The Structure and Functioning of Dryland Ecosystems— Conceptual Models to Inform Long-Term Ecological Monitoring

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By Mark E. Miller

Prepared in cooperation with the National Park Service

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The Structure and Functioning of Dryland Ecosystems— Conceptual Models to Inform Long-Term Ecological Monitoring

By Mark E. Miller

Abstract

The National Park Service (NPS) has undertaken the task of developing long-term ecological monitoring programs for 32 ecoregional networks of parks that have significant natural resources. As part of this effort, each network will select "vital signs" that are intended to represent the overall health or condition of park ecosystems, known or hypothesized effects of stressors, or elements that have important human values. As an aid to the consideration and selection of vital signs for long-term monitoring in NPS units of the Colorado Plateau region, this report presents a literature synthesis and a set of diagrammatic conceptual models that summarize existing knowledge and hypotheses concerning the structure and functioning of dryland ecosystems. These generalized conceptual models describe functional relationships among key structural components of dryland ecosystems; effects of climate, natural disturbances, and anthropogenic stressors on the functioning of selected ecosystem processes; and how these drivers of ecosystem change interact to produce particular patterns of ecosystem dynamics. Because NPS policies dictate that monitoring data will be used to help sustain the integrity of park ecosystems, conceptual models in this report emphasize common processes and pathways of dryland degradation—with the intent that this emphasis will best highlight ecosystem attributes that should be monitored for purposes of sustaining ecosystem integrity. Although developed to support the identification of long-term monitoring needs in NPS units, information in this report is broadly applicable well beyond NPS management boundaries and should be of use to other organizations or persons involved in management, conservation, and monitoring of dryland ecosystems in the Colorado Plateau or bordering ecoregions.

Acknowledgments

Introduction and Background

Purpose and Content of This Report

This report presents conceptual ecological models describing the structure and functioning of dryland ecosystems[1] of the Colorado Plateau and bordering ecoregions of North America. These models and the associated literature review were prepared in support of the Southern Colorado Plateau Network (SCPN) of the National Park Service's

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[1]An *ecosystem* is a spatially explicit unit of the Earth that includes all of the organisms, along with all components of the abiotic environment within its boundaries (Likens, 1992, cited by Christensen and others, 1996, p. 670). *Ecosystem structure* refers to the types, amounts, and spatial arrangement of biotic and abiotic components of an ecosystem. *Ecosystem functioning* refers to the flow of energy and materials through biotic and abiotic components of an ecosystem, and includes processes such as primary production, trophic transfer from plants to animals, nutrient cycling, water dynamics, and heat transfer (Díaz and Cabido, 2001).

Inventory and Monitoring Program (NPS I & M Program). In conjunction with the I & M Program, ecoregional networks of NPS units have been tasked with the identification of "vital signs" to be monitored for the purpose of tracking long-term trends in the "health" or condition of park ecosystems. This report was developed for SCPN policymakers and researchers to help inform them in the consideration and selection of vital signs for dryland ecosystems in 19 NPS units located in the Colorado Plateau region of Utah, Arizona, Colorado, and New Mexico (table 1). The SCPN and the Northern Colorado Plateau Network (NCPN; consists of 16 NPS units) are working together closely to coordinate planning and implementation of their respective monitoring programs. As a consequence, this document also is intended to support the NCPN in the development of its monitoring plan and to facilitate the coordinated development of monitoring across both networks in the Colorado Plateau region. Although developed to support the identification of long-term monitoring needs in NPS units, information in this report is broadly applicable well beyond NPS management boundaries and should be of use

to other organizations or persons involved in management, conservation, and monitoring of dryland ecosystems in the Colorado Plateau or bordering ecoregions.

This report begins with background information regarding the vital-sign concept, intended purposes of conceptual models in relation to ecosystem monitoring, and the geographical and ecological scope of the report. Following the background information section, a general conceptual model and literature review are presented to characterize important functional relationships among biotic and abiotic components of dryland ecosystems. In the third section, several additional models are presented to describe particular patterns and processes of dryland ecosystem dynamics that have significant implications for ecosystem monitoring and management. Models in this section emphasize common processes and pathways of dryland degradation—with the intent that this emphasis will best highlight ecosystem attributes that should be monitored for purposes of sustaining ecosystem integrity. Supplementary material is presented in accompanying appendix tables A–C.

