species, poaching of cacti and other plants for landscaping, and the introduction of nonindigenous grasses as livestock forage.

Scattered across the Southwest are smaller-scale landforms that include sand dunes, warm springs, and seasonally flooded playa lakes. Some of these azonal (in the sense of MacMahon 1979) areas, such as washes or arroyos, are locally dominant and may exhibit considerable endemism, as in the White Sands of New Mexico. Playas are low, internally drained basins that, because of water inundation and evaporation, become saline over time; vegetation in such areas typically consists of salt-loving plants such as saltbush. These smaller-scale landforms add considerably to regional biological diversity of plants and invertebrates and some are important to larger vertebrate wildlife, at least seasonally. Desert springs, for example, are quite important to many endemic plants and fishes.

Riparian Ecosystems

Riparian landscapes occur along streams and rivers and represent an interface, of varying width, between dry and wet systems; these landscapes are defined by the plants that inhabit them, that is, plants occurring near streams or rivers and not in drier environments. Riparian plants are dependent on an intact hydrological regime where groundwater is maintained and natural surface flows occur. Vegetation dynamics are integrated with, and dependent on, annual cycles of flooding and minimal flows, as well as sediment availability (Crawford et al. 1993). At lower elevations in the Southwest, riparian zones are the only places where sufficient moisture exists for large, broad-leaved trees to germinate and grow. These zones typically consist of cottonwood gallery forests, usually with an admixture of willows and other water-dependent plants. Historically, disturbances in flood-prone channels in the Southwest created vegetational mosaics of wetland communities, with different combinations of species dominating different areas (Campbell and Green 1968). Along the Rio Grande in New Mexico, for example, the historical vegetation probably consisted of patches of cottonwood–willow forest (bosque) and other wetlands, including wet meadows, marshes, and newly deposited alluvium (Crawford et al. 1993; Durkin et al. 1995). Riparian systems are now increasingly characterized by nonindigenous plants such as saltcedar, Russian-olive, and Siberian elm (Crawford et al. 1993).

In the Southwest, riparian landscapes are invaluable. Although they represent less than 1% of the region's area (Knopf et al. 1988), a large proportion (75%–80%; Gillis 1991) of vertebrate wildlife species depends on riparian areas for food, water, cover, and migration routes. Riparian zones also improve water quality because they filter sediments and nutrients; accumulated sediments in riparian zones store large amounts of water, which helps sustain streamflow during drier times. Abundant riparian vegetation, however, sustains high levels of photosynthesis and transpiration; 99% of water entering a plant through the root system is lost by transpiration from the leaves (Knight 1994). This water transpired by plants is lost to downstream users. Most land managers accept such losses in exchange for benefits of shade (which lowers losses by evaporation), increased forage, sediment accumulation, biological diversity, wildlife habitat, and longer sustained flows in late summer.

In many areas, especially at higher elevations, beaver probably played an important role in creating and maintaining riparian areas (Knopf and Scott 1990). Tree cutting and dam building by beavers trap alluvial sediments, provide opportunities for new plant growth, and increase the diversity of wildlife habitats. Removal of beavers or their dams, together with livestock grazing, has contributed to arroyo cutting and gullying of the landscape (see Denevan 1967 for a review on relative roles of grazing and climate on arroyo-cutting episodes). As the channel cuts deeper and the gradient increases, the water table is lowered and surface sediments begin to dry out; gradually, the vegetation becomes composed of plants tolerant of drier conditions.

Many of the conditions that make riparian zones relatively rare and valuable, particularly in a semiarid landscape, also make them fairly sensitive to disturbance and change. When free-flowing water is impounded or diverted from the main channel (by dams, diversions, irrigation, or channelization), the nature of the riparian landscape changes (see box on Impounded River Systems in Water Use chapter). Construction of impoundments, whether for flood control or water storage, has largely decreased or eliminated the shifting of river channels that historically created mosaics of riparian vegetation, especially cottonwood and willow habitat (Crawford et al. 1993). With less flooding, there is less channel shifting and less suitable habitat for establishment of cottonwood seedlings, which are dependent on recently inundated sediments to become established. Where inundation does not occur, seedlings will not establish, thereby leaving the ground available for other species (Durkin et al. 1995). Modification of historical disturbance regimes results in a decline in diversity of native species because when the frequency or intensity of a natural disturbance is decreased, competitively superior nonindigenous plants may invade (Hobbs and Huenneke 1992). As existing riparian forests age without replacement, they become a monoculture of maturing trees that eventually senesce, die, become victims of fires (caused by vandals or carelessness), and disappear from the landscape (Howe and Knopf 1991).

Overgrazing has been a major factor in the alteration and degradation of riparian areas (Cooperrider and Hendricks 1937; Armour et al. 1991). Livestock grazing typically results in reduction of plant species diversity and density, especially of palatable species such as willows and cottonwood saplings (Rickard and Cushing 1982; Cannon and Knopf 1984; General Accounting Office 1988; Schultz and Leininger 1990). Changes in species composition, relative abundance of species, and plant density cause overall plant community structure to change.

With heavy grazing, whether by big game or livestock, stabilizing vegetation deteriorates,

banks are eroded, water storage capacity declines, water quality declines, streambeds become wider and stream depths shallower, water temperatures increase, and fish and aquatic invertebrate habitat quality declines (Crawford et al. 1993). Cottonwoods do not tolerate water stress well and may decline as groundwater becomes less available.

Additional causes of bank erosion include road building, construction, and other developments. Stream degradation also is caused by nutrients and fertilizers entering the water and resulting in increased eutrophication and by interactions of factors such as logging, fires, and overgrazing.

We probably know more about the responses of southwestern bird communities to riparian landscape changes due to grazing than we do about the responses of other animal groups (Rea 1983; U.S. Fish and Wildlife Service 1995). Reduction, modification, or removal of cattle grazing led to increases in abundance for several bird species associated with cottonwood–willow habitat on the San Pedro River (Krueper 1993). At other sites, 40% of the riparian bird species were negatively affected by livestock grazing (Bock et al. 1993), and a negative correlation between recent cattle grazing and abundance of several riparian birds was found (Taylor 1986). Farley et al. (1994) showed the importance of even young cottonwood riparian habitat to migrant birds in the middle Rio Grande ecosystem.

About 90% of total water consumption in western states is accounted for by agriculture and evaporation from reservoirs (Crawford et al. 1993). Irrigation by flooding has some negative effects, including nutrient leaching, which leads to fertilizer losses and to eutrophication of streams and groundwater. In addition, salts that have accumulated in soils may be transported downstream, creating saline water supplies. Irrigation water that is high in dissolved salts also favors nonindigenous saltcedar, which is more tolerant of high salt levels, at the expense of native cottonwood and willow (Kerpez and Smith 1987; Busch and Smith 1993).

Increased channelization of the lower Colorado River appears to have led to floodplain groundwater declines and has isolated riparian vegetation from its moisture source (Busch et al. 1992). Cottonwoods are now rare along the lower Colorado River and are represented mostly by old senescent individuals with little or no regeneration. Willows are somewhat more common but are increasingly challenged by nonindigenous species, particularly saltcedar (Busch et al. 1992). These changing water regimes give saltcedar a competitive edge, as it does not need floods to establish. Also, cattle won't eat saltcedar but do graze on shoots and seedlings of cottonwood and willow. The deep root system of saltcedar allows it to survive when water tables are lowered and surface flows are no longer present. Furthermore, establishment of saltcedar results in a regime of episodic fires, which researchers believe are uncommon in most native riparian woodlands (Busch and Smith 1993).

Noss et al. (1995) ranked riparian forests in Arizona and New Mexico as endangered, with 85%–98% declines due to destruction, conversion to other uses, or significant degradation in structure, function, or composition since settlement by Europeans. Large-scale losses of southwestern wetlands have occurred; the cottonwood–willow plant community has declined the most with modern river management (Rosenberg et al. 1991; U.S. Fish and Wildlife Service 1995). Exact amounts of loss vary from site to site, but in some places, such as the lower Colorado, lower Gila, lower Salt, and Rio Grande rivers, loss or modification of riparian habitat may be close to 100%. Overall, a 90% loss of presettlement riparian ecosystems has occurred in Arizona and New Mexico (Arizona State Parks 1988). Of the riparian areas under Bureau of Land Management control, an estimated 83% is in unsatisfactory condition (Almand and Krohn 1979). All major watercourses in southern Arizona suffered entrenchment and became more ephemeral in flow by about 1890, and riparian habitats were significantly altered by 1900 (Hastings and Turner 1965; Bahre 1991).

Riparian areas are not the only wetland losses in the Southwest. Dahl (1990) estimated losses of wetlands between 1780 and 1980 at 36% in Arizona, 33% in New Mexico, and 30% in Utah. *Cienegas*, a unique southwestern form of wetland upon which many animals depend, have suffered a 70% loss in Arizona since settlement, which places them in the threatened category (70%–84% decline) of Noss et al. (1995).

Even before settlement by Europeans, people and animals congregated along riparian strips in the Southwest. Following settlement by Europeans, however, livestock congregated there too. Metropolitan centers usually occur in riparian areas, and land ownership is overwhelmingly private. Urbanization, as exemplified by growth in large southwestern cities such as Albuquerque, El Paso, Phoenix, and Tucson, is changing riparian landscapes dramatically—in some cities the rivers have ceased flowing (for example, the Gila and Salt rivers in Phoenix and the Santa Cruz River in Tucson). At present, only relatively small patches of riparian habitat remain that are managed for their inherent values by local municipalities, Native American tribes, and the U.S. Fish and Wildlife Service.

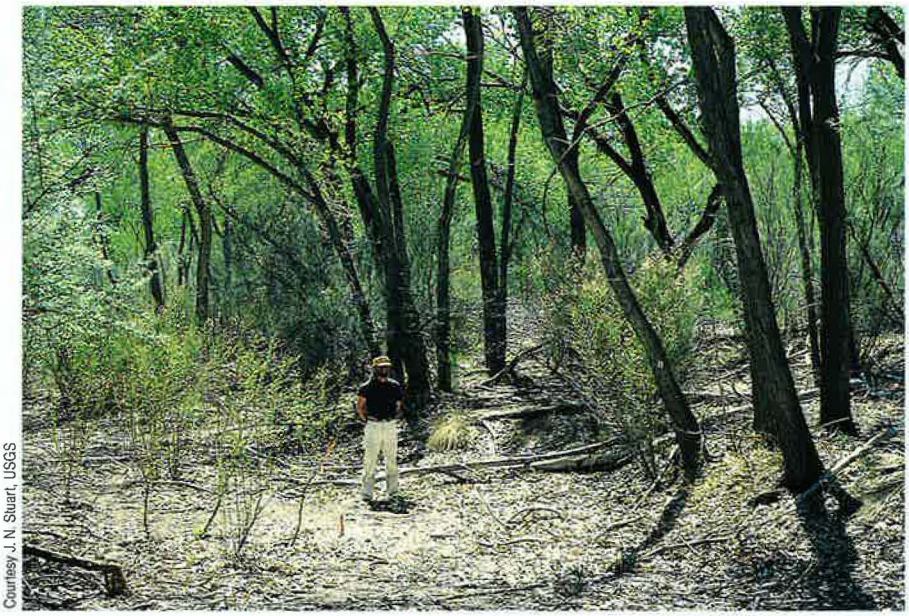
Changing Landscapes of the Middle Rio Grande

Before the fourteenth century, the Rio Grande between Cochiti and San Marcial, New Mexico, was a perennially flowing, sinuous, and braided river (Crawford et al. 1993). The river migrated freely over the floodplain, limited only by valley terraces and bedrock outcroppings; this shifting of the river created ephemeral mosaics of riparian vegetation (forests and shrublands) and wetlands (ponds, marshes, wet meadows) (Durkin et al. 1995). Water diversion for irrigated agriculture by Native Americans and later by European immigrants may have somewhat diminished river flows during growing seasons before 1900. Increased sediment loading, the result of climatic variations and agriculture, caused the river's channel to become broader and shallower, which increased the river's tendency to flood.

In the late 1800's, groundwater levels in the Rio Grande floodplain rose dramatically because of a rising riverbed, irrigation, and poor return of irrigation water. Salts, leached upward by the rising groundwater, created salinity problems. Levees, built in the 1920's and 1930's to cope with floods, tended to constrain the floodway and channel, thereby reducing the river's tendency to meander, which is critical for establishment of native bosque (cottonwood–willow) vegetation. In addition, the riverbed aggraded inside the levees so that by the 1950's it was higher than adjacent downtown Albuquerque. Upstream dams were built largely for flood and sediment control, as well as water storage, and drainage systems were established to lower water tables in the floodplain. These actions, combined with water diversion channels and increased groundwater pumping in Albuquerque, disrupted the connection between the river water and groundwater in the floodplain; thus, hydrological conditions in the riparian zones were no longer linked in a natural historical way (Crawford et al. 1993).

Cottonwood–willow forests have also been reduced by land clearing, tree harvesting, water diversion, and agricultural uses. About 90% of the Rio Grande's water is used for agriculture in the middle Rio Grande valley (Crawford et al. 1993). Livestock graze back new riparian vegetation (young cottonwood and willow), which contributes to watershed erosion and leads to increased sediment loading in the river. Groundwater drainage and the absence of periodic flooding caused most of the valley's wetlands to dry up. Plant and animal species dependent on such areas have disappeared or are confined to restricted habitats. Cottonwood and willow have been widely replaced by species that are not as reliant on spring flooding and inundation to reproduce—saltcedar in southern reaches and Russian-olive in northern ones (Figure).

Roelle and Hagenbuck (1995), who documented surface cover changes in the Rio Grande floodplain from 1935 to 1989, found that five of eight wetland cover types declined by 17,000 hectares (45%) in that period; largest gains during the period were in urban and agricultural cover types. Only



Courtesy J. N. Stuart, USGS



Courtesy J. N. Stuart, USGS

Figure. Riparian vegetation. Mature cottonwood site (top) at Bosque del Apache National Wildlife Refuge, Socorro County, New Mexico, showing the relatively open nature of such stands, and a stand of nonindigenous saltcedar (bottom) on the Rio Hondo, Chaves County, New Mexico, showing the almost impenetrable nature of invading stands.

three wetland or riparian cover types increased: lake, wetland forest, and dead forest or scrub–shrub. The lake increase, though, was due to higher water levels in a large impoundment (Elephant Butte Reservoir), and wetland forest increase was primarily due to increasing forest cover between levees and the river channel, which has become narrower and straighter because of channel stabilization. Only 27% of the area forested in 1935 still supports forests. The flow regime of the river has been altered significantly, with lower peak flows, which means that cottonwood regeneration rarely occurs. Under current hydrological conditions, Russian-olive and saltcedar are likely to continue to replace cottonwood. Even though the middle Rio Grande valley in New Mexico supports the most extensive cottonwood gallery forest remaining in the entire Southwest (W. Howe, U.S. Fish and Wildlife Service, Albuquerque, New Mexico, personal communication), human-induced changes in hydrology and land use are rapidly shrinking remaining forests.

See end of chapter for references

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Because riparian ecosystems are critically dependent on disturbance caused by occasional high water flows, if these flows have been diminished or halted, natural riparian zones are being lost, along with their associated faunas. Some way must be found to produce or preserve flows that aid in the establishment, growth, and survival of riparian-dependent species.

Status and Trends of Plants

The diversity of vascular plant species is high throughout the Southwest; New Mexico and Arizona, especially, may be the most floristically rich areas in the United States (Morin 1995). New Mexico is estimated to have about 3,900 taxa of vascular plants (Martin and Hutchins 1980, 1981), and Arizona is similarly diverse with about 3,370 species of flowering plants and ferns (Kearney and Peebles 1960). Statewide, Utah has about 2,500 species of indigenous vascular plants (MacMahon 1988b) and 580 introduced species (Welsh et al. 1987). Despite the richness of regional species, endemism among southwestern vascular plants is not striking. About 150 taxa of vascular plants are endemic to New Mexico (Dick-Peddie 1993)—less than 4% of the total flora. Of these endemics, 24 are cacti, 10 are annual plants, 9 are woody shrubs, 3 are biennials, and 2 are indeterminate, having been collected only once, more than a century ago. About 5% of Arizona plants are endemic with 46 species confined to northern Arizona, 28 to central Arizona, 74 to southern Arizona, and 16 others widely distributed through the state (Kearney and Peebles 1960). Researchers believe that endemism is high among plants on the Colorado Plateau of Utah (Welsh et al. 1987).

Regionwide, the U.S. list of endangered and threatened plants shows that about 40 southwestern species are jeopardized. Although vertebrates dominated these lists during the early years of the U.S. Endangered Species Act, invertebrates (13%) and plants (48%) now represent the largest proportion of listed taxa (Flather et al. 1994). Arizona, New Mexico, and Utah each list from 50 to 140 taxa of plants as sensitive (formerly candidates for listing under provisions of the U.S. Endangered Species Act of 1973; memorandum from the director of the U.S. Fish and Wildlife Service, 19 July 1995). Sensitive plants in the region include cacti, wild buckwheats, prickly poppies, milk-vetches, paintbrushes, penstemons, sagebrushes, saltbushes, and others. The sunflower, pea, cactus, and figwort families account for more than half of the species of special concern in New Mexico (Dick-Peddie 1993).

Habitat alteration and incompatible land use are major threats to the region's rare plants. Some species, primarily cacti and those with showy flowers, are also threatened by overcollecting for the horticultural trade (Morse et al. 1995). Other species (for example, cacti, yuccas, agaves, penstemons) also are subject to poaching and commercial exploitation (Dick-Peddie 1993).

In general, most southwestern life zones have sensitive species of plants, and most of these zones have been subjected to perturbations such as grazing, fire suppression, road construction, and urbanization, which account for many of the threats to sensitive plants.

Arizona, California, New Mexico, Texas, and Utah have some of the highest proportions of globally rare native plants in the country (Morse et al. 1995), with proportions ranging from 12% to 17%. Still, less than 1% of the native flora may have been extirpated in these states (Morse et al. 1995). From a community perspective, 56% of rare plant communities occur in the western United States, including the Southwest (Grossman and Goodin 1995).

Many southwestern plants are poorly known, especially the small, unobtrusive species. For example, the moss flora of the

Southwest is one of the least known in the United States, and our knowledge of liverworts and hornworts in New Mexico, Arizona, and surrounding regions is the poorest in the country (Whittemore and Allen 1995). Some of the most poorly known areas for vascular plants are also in the Southwest, including parts of Arizona north of the Colorado River, portions of New Mexico, and parts of the Colorado Plateau (Morin 1995). Thus, in much of the Southwest, a considerable amount of basic floristic research needs to be done.

Status and Trends of Animals

Invertebrates

Invertebrates, like plants, are relative latecomers to state and federal lists of endangered and threatened species. At present, invertebrates represent about 13% of all federally listed threatened and endangered species (Flather et al. 1994), although worldwide they represent 90% of all animals (Mason 1995). As of 31 August 1992, there were 91 taxa of invertebrates on the U.S. list of endangered and threatened wildlife. Invertebrate species listed as threatened or endangered in the Southwest include one ambersnail in Arizona and Utah, and two springsnails and one isopod in New Mexico—about 4% of the total number of federally protected invertebrates.

Increasing numbers of invertebrates are showing up on more recent listings of sensitive species (U.S. Fish and Wildlife Service 1994a). In the last few years, listed sensitive invertebrates included a millipede from New Mexico, a pseudoscorpion from Arizona, two

Rare Aquatic Snails

State Natural Heritage Programs in the Southwest have identified 30 species of rare aquatic snails (Figure a), most in the mollusk family Hydrobiidae. The Hydrobiidae are at risk throughout North America, with 16 endangered, threatened, or U.S. Fish and Wildlife Service Category 1 candidate species, and 90 species of concern (Mehlhop and Vaughn 1994).

Several physiological and ecological aspects of rare southwestern snails render them vulnerable to extirpation. All are gill breathers and thus are intolerant of drying or anaerobic conditions. Individual snails tend to live about one year, making annual reproduction essential. Most snail species are geographically restricted to natural springs and nearby wetlands, with 83% of the species having a total range of less than 10 square kilometers. These mostly isolated habitats inhibit migration—of 30 snail species, most occur at only a single spring, and most of the others are found at only two or three springs (Figure b). Water-use activities that have altered the quantity or quality of many spring waters also threaten the snails (Figure c). Of 26 species for which threats have been assessed, only two were found to have no substantial identified threats.

Although the status of most of these rare aquatic snails is vulnerable (Mehlhop and Vaughn 1994), there are reasons for optimism. More than half (53%) of the snail habitats are in springs that are managed fully or in part by federal or state agencies or by private conservation organizations (Figure d). Also, although water-use activities appear to pose significant threats to the long-term viability of these species, these threats have existed for most of these species for decades, suggesting that such activities and snails may be able to coexist.

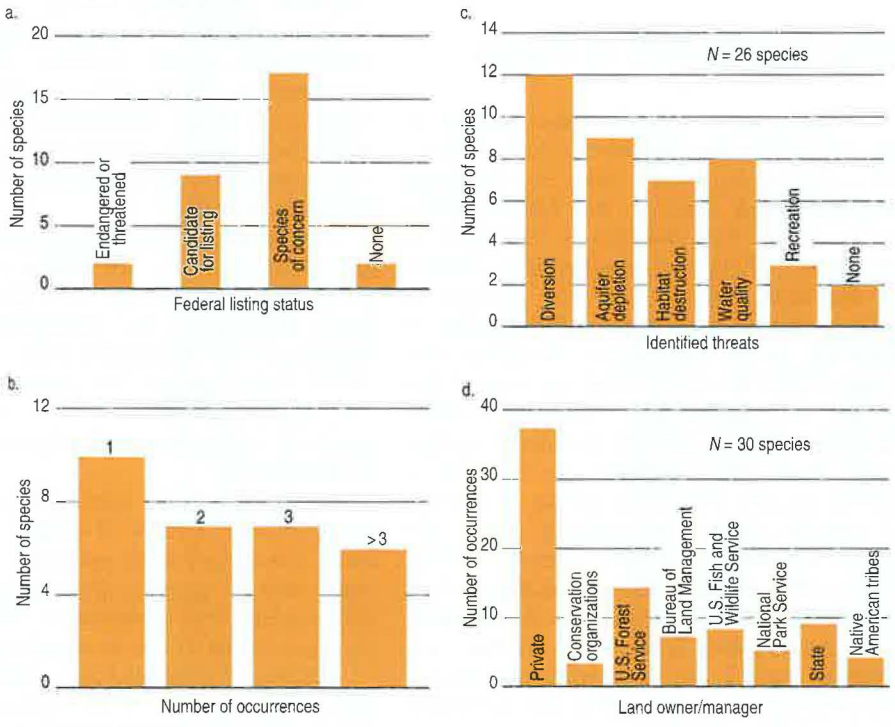


Figure. a) Federal status of rare or declining snails in the Southwest; b) number of known occurrences per species of rare aquatic snails; c) reported threats to rare aquatic snails in the Southwest; d) landowner or management agency of sites where aquatic snails in this study occur.

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amphipods—one from Arizona and another from New Mexico—and several mollusks, mostly springsnails, talussnails, and physas. Almost all sensitive invertebrates are from aquatic habitats and probably are subject to the same type of environmental threats that also affect southwestern fishes. Beyond that, individual state lists of sensitive species seem to represent local and existing expertise and concerns.

Sensitive insect species include 18 taxa from Arizona, 3 from New Mexico, and perhaps 4 from southern Utah. Lepidoptera (moths and butterflies) represent about 13% of North American insect species and attract attention from laypersons and professionals. Nonetheless, much remains to be learned of the basic taxonomy, distribution, and status of butterflies and moths (Powell 1995). A survey for large Lepidoptera in a 10-square-kilometer area in Arizona has taken 13 years, is 95% complete, and has identified over 900 species (Powell 1995). The highest species richness of butterflies and selected moth families in the western United States is found in Arizona (437 species), New Mexico (410 species), Utah (281 species), and western Texas (Big Bend, 199 species) (Opler 1995). Species richness of western Lepidoptera is usually highest in areas that adjoin the Mexican border. Each of five subregions, mostly in the Southwest, has many endemic species, of which 20 or more are potential candidates for listing as endangered species (Opler 1995). Threats to moths and butterflies include overgrazing, urbanization, and excessive modification or recreational use of specialized habitats such as wetlands or dunes (Opler 1995).