USGS plant ecologists evaluating sampling methods in support of the National Park Service Inventory and Monitoring Program. San Juan County, Utah. Photograph by Lisa Thomas, NPS.

Table 1. Selected characteristics of NPS units included in the Southern and Northern Colorado Plateau Networks. Ecoregion designations follow The Nature Conservancy and NatureServe (Groves and others, 2002), as modified from Bailey (1995).

Network/Park	Code	State	Size (ha)	Altitude (m)	Ecoregion
Southern Colorado Plateau Network					
Aztec Ruins National Monument	AZRU	NM	130	1705–1764	Colorado Plateau
Bandelier National Monument	BAND	NM	13,254	1626–3081	Southern Rocky Mts.
Canyon de Chelly National Monument	CACH	AZ	37,448	1687–2336	Colorado Plateau/Arizona-New Mexico Mts.
Chaco Culture National Historic Park	CHCU	NM	14,090	1832–2096	Colorado Plateau
El Malpais National Monument	ELMA	NM	46,559	1950–2554	Arizona-New Mexico Mts.
El Morro National Monument	ELMO	NM	518	2183–2304	Arizona-New Mexico Mts.
Glen Canyon National Recreation Area	GLCA	AZ/UT	505,868	930–2319	Colorado Plateau
Grand Canyon National Park	GRCA	AZ	493,050	348–2798	Colorado Plateau
Hubbell Trading Post National Historic Site	HUTR	AZ	65	1920–1946	Colorado Plateau
Mesa Verde National Park	MEVE	CO	21,093	1833 – 2613	Colorado Plateau
Navajo National Monument	NAVA	AZ	146	1658–2294	Colorado Plateau
Petrified Forest National Park	PEFO	AZ	38,024	1618–1891	Colorado Plateau
Petroglyph National Monument	PETR	NM	2,915	1519–1838	Arizona-New Mexico Mts.
Rainbow Bridge National Monument	RABR	UT	65	1129–1492	Colorado Plateau
Salinas Pueblo Missions National Monument	SAPU	NM	433	1815–2058	Arizona-New Mexico Mts.
Sunset Crater Volcano National Monument	SUCR	AZ	1,227	2076–2441	Arizona-New Mexico Mts.
Walnut Canyon National Monument	WACA	AZ	1,456	1896–2106	Arizona-New Mexico Mts.
Wupatki National Monument	WUPA	AZ	14,350	1304–1744	Colorado Plateau
Yucca House National Monument	YUHO	CO	14	1767–1805	Colorado Plateau
Total			**1,189,205**		
Northern Colorado Plateau Network					
Arches National Park	ARCH	UT	30,966	1206–1725	Colorado Plateau
Black Canyon of the Gunnison National Park	BLCA	CO	12,159	1636–2752	Southern Rocky Mts.
Bryce Canyon National Park	BRCA	UT	14,502	2000–2777	Utah High Plateaus
Canyonlands National Park	CANY	UT	136,610	1140–2189	Colorado Plateau
Capitol Reef National Park	CARE	UT	97,895	1182–2730	Colorado Plateau
Cedar Breaks National Monument	CEBR	UT	2,491	2461–3247	Utah High Plateaus
Colorado National Monument	COLM	CO	8,310	1411–2160	Colorado Plateau
Curecanti National Recreation Area	CURE	CO	17,433	1982–2898	Southern Rocky Mts.
Dinosaur National Monument	DINO	CO/UT	85,097	1442–2747	Utah-Wyoming Rocky Mts.
Fossil Butte National Monument	FOBU	WY	3,318	2012–2466	Wyoming Basins
Golden Spike National Historic Site	GOSP	UT	1,107	1317–1613	Great Basin
Hovenweep National Monument	HOVE	CO/UT	318	1548–2056	Colorado Plateau
Natural Bridges National Monument	NABR	UT	3,009	1702–2019	Colorado Plateau
Pipe Spring National Monument	PISP	AZ	16	1495–1559	Colorado Plateau
Timpanogos Cave National Monument	TICA	UT	101	1669–2452	Utah-Wyoming Rocky Mts.
Zion National Park	ZION	UT	59,900	1112–2661	Colorado Plateau
Total			**474,709**		