About 90,000 species of insects have been described from North America (north of Mexico) alone, with an estimated 72,500 species yet to be described (Hodges 1995). Given the diversity of invertebrates in the Southwest, we suspect that they are underrepresented as listed or sensitive species. Clearly, much basic collection and taxonomic work remains before we can meaningfully interpret status and trends of many invertebrates. Nonetheless, many invertebrates are threatened by the same factors that threaten other animal species—changes in water regimes, habitat modification and alteration, pollutants, urbanization, and nonindigenous species. For example, Africanized honey bees recently invaded the Southwest. (The ecological implications of this invasion on the biota of the region were discussed by Kunzmann et al. 1995; additional studies are needed.) Status studies of southwestern invertebrates and delineation of specific threats are clearly and urgently needed. Notably missing from most lists of sensitive invertebrates are desert arthropods, especially those of specialized habitats such as dunes, playas, and oases; their status needs to be assessed.

Fishes

Freshwater fishes are the most imperiled vertebrate group in the United States (Williams et al. 1989; Minckley and Deacon 1991; Warren and Burr 1994). In the United States, about 20% of fishes are extinct or imperiled, as compared with 7% of the country's mammals and birds (Master 1990). Almost 30% of the surface land area in the conterminous United States occurs west of the Continental Divide, but only about 21% of the roughly 800 freshwater fishes native to the United States are found there (Page and Burr 1991). Aquatic ecosystems in western North America, however, particularly in the Southwest, are endowed with some of the highest rates of endemism on the continent. In the Colorado River basin, for example, 35% of all native genera and 64% of the 36 fish species are endemic (Carlson and Muth 1989). The other southwestern watershed that demonstrates a high degree of fish endemism (30%) is the Rio Grande in New Mexico. Endemism in western fishes generally reaches its highest level in small systems such as isolated lakes and desert springs.

The level of threats to western fishes is also high and is probably best reflected in the number of imperiled species found in each state. Southwestern states have some of the highest percentages of threatened fish fauna: Arizona, 85%; California, 72%; New Mexico, 30%; and Utah, 42% (Warren and Burr 1994; Fig. 11).



Fig. 11. Numbers of native freshwater fish species in the lower 48 states (purple number) and number of fishes recognized by fisheries professionals as endangered, threatened, or of special concern (red number; based on Warren and Burr 1994).

Regionally, more than 48% of the fishes in the Southwest have been identified as jeopardized, compared with 19% in the Northwest and 10% in the Southeast (Warren and Burr 1994).

Because we cannot present all possible situations affecting southwestern fishes, we emphasize factors relevant to the decline and demise of these fishes by using shared ecological traits to illustrate the problems faced by these fishes. Fish communities of the main-stem Colorado River and associated major tributaries, mountain headwater systems in the Gila River drainage (see box on Gila Trout), the main-stem Rio Grande, and desert spring systems are discussed here (Fig. 12). The fishes in these communities range from long-lived, large-bodied fishes found in large, highly variable rivers to small, specialized fishes that have been isolated for thousands of years in relatively stable environments.



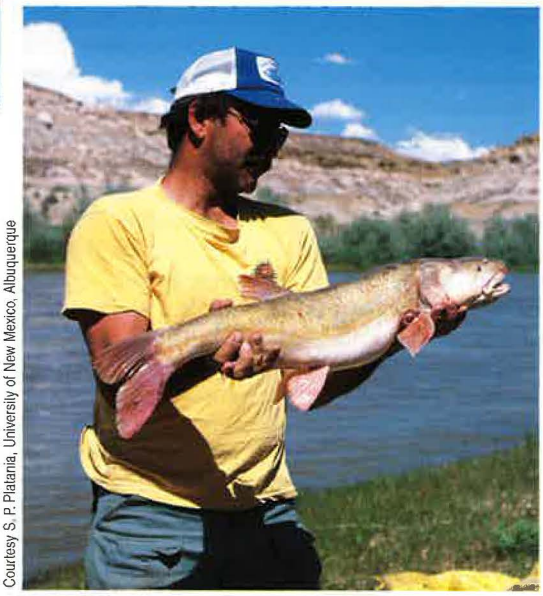
Fig. 12. Major river drainages in the Southwest.

Colorado River Fishes

Perhaps no other group of fishes better exemplifies the problems confronting aquatic ecosystems in the Southwest than the fishes of the Colorado River basin. More studies have been conducted and reports written on this group of fishes than any other assemblage of nongame fishes in the region. The Colorado River basin is the largest watershed in the Southwest, draining portions of seven western states, including about one-twelfth of the land area in the contiguous United States. The threats to this ecosystem are numerous and synergistic. Numerous dams on the main-stem river represent the most significant environmental perturbation facing these fishes. Main-stem impoundments have drastically changed water temperature, converted the river from sediment-laden to relatively clear, altered historical patterns of spring floods and the general waterflow regime, and blocked migratory pathways for fishes. Consequent modification or loss of habitat for native species and the creation of suitable habitat for nonindigenous fishes have irreversibly altered the Colorado River aquatic ecosystem.

Although only 36 native freshwater fish species formerly lived in the Colorado River basin—a low number relative to basins east of the Continental Divide—species-level endemism is high (64%) (Carlson and Muth 1989). The number of native species in the major Colorado River basin drainages ranges from 5 (Bill Williams River) to 18 (Gila River). Although many of these endemic species are restricted to specific river systems in the Colorado River (for example, Virgin spinedace—Virgin River; spikedace and loach minnow—Gila River; woundfin—Virgin, Salt, and Gila rivers), several endemic taxa once were found generally distributed in main-stem habitats throughout the basin.

Fishes that inhabit and evolved in large rivers in the Colorado River basin are members of the chub complex (roundtail chub, humpback chub, and bonytail), Colorado squawfish (Fig. 13), and the razorback sucker. Of this group, four species are listed as endangered and one (roundtail chub) is a sensitive species (formerly Category 2 candidate; U.S. Fish and Wildlife Service 1994a). Most recent fisheries investigations have been directed at the three endangered Colorado River cyprinids—Colorado squawfish, humpback chub, and bonytail.



Courtesy S. P. Platania, University of New Mexico, Albuquerque

Fig. 13. Colorado squawfish, held by D. L. Propst, New Mexico Department of Game and Fish. This female fish was captured in the San Juan River, near its confluence with the Mancos River in New Mexico. The fish, 780 millimeters in total length and an estimated 8 kilograms in weight, was released unharmed. Anecdotal accounts refer to squawfish 2 meters long and weighing 45 kilograms. The maximum weights recorded in historical collections were 30 to 40 kilograms.

Studies on the Colorado squawfish demonstrated that it is a highly migratory species that formerly occurred throughout the basin but is now reduced to about one-third of its original range. Natural populations of this large-river fish have been eliminated from the lower basin, and the species is rare in the upper basin.

Humpback chubs inhabit relatively inaccessible reaches of the Colorado River system. Although this endemic Colorado River fish probably was found historically in most large-river habitats of the Colorado River, it now exists in only five canyon reaches in the upper basin—in the Grand Canyon in Arizona and near the confluence of the Colorado and Little Colorado rivers. Researchers believe that this last locality harbors one of the largest remaining humpback chub populations and that it is the spawning locality of Grand Canyon populations.

Bonytails (also called bonytail chubs) are the rarest of the endemic big-river fishes of the Colorado River. This fish species experienced the most abrupt decline of any of the long-lived fishes native to the main-stems of the Colorado River system and, because no young individuals have been found in recent years, has been called functionally extinct (Carlson and Muth 1989). Bonytails were one of the first fish species to reflect the changes that occurred in the Colorado River basin after the construction of Hoover Dam; the fish was extirpated from the lower basin between 1926 and 1950. In reference to the rapid demise of bonytails, Behnke and Benson (1980:20) said, "If it were not for the stark example provided by the passenger pigeon, such rapid disappearance of a species once so abundant would be almost beyond belief." Bonytails were also extirpated from several upper basin rivers (Green, Gunnison, and Yampa rivers) where they were once common. Populations in free-flowing waters now apparently survive only in the Colorado River in Colorado and Utah. The largest population of bonytails occurs in Lake Mohave (Mueller and Marsh 1995), but this population consists only of old individuals, and there is no evidence of reproduction.

Only recently have investigations begun to focus on the razorback sucker—one of the most threatened big-river fishes in the Colorado River basin (Mueller and Marsh 1995). This fish was formerly so abundant throughout the main-stem and major tributaries of the Colorado River basin that in the early 1900's it was one of the principal fishes taken by a commercial fishery in southern Arizona (Hubbs and Miller 1953). Additional anecdotal accounts of the abundance of razorback suckers occur in historical reports from the 1880's through the 1940's. This unique fish now inhabits only 1,208 (river) kilometers in the upper basin, while the only substantial population in the lower basin occurs in Lake Mohave (McAda and Wydoski 1980; Marsh and Minckley 1989). The most serious problem for the razorback sucker is the lack of any significant reproduction in recent years.

The dilemma of big-river fishes in the Colorado River basin is not limited to these species, which are accorded some level of federal protection. For example, the flannelmouth sucker, one of the most common suckers in many portions of the upper basin, has been eliminated from the Gila River drainage.

Concurrent with the decline in native fish species has been an increase in the species richness and abundance of nonindigenous fishes. Maddux et al. (1993) reported the introduction of at least 72 fish species, twice the number of native fishes, into the Colorado River basin. Many of these introduced fishes have established successful populations in parts of the Colorado River system and now are serious predators of young suckers, chubs, and squawfish.

Rio Grande Fishes

Fish communities of the Rio Grande consist of plains fishes that belong to the westernmost drainages of the Mississippi River basin. Fishes in the New Mexico portion of the Rio Grande exhibit a high degree of endemism and special biological characteristics that reflect their evolution in this variable system. Researchers believe that the native fish community of these middle reaches of the Rio Grande has between 16 and 27 species (Hatch 1985; Smith and Miller 1986; Propst et al. 1987; Sublette et al. 1990). Three of the six Rio Grande endemics—Rio Grande shiner, phantom shiner, and Rio Grande bluntnose shiner—no longer occur in the New Mexico portion of the Rio Grande (Bestgen and Platania 1990). In addition, the endemic Rio Grande chub and Rio Grande silvery minnow are reduced in range and abundance, with Rio Grande chubs now generally found only in tributary streams and Rio Grande silvery minnows only in main-stem habitats.

The history of the decline and extirpation of these formerly widespread species is relatively well documented. The Rio Grande shiner was last found in the middle Rio Grande in 1949, whereas phantom shiners and Rio Grande bluntnose shiners were last collected in the upper Rio Grande in 1939 and 1964, respectively (Chernoff et al. 1982; Bestgen and Platania 1990). The speckled chub, a nonendemic main-stem cyprinid, was last found in the middle Rio Grande in 1964. The Rio Grande silvery minnow is the only endemic main-stem Rio Grande cyprinid that survives in New Mexico (Bestgen

and Platania 1990), although the species had formerly been abundant, occurring from the confluence of the Chama River and Rio Grande to the Gulf of Mexico (Fig. 14). The 95% reduction in the Rio Grande silvery minnow's range resulted in its listing as an endangered species (U.S. Fish and Wildlife Service 1994b).

The decline and demise of the middle Rio Grande fish fauna may be partly explained because habitats that formerly supported small isolated outlier populations of Rio Grande fishes may have relied on emigrants from upstream or downstream reaches to supplement isolated populations. When dams eliminated these dispersal avenues, populations of these short-lived fishes dwindled and eventually were extirpated. Life-history characteristics of these fishes support this assumption. For example, these species take advantage of changes in natural water flow for reproduction because their eggs and larvae occur in times of peak water flow; a generalized hydrograph for plains streams indicates that spawning takes place during spring runoff or summer rainstorms. Many fishes that are found only in these streams produce semibuoyant eggs that are carried along with these spates and hatch 24 to 48 hours after being spawned. The larval fish develop quickly in the warm waters characteristic of summer flow, and after about 3 days, they move into the highly productive waters typical of slow-velocity habitats, where they grow quickly (S. P. Platania and C. S. Altenbach, University of New Mexico, Albuquerque, personal observation).

Perils Facing the Gila Trout

The plight of Gila trout provides a case study of problems confronting fish inhabitants of mountain headwater streams in the Southwest. This endemic salmonid once occurred in much of the Gila River drainage—a Colorado River basin tributary in New Mexico and Arizona—but by the time the species was first described in 1950, its range had been reduced to a few headwater streams in New Mexico (Propst et al. 1992). The first attempts to conserve and recover populations of this fish occurred in 1923, when the New Mexico Department of Game and Fish established hatchery stocks of Gila trout and prohibited stocking of nonindigenous trout species in stream reaches where the Gila trout occurred. The U.S. Endangered Species Preservation Act of 1966, the U.S. Endangered Species Act of 1973, and the New Mexico Wildlife Conservation Act of 1974 legally protected the remaining populations.

The Gila trout recovery plans of 1979 and 1983 (U.S. Fish and Wildlife Service 1987) identified the need to replicate and safeguard the remaining populations as genetically distinct evolutionary units. These plans provided the guidelines to recovery, requiring the selection of stream reaches suitable for reestablishment, mechanical and chemical removal of nonindigenous trout, and transplanting Gila trout to the renovated systems. Streams selected as donor sites for Gila trout populations were generally headwater reaches within the historical range of the fish. By 1987 recovery efforts had resulted in the establishment of Gila trout populations at nine localities, eight in New Mexico and one in Arizona. After meeting benchmark requirements of the recovery plans, the U.S. Fish and Wildlife Service proposed downlisting the Gila trout from endangered to threatened (U.S. Fish and Wildlife Service 1987); concurrently, the New Mexico Department of Game and Fish delisted the McKnight Creek population and downlisted all other New Mexico populations from endangered to threatened (Propst et al. 1992). No one anticipated the natural events and their repercussions that would transpire over the next 6 months.

Before the end of the comment period for the proposed downlisting, a flood eliminated more than 80% of the Gila trout population from McKnight Creek, a forest fire and subsequent flooding eliminated the Main Diamond Creek population (the type locality), and drought and forest fire eliminated more than 90% of the South Diamond Creek population. The occurrence of these chance events concurrent with attempts to downlist this fish demonstrates the fragility of small populations and dramatically shows the potentially serious problems in recovery strategies implemented during the 20-year recovery period.

Threats to Gila trout were comparable to those identified for other interior North American headwater stream trout—competition, predation, and hybridization by introduced trout such as the rainbow trout and brown trout, habitat loss and degradation, and decreased water quality and quantity. In addition, fragmentation of range and recovery attempts relying on establishment of isolated populations are principal problems for Gila trout. Additional threats identified after the catastrophes of the late 1980's were associated with the preferred habitat of this species or with changes within that habitat (for example, fire suppression and riparian habitat degradation).

The attempt to propagate Gila trout by adhering to the historical approach of multiple but small populations had several flaws. Translocated fish were isolated from other populations in habitats that could support only relatively small populations. The limited area for reintroduction and the small population sizes made Gila trout at these sites extremely susceptible to loss through natural events (fire and flooding) or excessive human-related activities (livestock grazing, timber harvest, and mining). This propagation strategy—where more populations were equated with higher levels of protection—caused a false sense of security. Another, and more difficult, conclusion reached by Gila trout biologists concerned the potential need to place the survival of the species as a higher priority than the maintenance of genetically distinguishable populations. They concluded that there was a need to investigate transplanting populations to longer and larger streams outside of the current range of the species and to introduce more individuals more frequently (Propst et al. 1992).

See end of chapter for references

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Disturbances in natural river-flow regimes undoubtedly have adversely affected reproduction in these fishes.

Desert Spring Fishes

Desert springs and associated isolated pools are characteristic of the Southwest. These habitats are often marginal for fishes and are typically geographically isolated, have small surface volumes and relatively constant physicochemical features, and discharge warm, oxygen-poor water. Although each spring or pool is species-poor, most aquatic inhabitants of each pool are endemic. Most fishes in these habitats are short-lived (1–2 years) and are native to only a single locality. The fish communities of these habitats are generally composed of pupfishes, poolfishes and springfishes, killifishes, and livebearers.

Minckley et al. (1991) summarized the conservation status of 76 taxa of killifishes from the southwestern United States and northern Mexico. Of this group, 38% are classified as threatened or endangered, 30% as rare or vulnerable, and 9% as extinct. Minkley et al. (1991) reported that 6 poolfishes, springfishes, and pupfishes are extinct, and only 2 of the remaining 46 fish species are considered free from jeopardy. All 10 species and subspecies of poolfishes and springfishes are considered imperiled (Minckley et al. 1991).

Although there are numerous problems confronting desert spring fishes, perhaps the best known are those facing the Devils Hole pupfish. The life-history traits of this fish and the geologic nature of its habitat are similar to those of other southwestern pupfish. Devils Hole pupfishes became isolated at the mouth of a water-filled limestone cave in Ash Meadows of southern Nevada about 20,000 years ago when waters retreated from the last Ice Age. These fish congregate around a 6- by 3-meter limestone shelf, the smallest known habitat of any vertebrate animal. The algal mat that grows on this shelf is the base of a food chain composed of protozoa, diatoms, amphipods, and pupfish. The Devils Hole pupfish population numbers are greatest in summer (about 700 individuals), when primary productivity is also highest. In winter, when less sunlight reaches the shelf, the algal mat dies and the number of pupfish may be as low as 200 (Ono et al. 1983).

The greatest threat to this species occurred when farmers in the Ash Meadows Valley drilled numerous wells to pump groundwater from the aquifer. As predicted, these pumping activities lowered the water table, thereby threatening the pupfish with the exposure and subsequent drying of their shelf habitat. In addition, the lowering of the water table also imperiled the other endemic animals in several other springs in the valley. When groundwater-pumping activities stopped in the mid-1970's, temporary relief occurred for this species and the other inhabitants of isolated spring pools throughout Ash Meadows Valley.

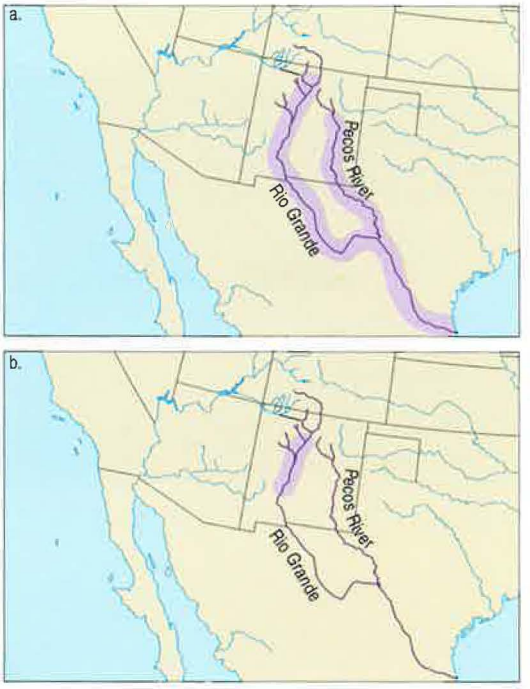


Fig. 14. a) Historical and b) present distribution of the Rio Grande silvery minnow.

Recovery efforts involving fishes of these isolated habitats seem relatively simple compared with those required to recover long-lived fishes in large, free-flowing rivers. Such efforts require that the spring, its associated spring pool, and the aquifer be secured. Although the first two conditions may be met, securing an aquifer is a daunting task. Other recovery options include measures such as those developed for the Pahrump poolfish, a species that was formerly restricted to Manse Spring in Pahrump Valley, Nevada. Overpumping of the water table and the introduction of nonindigenous fishes severely imperiled this species. In the 1970's and 1980's, stockings of this species occurred in state and federal refuge complexes, and the species was successfully established outside of its native range, providing it with additional security for its continued survival (Minckley et al. 1991).

Causes of Imperilment

Little debate occurs among fisheries professionals about the causes of imperilment and extinctions of southwestern fishes. Most frequently mentioned causes are construction of dams (Fig. 15), loss of physical habitat (Fig. 16), habitat degradation, chemical pollution, overexploitation, and introduction of nonindigenous species. Dam construction and regulation probably had the greatest adverse effect on native fishes of southwestern rivers, while



Fig. 15. Downstream side of a diversion dam on the Rio Grande at San Acacia, New Mexico, in autumn 1986.



Fig. 16. A Rio Grande pool drying near Socorro, New Mexico, in autumn 1987.

the effects of excessive groundwater pumping have imperiled many spring systems and their associated fauna. The number of nonindigenous fish species in the Southwest is considerable: Arizona has 71 species; New Mexico, 75 species; Utah, 55 species; and Texas, 96 species (Boydstun et al. 1995).

As a whole, fishes in the western United States are clearly more imperiled than those in the eastern United States. More than half of the fishes listed as endangered or threatened by the U.S. Fish and Wildlife Service, or being considered for such listing, occur west of the Continental Divide. The commonly observed pattern is the disappearance of the most sensitive fishes, followed by the collapse of whole fish faunas in major western river basins. If current efforts directed at recovery of native western fishes are not continued and successful, we could witness the disappearance of most of the region's endemic fish fauna.

Recovery strategies for aquatic organisms in the Southwest vary depending on their perceived problems and life-history strategies. In general, researchers know what is required to recover most threatened and endangered fishes, but some solutions (for example, removing dams) may be unrealistic and controversial. The most frequently cited solution is habitat preservation, which may be relatively simple for fishes with restricted distributions and small population sizes. Recovery strategies for long-lived, wide-ranging species, such as the Colorado squawfish, are more complex and require a long-term commitment. The unique ecological requirements of the various life-history stages of long-lived species dictate the need for protection of extensive river reaches and perhaps changes in water use. Realistic possibilities for recovery of the native fish fauna of the Southwest are decreasing as human populations increase and formerly uninhabited lands become developed, causing native fish populations to decline further.

Amphibians and Reptiles

Diversity of Southwestern Herpetofauna

More than 150 species of amphibians and reptiles occur in the Southwest; this is partly due to the region's diverse habitats. Compared with the moister habitats of eastern North America, the southwestern amphibian fauna is relatively poor, with only 3 salamander species and about 30 frog and toad species. About 25% of the amphibians, though, are found nowhere else in the United States. About 50 lizard and 56 snake species account for more than 70% of the reptiles and amphibians inhabiting this region; most of these live in the arid and semiarid desert grasslands and shrublands that make up most of the Southwest. Although aquatic turtles are relatively scarce in the Southwest (11 species), most are important components of the fragile riparian ecosystems in this semiarid region. In the Colorado Plateau, 18 amphibian and 62 reptile species have been described (Drost and Deshler 1995). Current status and trends for amphibians and reptiles are not as well known as those for fishes and birds. Additionally, these organisms face some threats not faced by other vertebrate animals (for example, rattlesnake roundups, and commercial collection for the pet trade).

Montane Forest Herpetofauna

Conservation concerns relative to southwestern amphibians and reptiles can be effectively summarized by elevation, as many species in similar habitats are often threatened by the same factors. Amphibians and reptiles in the Southwest are common in the warm, lowland deserts and grasslands but are relatively uncommon at cool, high elevations. Still, the presence

of several species found only in these high-elevation habitats makes certain coniferous forests important for herpetological diversity. For example, two species restricted to montane sky islands in New Mexico—the Jemez Mountains and Sacramento Mountain salamanders (Fig. 17)—are the only salamanders endemic to New Mexico. Both are federally listed as sensitive species (U.S. Fish and Wildlife Service 1994a) and are considered endangered by the state of New Mexico. Studies suggest that these salamanders are adversely affected by intensive logging operations, although to what extent remains unclear (Ramotnik and Scott 1989; Scott and Ramotnik 1992). The U.S. Forest Service has made significant efforts to protect known populations, including developing an agreement with the U.S. Fish and Wildlife Service and the New Mexico Game and Fish Department to protect all habitat occupied by the Jemez Mountains salamander while a management plan is produced.



Courtesy P. S. Corn, USGS

Fig. 17. Sacramento Mountains salamander, one of two endemic salamanders in New Mexico.

A few endemic reptiles also occur in montane habitats, and some are prone to being overcollected because of their novelty to reptile enthusiasts. Commercial collection of snakes such as the twin-spotted rattlesnake, the New Mexican ridge-nosed rattlesnake, and the rock rattlesnake (Fig. 18) for the pet trade has been a concern in recent years because of the vulnerability of these species to extirpation (Ernst 1992). Mining and logging development may also moderately threaten some of these species (Ernst 1992).