Vital Signs Definition

As defined by the NPS (see http://science.nature.nps. gov/im/monitor/vsm.htm#Definitions), vital signs are a subset of physical, chemical, and biological elements and processes of park ecosystems that are selected to represent the overall health or condition of park resources, known or hypothesized effects of stressors, or elements that have important human values. The elements and processes that are monitored are a subset of the natural resources that park managers are directed to preserve "unimpaired for future generations," including water, air, geological resources, plants and animals, and the various ecological, biological, and physical processes that act on those resources. Vital signs may occur at any level of the ecosystems including landscape, community, population, or genetic level, and may be compositional (referring to the variety of elements in the system), structural (referring to the organization or pattern of the system), or functional (referring to ecological processes). Although vital signs are used to support long-term monitoring in NPS units, they have relevance for other monitoring efforts useful for ecosystem management.[2]

Purposes of Conceptual Models

In the vital-sign selection process, conceptual models are used to summarize existing knowledge and hypotheses concerning the structure and functioning of park ecosystems. An important goal of the models is to depict how natural drivers (for example, climate) and anthropogenic stressors affect ecosystem structure and functioning. The ability of the monitoring program to detect the ecological effects of anthropogenic stressors is dependent upon interpreting trends in resource condition against the backdrop of natural ecosystem variation. Hypotheses concerning the effects of anthropogenic stressors on ecosystem structure and function must be grounded in an understanding of the relationship between natural drivers and the structure, functioning, and dynamics of ecosystems. Ecosystems can be characterized on the basis of far more structural and functional attributes than can be monitored affordably. Thus another important goal of the models is to guide the identification of a few important attributes that provide information about multiple aspects of ecosystem status (Noon, 2003).

No single conceptual model can satisfy all needs. Spatially explicit applications, such as ecological resource assessments, monitoring design, and landscape-level ecological modeling, ultimately require site-specific models, but monitoring programs also require generalized ecological models

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[2] *Ecosystem management* is the process of land use decision making and land-management practice that takes into account organisms and processes that characterize and comprise the ecosystem and is based on the best understanding currently available as to how the ecosystem works. Ecosystem management includes a primary goal of sustainability of ecosystem structure and function, recognition that ecosystems are spatially and temporally dynamic, and acceptance of the dictum that ecosystem function depends on ecosystem structure and diversity (Dale and others, 2000, p. 642).

to facilitate communication among scientists, managers, and the public regarding ecosystems and how they are affected by human activities and natural processes. Together, the NPS and USGS have adopted an iterative approach of first developing general conceptual models for broadly defined ecosystem types, and then adapting and refining those models with site-specific data concerning abiotic constraints, land use history, current condition, and specific patterns of ecosystem dynamics. Models presented in this report are generalized because of the great diversity of dryland ecosystems found in SCPN and NCPN parks.

Previous NPS reports established a framework for the conceptual modeling effort associated with the NCPN and SCPN monitoring programs (see Evenden and others, 2002; Thomas and others, 2003; Miller and others, 2003). The conceptual framework presented in these earlier documents provides a basis for the material included in this report, but it is not repeated here in detail.

Geographical and Ecological Scope

Given the distribution of parks included in the NCPN and SCPN, the geographic scope of this report extends from northern Utah and southwestern Wyoming southward to north-central Arizona and New Mexico (fig. 1). This region is centered on the Colorado Plateau physiographic province, but the region also includes parts of the Wyoming Basin, the Southern and Central Rocky Mountains, and the Basin and Range physiographic provinces (Hunt, 1974). Park altitudes range from 348 m at the lower end of the Colorado River corridor in the Grand Canyon to 3,247 m at Cedar Breaks National Monument (NM) in southwestern Utah (table 1). Mean annual precipitation (MAP) at National Weather Service Cooperative Network (NWS) stations located in or near NCPN and SCPN parks ranges from 162 mm at Page, Arizona, to 752 mm at Cedar Breaks NM (fig. 1). Because this report focuses on characteristics of dryland ecosystems, it is generally restricted to those areas where MAP is less than 450 mm—the upper limit for piñon–juniper vegetation (pygmy woodlands and forests dominated by *Pinus edulis* and *Juniperus osteosperma*) at Mesa Verde National Park (NP; Floyd, Colyer, and others, 2003). With the exception of the dry, high-elevation Gunnison Basin where Curecanti National Recreation Area (NRA) is located, areas receiving less than 450 mm in this region are generally found below 2,100–2,300 m altitude. Approximately 90–95 percent of NCPN park lands and 85–90 percent of SCPN park lands fall below these precipitation and altitude zones (estimated from data presented by Evenden and others, 2002, and Thomas and others, 2003). [See reports by Evenden and others (2002) and Thomas and others (2003) for additional park-specific information.] Dryland ecosystems within the scope of this report are characterized by mixtures of pygmy conifers (*Juniperus* and *Pinus* spp.), shrubs, dwarf shrubs, herbaceous plants, and biological soil crusts. Excluded from this report are montane shrublands (or "petran chaparral") and forests that are typically above the piñon–juniper zone.