Pinyon–Juniper Woodland Herpetofauna

Lower-elevation coniferous woodland is widely distributed in the Southwest and supports a variety of amphibians and reptiles, although there are few endemic species because few are specialists in using these habitats. Studies are needed on the potential effects of the increasing urban development that is occurring in pinyon–juniper woodland and savanna habitats, especially in north-central New Mexico and northern Arizona. At present, this habitat type is sufficiently common that current effects on reptiles and amphibians are probably not significant.

Encinal Woodland Herpetofauna

Encinal forests in southwestern New Mexico and southeastern Arizona support a distinctive assemblage of species whose range occurs primarily in Mexico—most are found in the Sierra Madre Occidental and occur in the United States at the northern limits of their ranges. These species include the Tarahumara frog, canyon spotted whiptail, and Mexican garter snake—all sensitive species (U.S. Fish and Wildlife Service 1994a), and the endangered New Mexico ridge-nosed rattlesnake. The Tarahumara frog, once known from 30 localities in southern Arizona and northern Mexico, appears to be extirpated in the United States but is not threatened with extinction throughout its range (Hale et al. 1995). Disappearance of U.S. populations of the Tarahumara frog may be tied to acid rain, heavy metals, air particulates, or solar radiation (Hale et al. 1995), whereas habitat modification and collection for the pet trade (Bender 1981) threaten the other species mentioned.

Sonoran Desert Herpetofauna

In the Sonoran Desert, reptiles such as the chuckwalla, rosy boa, and desert tortoise have



Courtesy J. N. Stuart, USGS



Fig. 18. Banded rock rattlesnake in the Magdalena Mountains, New Mexico (top), and ridge-nosed rattlesnake in the Animas Mountains, New Mexico.

Courtesy C. W. Painter, New Mexico Department of Game and Fish, Santa Fe

apparently declined (U.S. Fish and Wildlife Service 1994a), in part because of overcollection for the pet trade, although habitat modification may also be a factor. The effects of grazing on herpetofaunal communities in the Sonoran Desert are not well studied, although trampling of young desert tortoises and damage to burrows and vegetation have been attributed to livestock (Berry 1978; Campbell 1988). Likewise, Szaro et al. (1985) found the wandering garter snake to be five times more abundant in ungrazed sites than in grazed sites in the White Mountains. Other communities appear to show few effects from grazing. For example, Jones (1981) found that lizard abundance and diversity in Arizona's Sonoran Desert were not significantly affected by heavy cattle grazing if overall vegetation structure was unaltered. However, lizard abundance and species diversity were greater on lightly grazed sites than on heavily grazed sites (Jones 1981). More intrusive activities, such as grazing by sheep, off-road vehicle use, and urban development, significantly alter vegetation structure (Busack and Bury 1974) and affect reptiles more. Declines of reptile species in the eastern Mohave Desert have been associated with increased disturbance (Stewart 1994); such changes are predictable as human populations and accompanying urbanization increase in the adjacent Sonoran Desert.

Chihuahuan Desert Herpetofauna

Relatively few studies have addressed the status and trends of Chihuahuan Desert herpetofauna. Conant (1977) and Scudday (1977) discussed human effects on this fauna, mainly in terms of aquatic amphibians and reptiles. Degenhardt (1977) suggested that some lizard species in Big Bend National Park had declined as plant cover increased in response to cessation of livestock grazing. Conversion of desert grassland to Chihuahuan Desert scrub over a 30-year period was implicated in the decline of several snake species and an increase in others along a road transect on the Arizona–New Mexico border (Mendelson and Jennings 1992). Bock et al. (1990) reported significantly reduced numbers of the bunch grass lizard and other lizard species in grazed grassland in southeastern Arizona. Long-term data, though, are generally lacking for most grassland herpetofaunal communities in the Southwest, thus permitting only tentative conclusions about local extirpations and distributional changes.

Grassland Herpetofauna

A number of amphibian and reptile species in the Southwest are restricted to plains and mesa grasslands, desert grasslands, or both. For many of these species we have little information on status and trends. The status of spadefoots, for example, is poorly known (Corn 1995). The advancement of juniper savanna into disturbed grasslands in New Mexico and Arizona (Dick-Peddie 1993) is expected to affect some grassland reptiles; for example, the grassland-dwelling little striped whiptail has been replaced by the woodland-adapted plateau striped whiptail at some localities in northern New Mexico (J. Stuart, U.S. Geological Survey, Albuquerque, New Mexico, unpublished data).

Aquatic Herpetofauna

Many frogs and toads and almost all aquatic turtles in the Southwest are dependent on rivers or surface waters associated with river floodplains. Among the species that have suffered significant losses in the Southwest are the Chiricahua and lowland leopard frogs, the Mexican and narrow-headed garter snakes, and the southwestern toad—all sensitive species (U.S. Fish and Wildlife Service 1994a). The status of the Big Bend slider, a little-known turtle endemic to the Rio Grande basin, is uncertain in New Mexico (Degenhardt et al. 1996).

Documented declines of amphibians in the Southwest include some populations of the Huachuca tiger salamander, northern leopard frog, and western toad (see summary in Corn 1995). Most documented declines for southwestern amphibians have occurred in the leopard frog complex (Clarkson and Rorabaugh 1989; Degenhardt et al. 1996; Fig. 19). The Vegas Valley leopard frog is now extinct (Jennings 1988), and the relict leopard frog in southern Nevada and southwestern Utah was thought extinct until three small populations were recently rediscovered (Jennings 1993). In Arizona, biologists found northern leopard frogs were absent from 46% and Chiricahua



Courtesy P. S. Corn, USGS

Fig. 19. Northern leopard frog.

Arizona Leopard Frogs: Balanced on the Brink?

The low humidity, high summer temperatures, and other natural forces that helped shape the saguaro, spectacular canyonlands, and other familiar features of the Southwest would seem to be inhospitable to the highly aquatic frogs of the genus *Rana,* known as ranids. In spite of these conditions, leopard frogs were, until recently, common inhabitants of Arizona's wetland and riparian ecosystems; in fact, the Southwest boasts the greatest diversity of leopard frog species in the United States. The recent dramatic declines of some members of this species complex need to be examined and addressed immediately.

Establishing a Historical Baseline

In the Southwest, native members of the true frog family (Ranidae) include the leopard frogs and the Tarahumara frog. Arizona's leopard frog fauna, among the largest in North America, is surprisingly diverse and includes at least five (possibly six) native leopard frogs and one introduced species (Platz et al. 1990; Table). While it is unclear exactly when declines of these frogs began, they were first noticed during the 1970's, when the status of the Tarahumara frog was of concern. Population studies of the Tarahumara frog in the mid-1970's indicated that the future existence of populations of this species in Southeast Arizona and the northern Sonora could be in jeopardy (Hale and May 1983; Hale and Jarchow 1988; Hale 1992). During these studies, researchers suspected that native leopard frogs were also declining, but there were no baseline data to support this suspicion. One of the first studies to investigate the status of Southwest leopard frogs on a large landscape was that of Clarkson and Rorabaugh (1989), who surveyed 56 historical and 7 new localities between 1983 and 1987 for four species of native leopard frogs.

Although this seminal investigation concluded that all species of leopard frogs examined were declining, several points relevant to status determination and conservation planning were not addressed by the authors. First, by focusing on historical localities, the data set gathered by Clarkson and Rorabaugh (1989) was biased toward concluding that declines have occurred (P. Geissler, U.S. Geological Survey, Laurel, Maryland, unpublished report). Second, because the study was not specifically designed to identify new localities or systematically evaluate threats, this information, which is important to status assessment and recovery planning, was not discussed.

In an effort to gather such data, the Arizona Game and Fish Department began assessing the status and current distribution of all native Arizona ranids by conducting statewide visual encounter surveys (in the sense of Crump and Scott 1994) of historical and high potential habitats, and by recording detailed habitat data and herpetofauna observations. Because of the confused taxonomic history of this group (Hillis 1988) and the likelihood that specimens of this complex are misidentified even in museum collections (Jennings 1994), biologists at the Arizona Game and Fish Department gathered historical locality data from selected sources in the published literature or local museums whose collections reflect the current taxonomy. Our data base presently contains over 4,000 herpetofaunal observations, collected from more than 1,500 localities.

I present a preliminary analysis of our survey data for all species of Arizona ranids except the Tarahumara frog, whose status has been recently reviewed elsewhere (Hale et al. 1995). Presence or absence of frogs at historical localities has been determined since 1990, the beginning of our statewide survey efforts. Because large temporal differences exist in activity of many amphibians, determining their presence or absence from a locality is difficult and requires multiple visits. Corn and Fogleman (1984), studying northern leopard frogs in Colorado, suggested that if frogs or reproduction are not observed at a locality over a three-year period, a population can be considered extirpated. In most, but not all instances, I have determined the presence or absence of leopard frogs at a site by examining survey results from three or more visits to that site during times of peak activity (April through October).

Preliminary Status of Arizona Leopard Frogs

Rio Grande Leopard Frog

Researchers believe that this species was inadvertently released into the Colorado River near Yuma, Arizona, in the 1960's during sport-fish stockings (Platz et al. 1990). Although all native leopard frogs have declined in at least some part of their Arizona ranges, it is ironic that this non-indigenous leopard frog continues to expand its Arizona range and is now known from the Colorado River near Yuma, the Gila River up to its confluence with the Salt River, and the Gila, Salt, Agua Fria, and Hassayampa rivers and adjacent agricultural areas near Phoenix (M. J. Sredl, Arizona Game and Fish Department, unpublished data; J. C. Rorabaugh, U.S. Fish and Wildlife Service, Phoenix, Arizona, personal communication).

Plains Leopard Frog

Most of the range of the plains leopard frog occurs in the central and southern Great Plains, where it is an inhabitant of aquatic habitats in prairie and desert grassland ecosystems (Stebbins 1985). In Arizona, this species is restricted to the Sulphur Springs

Common name	Number of localities/number of surveys	Historical absent	Historical present	Historical unsurveyed	New sites
Rio Grande leopard frog[a]	—	0	1	1	9
Plains leopard frog	85/98	14	1	1	2
Chiricahua leopard frog	679/871	80	18	35	45
Relict leopard frog[b]	—				
Northern leopard frog	477/566	24	2	21	29
Ramsey Canyon leopard frog	—		1	0	5
Yavapai leopard frog	648/797	35	28	35	167

[a] Introduced to Arizona.
[b] No verifed Arizona records.

Table. For each species of Arizona leopard frog, numbers of localities visited, numbers of surveys conducted within the range of that species, and frequency within each status category are listed. The status of each locality was evaluated relative to pre- and post-1990 surveys.

Valley in southeastern Arizona (Frost and Bagnara 1977), an area separated from the main portion of the range of this taxon by about 350 kilometers (Mecham et al. 1973). Specimens have also been collected from Ashurst Lake, southeast of Flagstaff in northern Arizona (J. E. Platz, Creighton University, Omaha, Nebraska, personal communication), but there have been no recent leopard frog records to verify this species at that site. Within the Arizona range of the plains leopard frog, Arizona Game and Fish biologists have conducted 98 surveys at 85 localities and found the species absent from nearly 93% of the localities surveyed historically (Table). Recent surveyors have only found this species at three localities, two of which were found after 1990.

Chiricahua Leopard Frog

Of all of Arizona's leopard frogs, the Chiricahua leopard frog has undergone perhaps the largest, most dramatic decline (Sredl and Waters 1995). The range of this species includes the southern edge of the Colorado Plateau in Arizona and New Mexico, southeastern Arizona, southwestern New Mexico, and the Sierra Madre Occidental in Mexico (Platz and Mecham 1979). The Arizona range of this frog consists of a northern part, which extends from the White Mountains and Mogollon Rim (the southern edge of the Colorado Plateau) in central Arizona, and a southern part in drainages associated with the Madrean oak woodlands and semidesert grasslands of the Madrean Archipelago (Sredl and Howland 1995). To evaluate the status of this frog, Arizona Game and Fish biologists have conducted 871 surveys at 679 localities, 98 of them historical. To date, the Chiricahua leopard frog appears absent from 82% of the historical localities surveyed since 1990 (Table). While surveyors found the Chiricahua leopard frog at 45 new sites, many of these observations consisted of as few as one or two frogs observed at localities adjacent to extant populations, making it likely that these individuals had dispersed from nearby populations.

Relict Leopard Frog

The relict leopard frog has the dubious distinction of being the first North American amphibian thought to have become extinct (Platz 1984) only to be rediscovered (Jennings 1993). No Arizona records of this species exist, but further clarification of relationships of southwestern leopard frogs may result in populations now classified as other species being included in this species.

Northern Leopard Frog

Until the late 1960's, all currently recognized leopard frogs, including those found throughout the Southwest, were classified as the species *Rana pipiens*, now known by the common name of northern leopard frog. During the 1960's, though, taxonomists realized that what was recognized as *R. pipiens* was really a multispecies complex (Hillis 1988). In Arizona, *R. pipiens* has been found in the lakes, earthen tanks, springs, creeks, and rivers of the Colorado Plateau in the northeast portion of the state. During these surveys, Arizona Game and Fish biologists visited 477 localities and conducted 566 surveys within the Arizona range of this frog, and found it at 8% of the historical localities visited. Although Arizona Game and Fish biologists found 29 new sites of occurrence, few of these populations are large. Within Arizona, there are probably fewer than five metapopulations, many of which are small.

Ramsey Canyon Leopard Frog

The Ramsey Canyon leopard frog is the most recently described of Arizona's leopard frog species (Platz 1993). This frog is known only from the Huachuca Mountains in southeastern Arizona, where six populations have been found in three drainages. A conservation team composed of agency and academic biologists as well as biologists from private institutions is developing a conservation agreement that is expected to be implemented soon. The continued viability of this species will depend on swift conservation actions by this group.

Yavapai Leopard Frog

Within the Southwest, the Yavapai leopard frog occurs in aquatic systems from desert scrub to pinyon–juniper habitats (Platz and Frost 1984). While the continued existence of this species in some parts of its range appears uncertain (Jennings 1995; Jennings and Hayes 1995), the status of this species in central Arizona seems good. Our intensive surveys of the range of this species have revealed that the species was present in 44% of the historical localities we visited. This percentage of occupancy of historical localities is by far the highest of any species of Arizona leopard frog. In addition, this frog has been found at 167 new localities, mostly in central Arizona (Table).

Mitigating Threats and Searching for Solutions

Analysis of historical and recent information reveals that the status of Arizona's six native ranids falls along a spectrum of endangerment. Although none is federally listed as threatened or endangered, two are candidates or species of special concern, and if declines continue, more species will be added. A general approach to stabilizing these declines or initiating recovery must incorporate traditional wildlife management techniques and techniques from endangered species recovery efforts. To have the greatest chance of success we need to begin formulating these plans now. Conservation and management activities should be implemented long before they become actions of last resort (Griffith et al. 1989).

See end of chapter for references

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leopard frogs from 94% of known localities previously studied by Clarkson and Rorabaugh (1989). Yavapai leopard frogs have been extirpated from the Imperial Valley in California and the lower Colorado River of California and Arizona.

Causes for declines of semiaquatic amphibians and reptiles remain elusive but include habitat destruction and alteration, introduced predators, pollutants, disease, and climate change (Corn 1995). Most declines are human-induced. For example, urban and agricultural water demands can result in drainage of isolated surface waters (such as springs in arid areas) through lowering of water tables; increasing human populations in riparian areas have led to reduced surface waters. Urbanization also may cause more pollutants to be introduced into surface water and groundwaters; pollutants may be further concentrated by reduced water supplies.

In addition, drainage of shallow wetlands and playas can eliminate breeding habitat for many amphibians. Riparian corridors and their associated amphibian and reptile populations may become fragmented by dam construction, agricultural and urban development in floodplains, and dewatering of streams and rivers (Knopf 1989). Such fragmented, reduced populations of reptiles and amphibians may have lowered genetic variability and may be more vulnerable to environmental perturbations (Brode and Bury 1984; Corn and Fogleman 1984; Bradford et al. 1993).

Effects of Introduced Species

Although the effects of introduced species on native fishes in southwestern aquatic systems have been well documented (Miller 1961; Sublette et al. 1990), such effects have been less documented for amphibians and reptiles. The nonindigenous bullfrog has been implicated in the decline of native leopard frogs in California (Hayes and Jennings 1986) and of native leopard frogs and garter snakes in southern Arizona (Schwalbe and Rosen 1988). Rosen and Schwalbe (1995) provided additional evidence of the effect of bullfrogs on native herpetofauna and of the possibility of recovery of affected populations once bullfrogs are removed. The establishment of nonindigenous aquatic turtles in several southwestern river systems has been verified (Hulse 1980; Degenhardt et al. 1996), but the effect of these introductions on the native turtle fauna is largely unknown. Extirpation of native frogs by introduced warmwater fishes has occurred in some California drainages (Hayes and Jennings 1986; Bradford et al. 1993) and may also be a factor in the decline of some southwestern amphibian populations. Studies are urgently needed to determine the effects of such introduced predators on vulnerable populations of amphibians and reptiles.

Birds

Baseline Surveys

Recent survey efforts focusing on Neotropical migrant birds have highlighted the ecological problems these birds face. Overall, moderate amounts of data on status and trends exist for birds. Although our knowledge of population trends in breeding birds is augmented considerably by surveys such as the U.S. Geological Survey Breeding Bird Survey (Peterjohn 1994), reliance on such indexes is not always possible in the topographically diverse Southwest, where higher-elevation habitats may not be routinely surveyed for breeding birds. Lowland areas, however, including some important habitats, are usually well covered by such surveys.

Riparian Birds

Riparian areas of the Southwest are the most productive habitats in terms of abundance and diversity of birds (Knopf et al. 1988). An estimated 78 of the 166 (47%) bird species that breed in the complex deciduous vegetation associated with watercourses breed only in this vegetation type (Knopf and Samson 1994). The presence of foliage of various height classes, the richness of plant species and forms, the heterogeneous mix of open and densely vegetated areas, and the relatively high frequency of nesting cavities form a complex association that can support a large variety of birds. These corridors of woody vegetation also appear important for migrant land birds, including species that overwinter in the Neotropics and short-distance migrants that usually winter in the southern United States and northern Mexico (Farley et al. 1994).

In New Mexico and Arizona, 11 of 40 (27.5%) land bird species known to have declined in numbers over the last 100 years may have done so because of degradation and destruction of riparian habitats (DeSante and George 1994). Maintenance of historical overbank flooding regimes, if combined with cessation of cattle grazing or at least if allowing grazing only at times other than nesting season, results in more successful recruitment of native vegetation in riparian areas and consequent increased use of these habitats by breeding and migratory birds (Farley et al. 1994). Many of the birds in riparian habitats migrate long distances to the Neotropics during the nonbreeding season, and 25% of those that breed in New Mexico are considered high-priority conservation risks (Carter and Barker 1993; Mehlman and Williams 1995).

Data from the Breeding Bird Survey for 1966–1993 show significant declines for a number of birds associated with southwestern riparian ecosystems. For example, vermilion flycatchers declined an average of 3.1% annually, and Lucy's warblers declined 0.5% annually (Peterjohn et al. 1994). Statistically significant trends require repeated sampling over large areas for lengthy periods, and the restricted distribution and limited sampling of this habitat (Peterjohn et al. 1994) reduced the number of statistically testable declines.

Woodland and Forest Birds

Fluctuating bird populations also have been recorded in pinyon–juniper and ponderosa pine woodlands. In these habitats, the processes associated with the decline of birds may be less clear, but researchers believe that overgrazing and timber and snag removal are at least partially responsible (DeSante and George 1994;

Hejl 1994). Although there is no significant overall decline among all woodland-breeding birds in the western United States (Peterjohn and Sauer 1994), a number of species have experienced quantifiable reductions in their populations. For example, the ladder-backed woodpecker, Bendire's thrasher, and gray vireo, which all breed primarily in pinyon–juniper habitat, have exhibited declines in numbers based on Breeding Bird Survey sampling from 1966 to 1993 (2.4%, 3.7%, and 0.8% per year, respectively).

The buff-breasted flycatcher, a regular breeder in ponderosa pine woodlands, has also experienced significant reductions in range and population size. Trends using Breeding Bird Survey data are unavailable for the buff-breasted flycatcher because this bird is observed irregularly on census routes.

Many primarily Mexican highland bird species range into parts of Arizona, New Mexico, and Texas. Although several of these species are listed as endangered or threatened in the southwestern states (for example, thick-billed parrot, ferruginous pygmy-owl, violet-crowned hummingbird, elegant trogon, and varied bunting; Flather et al. 1994), accurate estimates of their population trends are frequently lacking. The presence of a few relatively small, isolated populations at the periphery of the ranges of these species makes field biology difficult and effective management challenging. Moreover, complementary or more extensive data from the relatively densely populated central portions of the ranges of these species in Mexico are mostly unavailable.

Recovery of Peregrine Falcons

The American peregrine falcon is a southwestern bird that is experiencing a notable positive trend even though the species had experienced significant declines 40 years ago. Concentrated reintroduction and recovery efforts led by the Peregrine Fund are now coming to fruition in many areas. For example, the canyon country of northern Arizona and southern Utah supports the highest densities of nesting peregrines south of Canada (Brown et al. 1992).

Demographic Studies Needed

A valuable form of data collection for many of the Neotropical migrant birds in this region could involve determining their demographic variables at the population level. For example, scientists do not know the levels of reproductive success, survivorship, interyear site fidelity, or population persistence for the southwestern willow flycatcher, a riparian obligate recently listed as federally endangered (U.S. Fish and Wildlife Service 1995). Although population location and habitat associations are essential for the short-term maintenance of this species, its effective conservation will require additional detailed information.

The MAPS (Monitoring Avian Productivity and Survivorship) program (DeSante et al. 1993) is a sample protocol that defines standardized methods for determining and monitoring the species-specific demographic patterns of birds over regional and continental scales. To better understand the causes of population declines of southwestern birds, additional studies of individual bird species in each major ecosystem are necessary.

Mammals

Diversity of Southwestern Mammals

Cole et al. (1994) estimated that the mammalian fauna of the New World may be less threatened than that of other areas of the world. Of the estimated 1,750 New World mammal species, fewer than 5% are endangered, and about 15% are vulnerable or potentially vulnerable. Within temperate North America there are 37 families with 643 species of mammals; these figures include mammals in the Southwest. Cole et al. (1994) estimated that in North America about 65% of terrestrial mammal species were stable, 4% endangered, and 10% vulnerable; no assessment was possible for 20%.

The Southwest contributes impressively to continentwide diversity of mammals; native mammal species in southwestern states number about 120 in Texas, 138 in Arizona, 139 in New Mexico, and 163 in California (Findley et al. 1975). No other region in the country has so many mammal species—and many of these species and their named subspecies are endemic to the Southwest.

Effects of Human Settlement

It was this fundamental diversity, mammalian and otherwise, that helped attract early settlers to the region, although their concerns about the barren and arid nature of the region were clear. After European settlement, especially in the late 1800's and early 1900's, the first wave of changes in mammalian diversity was noted, with the first native species affected those that humans least tolerated—species originally characterized by large geographic ranges and home territories (Hall 1981). With the determined efforts and encouragement of employees of the Bureau of Biological Survey, large numbers of "predatory" animals, such as

grizzly bears, gray wolves, and mountain lions (one subspecies of which, the Yuma puma, is a federal candidate species), were trapped, and some were eventually extirpated from the Southwest (Brown 1983). These large native carnivores came into conflict with human activities, especially the raising of domestic livestock. With the decline of native ungulate populations (Mackie et al. 1982) during and following settlement, domestic livestock may have provided replacement protein for native carnivores before they too were extirpated.

Other human activities, especially agricultural conversion of natural habitats, resulted in the demise or decline of at least two other species whose life histories are intertwined, the black-tailed prairie dog and the black-footed ferret. The prairie dog's own activities, grazing and construction of burrows and mounds, put it on a collision course with farmers and ranchers. Eradication campaigns reduced prairie dog distribution from 40,000,000 hectares to 600,000 hectares by 1960—about a 98% decline in the original geographic distribution of the species (Miller et al. 1990). These eradication campaigns, primarily using poison, also doomed the black-footed ferret.

Other mostly Neotropical carnivores, such as the jaguar, jaguarundi, and ocelot, are now uncommon or absent from the northern portions of their ranges, which include southern Arizona, New Mexico, and Texas (Hall 1981; Hoffmeister 1986). The retraction of their ranges is probably due to their intolerance of humans and to some level of predator control in the Southwest. These carnivore species, though, were never as common as the grizzly bear, the gray wolf, or the black-footed ferret, although some information indicates that jaguars were more common than is often believed (Nowak 1994).