Piñon-Juniper woodland in Mesa Verde National Park, Colorado. Photograph by Mark Miller, USGS.

Characteristics and dynamics of these systems are addressed in a separate report (Vankat, 2004).

Across the geographic region included in the report, there is tremendous diversity in the composition, structure, and functioning of dryland ecosystems. This diversity is attributable to regional- and local-scale variations in climate, landforms, soils, and land use history. Variations in biogeographic history are reflected in the fact that the region also encompasses several distinct floristic areas (McLaughlin, 1986, 1989). As a consequence of these factors, SCPN and NCPN parks are found in seven broadly defined ecoregions (table 1, fig. 2).

Numerous schemes have been used to classify plant communities, ecosystems, and ecological land units of the region (for example, Küchler, 1964; Brown, 1982; Dick-Peddie, 1993; Spence and others, 1995; Creque and others, 1999; NatureServe, 2003; Comer and others, 2003). These schemes are based on various combinations of floristic, physiognomic, edaphic, topographic, and climatic parameters (Spence and others, 1995; Comer and others, 2003). Because this report focuses on ecosystem structure and function, it adopts a functional approach that generally corresponds with physiognomy rather than a particular classification scheme. On the basis of conceptual models presented below, this report concludes by offering recommendations concerning the type of classification best suited for the design of long-term monitoring in drylands.

Structure and Functional Relationships

This section begins with a brief overview of the ecosystem framework adopted by the SCPN and NCPN. Following this overview, a general conceptual model and literature review are presented to characterize important functional relationships among biotic and abiotic components of dryland ecosystems.

Background: The Jenny–Chapin Model of Ecosystem Sustainability

Jenny (1941, 1980) proposed that soil and ecosystem processes are determined by five *state factors*—climate, organisms, relief (topography), parent material, and time since disturbance. Jenny's state-factor approach has been widely applied as a framework for examining temporal and spatial variations in ecosystem structure and function (for example, Walker and Chapin, 1987; Vitousek, 1994b; Seastedt, 2001). Chapin and others (1996) recently extended this framework to develop a set of ecological principles concerning *ecosystem sustainability*. They defined "...a sustainable ecosystem as one that, over the normal cycle of disturbance events, maintains its characteristic diversity of major functional groups, productivity, and rates of