Increases of Deer and Elk

After the extirpation or decline of these carnivores and the black-tailed prairie dog, humans and other mammals coexisted for much of the twentieth century, albeit with some continued level of "damage control" on rodents (mostly prairie dogs) and carnivores (for example, coyotes). Continued trapping of carnivores (including mountain lions) in the Southwest, population management, and more restrictive hunting regulations have resulted in recovery of ungulates from turn-of-the-century population lows (Mackie et al. 1982). Elk numbers are now at an all-time high, with an estimated 782,000 elk occupying more suitable habitat than at any time in this century (Peek 1995; see box on Elk Reintroductions). In much of the

Elk Reintroductions

Rocky Mountain elk are native to north-central New Mexico, including the Jemez Mountains, whereas a different subspecies, Merriam's elk, inhabited southern New Mexico, east-central Arizona, and the Mexican border region (Hall 1981). Merriam's elk went extinct around 1900 in New Mexico, and native Rocky Mountain elk were extirpated by 1909 (Findley et al. 1975). Although elk were known to early inhabitants of the Jemez Mountains (Fig. 1), elk remains are seldom found in archaeological sites there. Indeed, two of three known elk remains from the Jemez Mountains (Table) came from archaeological sites dating to the late 1880's, while the third is represented by a single bone tool dated at A.D. 1390 to 1520. This scarcity of elk in archaeological remains suggests that only small, local elk populations were present between A.D. 1150 and A.D. 1600. Elk numbers may have been suppressed by the many ancestral Pueblo people who inhabited the area, as suggested for nearby Arroyo Hondo by Lang and Harris (1984) and for the intermountain West by Kay (1994). The gray wolf, the most important natural predator of elk in the Jemez Mountains, was extirpated from the area by the 1940's (Findley et al. 1975). Hunting has reduced local populations of another elk predator, the mountain lion (Allen 1989).



Courtesy C. D. Allen, USGS

Fig. 1. A drawing of elk from a rock art site in the Jemez Mountains, New Mexico. The elk was probably painted in the late 1800's.

Table. Ungulate remains (minimum number of individual animals) recovered from archaeological sites in and near the Jemez Mountains.

Locality	Deer	Elk	Bighorn	Antelope	Bison	Ungulate
Jemez Mts. (45 sites)	154	3	30	24	7	58
Arroyo Hondo (Santa Fe)	157	6	-	56	7	213
Total	311	9	30	80	14	271

Although Merriam's elk was driven to extinction, the Rocky Mountain subspecies survived farther north at places such as Yellowstone National Park; these northern animals were introduced widely in New Mexico (Findley et al. 1975). In 1948, for example, the New Mexico Department of Game and Fish released 21 cows and calves and 7 bulls captured at Yellowstone into the Jemez Mountains (S. Keefe, 25 September 1948, report on file at Bandelier National Monument, New Mexico). In 1964–1965, another 58 elk from Jackson Hole,

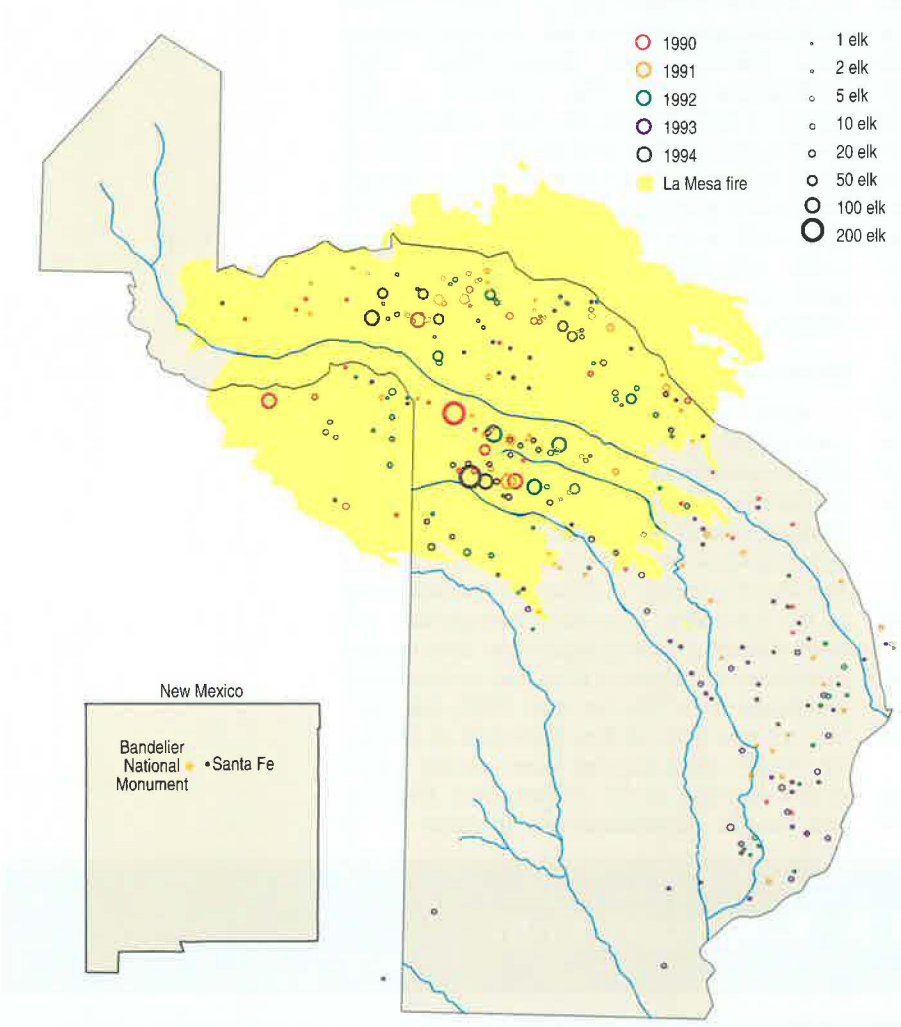


Fig. 2. Distribution of elk at Bandelier National Monument and vicinity, Jemez Mountains, New Mexico.

Wyoming, were released into the mountains of Los Alamos County adjacent to Bandelier National Monument (White 1981).

Elk populations have exhibited exponential population growth since at least the 1970's in Bandelier National Monument and the surrounding Jemez Mountains. The size of the Bandelier National Monument area elk herd has increased dramatically since the 1977 La Mesa fire (Allen 1996a; Fig. 2), which created about 6,000 hectares of grassy winter range. Estimated size of the wintering elk population in Bandelier National Monument has increased from less than 100 in 1977–1978 to 296 in 1978–1979 (Conley et al. 1979); 200–400 elk occurred in the La Mesa fire area in 1979–1980 (Rowland et al. 1983). By 1989, though, 1,000–2,000 elk wintered on Bandelier National Monument and adjacent Los Alamos National Laboratories and U.S. Forest Service lands (R. Isler, New Mexico Department of Game and Fish, Santa Fe, personal communication). Aerial surveys over Bandelier National Monument counted 907 elk in 1991, 867 in 1992, and 939 in 1994 (Allen 1996b). If we accept that 100 elk wintered in Bandelier National Monument in 1978 and 1,500 elk in 1992, the annual population growth rate was 21.3% with a 3.6-year population doubling time. Some of this population increase reflects concentration of animals into favorable wintering habitat from surrounding areas of the Jemez Mountains, where New Mexico Department of Game and Fish officials estimate that overall elk populations are between 3,500 and 8,000 animals.

Similar rapid population growth has also occurred in New Mexico as a whole, as well as throughout the West (Peek 1995). Elk were reintroduced into New Mexico beginning in 1911, with estimated statewide population levels of 3,500 animals by 1934 and 10,000–12,000 elk by 1976; the 1992 population was estimated at 40,000 elk (D. Weybright, New Mexico Department of Game and Fish, Santa Fe, personal communication). If we assume 10,000 elk in 1976, this translates into a 9% annual population growth rate and an 8-year doubling time for 1976–1992 (for 1976 = 12,000 elk; the result is a 7.8% annual increment and a 9.2-year doubling time). Because these large ungulates compete with domestic livestock for herbaceous forage, conflicts with ranchers have emerged in some areas.

Existing data are inadequate to determine whether rapid population growth continues today in the Jemez Mountains, although observations over the past several years clearly reveal that local elk populations are now colonizing lower-elevation sites in ever-increasing numbers, which is indicative of range expansions, if not continued overall population growth. These large elk populations are affecting resources ranging from plant communities to soils and even archaeological sites throughout the Jemez Mountains, especially in the Bandelier National Monument area. Given the uncertainties associated with current data, further population increases should be discouraged until the effects of large elk numbers on the area's resources can be quantified, desirable population levels that are based on resource-carrying capacities identified, and appropriate management strategies determined and implemented.

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Southwest, though, recovered elk populations are composed of nonindigenous elk introduced by state game departments (and other game agencies) from areas to the north, such as Yellowstone National Park (Findley et al. 1975; Hoffmeister 1986). In many areas, mule deer and white-tailed deer also have made remarkable recoveries from earlier lows, although in some areas nonindigenous deer have been transplanted (Hoffmeister 1986).

Other ungulate populations have remained at low levels. Despite considerable transplant efforts, bighorn sheep may only make up 2%–8% of their population levels at the time of European settlement; these animals have never recovered from unregulated harvesting, habitat destruction, overgrazing of rangelands, and diseases contracted from domestic livestock (Singer 1995). Desert bighorn sheep numbers are low, currently estimated at about 19,000, although the population trends have been upward since the 1960's (McCutchen 1995). Numbers of Sonoran pronghorn, listed as endangered by the U.S. Fish and Wildlife Service, are also low, and overall pronghorn numbers in the Southwest are probably below historical highs noted in the 1800's (Hoffmeister 1986).

Concern for Smaller Mammals

Only recently has concern been focused on other less conspicuous mammals that differ in habits from those that were in conflict with humans during settlement. The last list of candidate and sensitive species (U.S. Fish and Wildlife Service 1994a) includes a broad spectrum of mammals that are of concern. The list no longer emphasizes large carnivores, or many carnivores at all, but instead emphasizes smaller species such as insectivores (shrews), a wide array of bats, small relatives of rabbits known as pikas, cottontails and hares, pocket gophers, tree squirrels, and a variety of mice and rats. In general, we know little of the status and trends of these species.

Several unifying trends exist among mammals on these lists, excluding bats (U.S. Fish and Wildlife Service 1994a). Many of the mammals, including shrews, pikas, gophers, tree squirrels, mice, and rats, have small or restricted ranges, often on single mountaintops or other functional islands as well as on actual islands—such as those in the Great Salt Lake. Many mammals on the lists are isolated subspecies of wide-ranging species and often occur on different mountain ranges, a phenomenon particularly true of pikas and gophers (Hall 1981). Also, and perhaps more importantly from an ecosystem perspective, many of the species or subspecies live in wet or moist habitats, often montane. This is clearly the case for the shrews, voles, meadow jumping mice—a unique family of mice found in North America and China—and some other mice. A smaller number of mammals adapted to arid habitats (for example, kangaroo rats, pocket mice, and cotton rats), primarily in Arizona and Utah, are also on the sensitive species list (U.S. Fish and Wildlife Service 1994a).

Lists of species are sometimes idiosyncratic in nature, in that they reflect the activity, expertise, and concern of people, as well as their access to sources of data about particular species. Some mammals probably have been listed solely because of their restricted range and the absence of data on population trends. Although little information exists about the status or trends of mammals on mountaintops, it is unclear what might be threatening isolated populations of pikas on mountaintops that are not subject to extensive development or visitation. Although global climate change may result in different conditions at high elevations, such effects have not been proven. Likewise, the proliferation of pocket gophers on the sensitive species list (more than 20 southwestern species or subspecies; U.S. Fish and Wildlife Service 1994a) is somewhat puzzling but not yet addressed by any concerted information-gathering effort. Pocket gophers exhibit astounding diversity, with apparently distinct subspecies (or varieties) occurring within miles or even yards of one another (Thaeler 1968; Hall 1981; Patton and Smith 1990). Their subterranean existence promotes such diversity, but it is unknown whether the diversity in turn promotes concern because these different pocket gophers represent perceived dwindling endemism of small areas. Possible environmental threats to pocket gophers include habitat change through overgrazing, lowering of water tables, and poisoning campaigns directed against them or other rodents, such as prairie dogs. Gophers, like prairie dogs, perform ecologically important roles through their habit of turning over and aerating soils, thereby providing for percolation of water and creation of new substrates for vegetative succession.

Some additional species of concern in the Southwest include white-tailed deer in the Sonoran Desert, white-sided jackrabbits in southern New Mexico, and Mexican voles in Arizona. Baker (1977) cited other species for the Chihuahuan Desert, but for most taxa there are no data on status or trends. Species in mountainous areas have been affected by habitat alteration due to water diversions, forestry practices, fire suppression, and livestock grazing. Species in more arid areas are jeopardized by urbanization, agriculture, water diversion, off-road activities, and perhaps climate change.

Endemic Mammals of the Henry Mountains, Utah

Some species of small mammals may appear on lists of sensitive species (for example, U.S. Fish and Wildlife Service 1994) because they are known from only one or a few localities, have not been the subject of any studies, and are genetically distinct. The three endemic subspecies of mammals from the Henry Mountains of Utah illustrate some possibilities and problems faced by management agencies when such species are listed as sensitive species or as candidates for protection as endangered or threatened species. The Henry Mountains in south-central Utah were the last western mountain range to be discovered (Hunt et al. 1953; Figure), after being seen during one of John Wesley Powell's trips down the Colorado River and subsequently explored by a party sent out by Powell. The mountains provide habitat to three endemic subspecies of mammals: Mt. Ellen chipmunk, Mt. Ellen pocket gopher, and Mt. Ellen long-tailed vole (Hall 1981). Recent research in the Henry Mountains showed that the chipmunk is abundant with no apparent threats to its widespread habitat (Mollhagen and Bogan 1995). The vole, though less abundant, is commonly found in good habitat. Voles, however, cycle in abundance (Taitt and Krebs 1985) and surveys for them should be conducted over several seasons or years. Habitat for the vole could be jeopardized by overgrazing or drying of wetlands, but no studies in the Henry Mountains have documented such threats. These two species, the chipmunk and vole, are probably not in real danger from any perceivable threat. The pocket gopher, though, may represent a distinctly different case. Almost 40 years ago, Durrant (1958) commented that the gopher might be extinct, though the basis for his comment is unknown. More recent studies also found no sign of pocket gophers in the Henry Mountains (Mollhagen and Bogan 1995), though surveys are incomplete, and considerable habitat remains that must be searched. Additional surveys are needed to clearly determine the status of the Mt. Ellen pocket gopher so that management decisions can be made.



Courtesy M. Bogan, USGS

Figure. East face of the Henry Mountains in southeastern Utah.

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Introduced and Feral Mammals

Many kinds of introduced and feral mammals are now naturalized in the Southwest: Barbary sheep, gemsbok, ibex (Findley et al. 1975), and nonindigenous deer introduced for sport hunting; wild burros, horses, cattle, pigs, goats, sheep, dogs, and cats whose ancestors escaped from captivity; and mice and rats living commensally with humans. In general, little is known about the effect of these species on native vertebrate wildlife and their habitats. Drost and Fellers (1995) provided information on distribution and effects of some of these species on public lands, and Pogacnik (1995) discussed the status of wild horses and burros on public lands. Arizona is estimated to have about 4,000 wild horses, asses, and mules; New Mexico around 500 (most on White Sands Missile Range), and Utah about 2,000 (Pogacnik 1995). In New Mexico, gemsbok appear to be expanding their range northward from White Sands Missile Range, where they were introduced by the New Mexico Department of Game and Fish; they now routinely encroach on the San Andres National Wildlife Refuge and the White Sands National Monument (M. Bogan, unpublished data). In some areas, gemsbok seem to cause damage by trampling, but no studies have documented their effects on public lands.

Southwestern Bats

Concern for bats in the Southwest (Figure) is a relatively recent phenomenon, although two southwestern bats are listed as endangered by the U.S. Fish and Wildlife Service. Before November 1994, seven species or subspecies of bats in the Southwest were listed as candidates for eventual listing under provisions of the U.S. Endangered Species Act of 1973. The last list (U.S. Fish and Wildlife Service 1994) contained 15 bats, including 10 full species. The total bat fauna of the Southwest is about 30 species, depending on locality, so one-third to one-half of the region's bat species are now considered sensitive. No other group of mammals is a target for such recent concern. In general, we have no long-term population data on status and trends of these bats, mostly because bats, long-lived and with a low reproductive potential, are difficult to study, and their numbers are even more difficult to quantify. No nationwide survey of bat populations exists, and no attempt has been made to quantify existing data so that trends in bat populations can be discerned, although the U.S. Geological Survey has initiated such a study (T. J. O'Shea, U.S. Geological Survey, Fort Collins, Colorado, personal communication). Many of the species added as candidates—now considered species of concern—in November 1994 are widespread in the West and are thought to be relatively secure.

Although many bat biologists and state and national groups (for example, Bat Conservation International and Colorado Bat Society) have expressed concern about threats to bats for many years, most land managers have become aware of the potential for declining bat populations only in the last few years. In the West in general, a preeminent concern for bat welfare comes from the widespread closure of abandoned mine entrances. These mines, a historical and common feature of the American West, represent an extreme safety hazard to humans. With funding from the federal government, many western states have set up programs to close such mines, and thousands have been closed. Closures usually occur with no thought or concern that bats might be using these mines as roosting sites, even though many mines have become havens for western bats since the mines were abandoned (K. Navo, Colorado Division of Wildlife, Denver, and J. S. Altenbach, University of New Mexico, Albuquerque, personal communications). Bats have moved into abandoned mines after being driven or excluded from other roosting sites, such as vandalized caverns.



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Figure. Endangered lesser long-nosed bat (top), western red bat (center), and Townsend's big-eared bat (bottom).

Because topographic diversity, specifically the amount and nature of available roost sites, determines the species diversity of bats (Humphrey 1975), protection of roosts is essential. Thus, many individuals and groups are focusing their efforts on surveying the most likely mines that bats may be inhabiting before these mines are closed. In turn, many states are incorporating results of such surveys into their planning and, when necessary, erecting bat-friendly gates at the mine entrance instead of absolute closures (K. Navo, Colorado Division of Wildlife, Denver, personal communication). The National Biological Service (now the U.S. Geological Survey Biological Resources Division) recently helped fund a cooperative program (Bat Conservation International, Bureau of Mines Management and U.S. Geological Survey) aimed at assessing the magnitude of the threat that mine closures represent to bats. More data, especially long-term data, are needed to assess the status and trends of bats in the Southwest.

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Summary and Recommendations

Information Gaps

A striking lack of information exists about the status and trends of southwestern biota and ecosystems. To remedy this, researchers need to systematically collect and summarize the rigorously collected data on status and trends of plant and animal communities in the Southwest. For most groups we still lack information on population size and variability, recruitment, trends, effects of change due to human activity, interactions with nonindigenous species, and known threats to populations. However, for selected species of fishes and birds we have sufficient information not only to reveal the problems but also to start to understand the answers as well.

One wonders how far the current conservation effort for birds, Partners in Flight, would have gotten without the availability of detailed trend information gathered over the last 32 years by the U.S. Geological Survey Breeding Bird Survey. With well-designed efforts over the next 30 years, we eventually could have equivalent surveys for butterflies, snails, or other lesser known invertebrates or plants. We think caution is required in applying conservation strategies developed for well-understood groups to little-understood groups because such strategies may not provide workable answers in all cases. Some efforts, such as those directed at bats, are now under way (see box on Southwestern Bats), but additional conservation efforts need planning and implementation now.

The effect of habitat fragmentation—the division of solid habitat blocks by roads, right-of-ways, or development—on ecosystem integrity and on the species of the area affected is still incompletely understood and is a pervasive issue in the Southwest. For many areas our understanding of even the extent of habitat fragmentation is poor; available technology (such as geographic information systems and satellite imagery) should be used to assess status and trends of fragmentation. In addition, field studies are required to better understand the effects of fragmentation on populations and communities of southwestern plants and animals. Particularly important is acquiring knowledge of how organisms respond to shrinking habitats and whether linking habitats by corridors will compensate for some degree of absolute habitat loss (Simberloff et al. 1992).

Given that many human-related disturbances, such as livestock grazing and timbering, were more severe 90 or more years ago, and that some ecosystems are in better condition now than at the turn of the century, research should address the responses of ecosystems and their components to such recovery. Not only have many deer, elk, and related grazer populations recovered from population lows, but some are now posing real management concerns (see box on Elk Reintroductions). Issues such as the control of ungulate (or carnivore) populations on federal lands, especially on national parks, can best be resolved with rigorous studies that assess current effects of expanding animal populations on localized environments. Studies that are firmly grounded in knowledge of the history of southwestern ecosystems seem to us to provide the best opportunity to resolve such issues.

Large information gaps persist regarding the effects on ecosystems and species of the three most important types of human landscape management in the Southwest. In spite of the plethora of studies cited in Fleischner's (1994) overview, the effects of grazing on natural ecosystems and species continue to be controversial. We believe that more studies on these effects are needed and that they must be carefully designed so that it is possible to "tease out" effects due to grazing from those due to climate, soils, or other factors. Furthermore, it is likely that results from some grazing studies are not widely applicable beyond the local environment; this implies a need for more site-specific studies. Likewise, although we have learned much of the history and effects of fire suppression, a great deal of additional site-specific information is needed to understand the ecological effects of fire on southwestern ecosystems and biological diversity. Finally, although the pervasive effects of water diversion and impoundment structures on southwestern aquatic habitats and their biota are becoming clear (see chapter on Water Use), little knowledge exists of how to mitigate or reverse such trends. A key approach to addressing these information gaps is through additional experimental studies (e.g., alternative grazing regimes, spring versus fall burning, altering reservoir water levels and release rates), which would rigorously assess the response of biota and ecosystem processes to alternative management actions at specific sites. Once enough site-specific information is available, it may be possible to develop regional summaries to allow improved extrapolation of results to unstudied areas.

In many portions of the Southwest, human populations can be expected to continue to grow rapidly, yet there appears to be little research that directly addresses the effect of increasing human numbers on natural communities and their constituent species. Although some national park research programs attempt to address the issue of visitor effects on park ecosystems,

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more rigorous studies are needed. For nature reserves (for example, wildlife refuges, national parks, wilderness areas) we particularly need continued but expanded baseline inventories to assure that we fully understand what ecosystem components are present. Once baseline information is adequate, monitoring of critical populations needs to begin. In addition, more data are needed on the effects of activities such as mining, timber harvest, road building, application of biocides, pollution, and conversion of land to agricultural or urban uses. With new and better data, we will better understand exactly how human population growth will affect southwestern ecosystems and their biota.

Fundamentally, many conservation biology concerns are related to habitat management issues. If sufficient habitat is maintained, then most biotic components of that ecosystem will likewise be maintained. At present, however, we have an inadequate understanding of how biotic components interact in the mosaic of habitats that characterize the Southwest. New studies should include attempts to better understand the history of southwestern ecosystems; the historical picture can then provide a context for understanding current patterns and predicting future trends.

An important avenue of research that we have not mentioned previously is the need for studies on sociological aspects of status and trends of southwestern biota. To what extent are citizens committed to maintaining some semblance of natural conditions in the Southwest? Studies that assess the nonmarket values of natural resources will be important in helping to set priorities for future research on southwestern ecosystems. Fully successful conservation results will require a greater degree of social consensus than has been achieved recently. We believe that the lack of adequate unbiased data on both natural and cultural systems in the Southwest is a major impediment to achieving social agreement on needed actions.

Conclusion

Finally, we recognize that this overview sketch of the condition of southwestern biota necessarily shares the flaws of incompleteness and uncertainty common to this genre of summary reviews, reflecting the backgrounds of the few authors involved. Much additional, unsummarized information currently exists on the status and trends of southwestern biota, but this information is in widely dispersed and disparate forms, and much remains unpublished and generally inaccessible. One of several possible ways to begin to fill in known information gaps is to begin a series of actual or "virtual" regional scale workshops that bring together available experts to present and collate existing knowledge on the status and trends of southwestern biota, including much currently unavailable information. The initial workshops might be organized by regional ecosystem (for example, the Colorado Plateau or the Sonoran Desert) or by state, building to a regional scale synthesis. Such workshops or similar information-gathering efforts could play a key role in the development of the National Biological Information Infrastructure and would allow research needs to be better prioritized.

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