Legend:
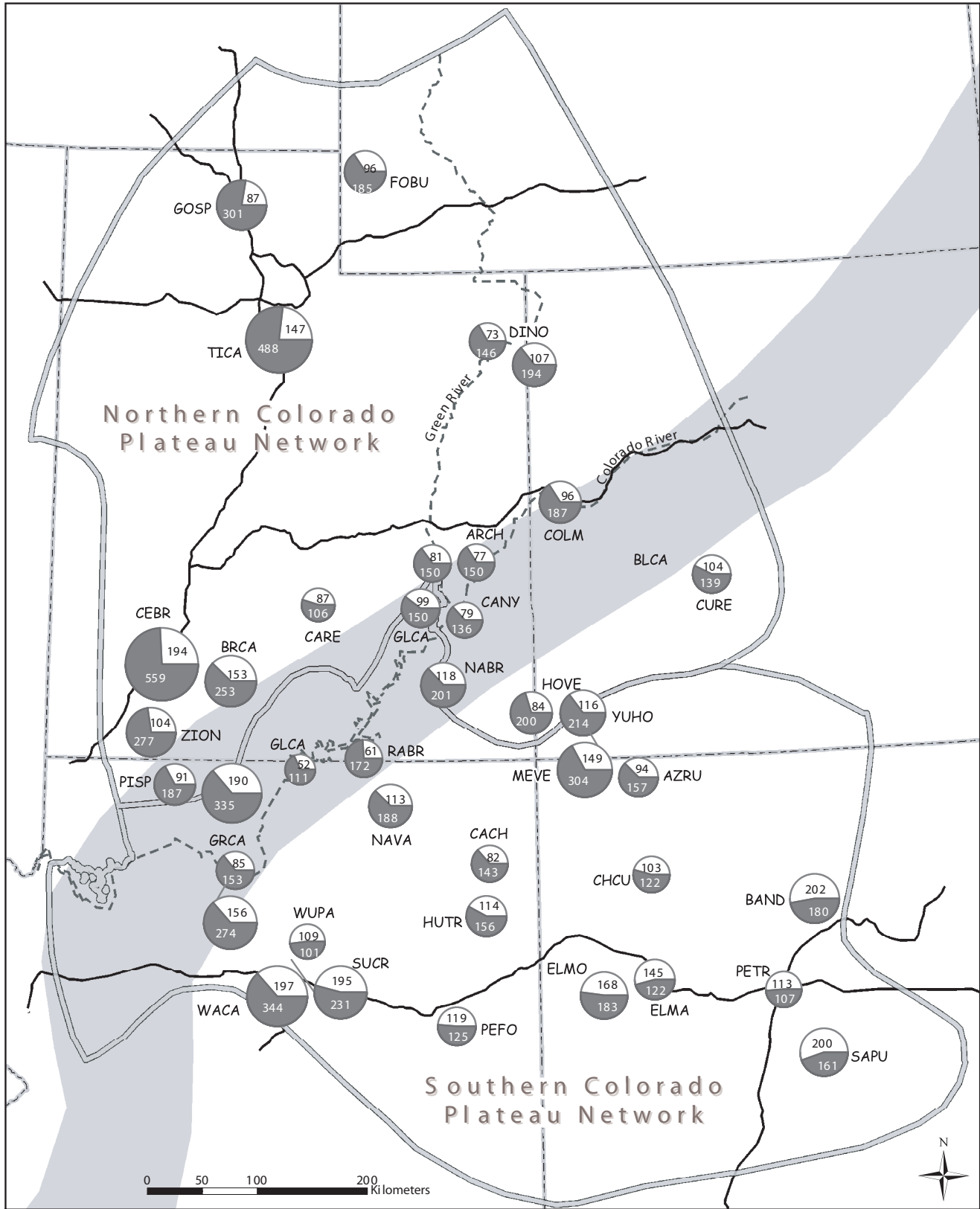
103 — Mean June to September Precipitation (mm)

122 — Mean October to May Precipitation (mm)

Symbol size scaled to indicate Mean Annual Precipitation

Interstate Highway

State Boundary

River

Monsoon Northern Boundary

Network Boundary

Figure 1 (facing page). Map showing mean annual precipitation (symbol diameter) and mean seasonal precipitation (symbol segments) for National Weather Service Cooperative Network stations located at or near NPS units of the Southern and Northern Colorado Plateau Networks. Shaded zone approximates the mean northwestern extent of summer monsoon moisture (from Mitchell, 1976). Precipitation data were acquired from the Western Regional Climate Center (see *http://www.wrcc.dri.edu/climsum.html*). See table 1 for key to four-letter park codes.

biogeochemical cycling" (Chapin and others, 1996, p. 1016). These ecosystem characteristics are determined by a set of four *interactive controls*—climate, soil-resource supply, major functional groups[3] of organisms, and disturbance regime—and these interactive controls both govern and respond to ecosystem attributes. Interactive controls are constrained by the five state factors, which determine the *constraints of place* (Dale and others, 2000). The SCPN and NCPN have adopted a modified version of the Jenny–Chapin model as a general ecosystem framework for guiding the development of additional conceptual models, the consideration and selection of vital signs, and the design of long-term monitoring (fig. 3).

For long-term monitoring associated with goals of sustaining the *health*[4] or *integrity*[5] of ecosystems, a key aspect of the Jenny–Chapin model is the associated hypothesis that interactive controls must be conserved for an ecosystem to be sustained. Large changes in any of the four interactive controls are predicted to result in a new ecosystem with different characteristics than the original system (Chapin and others, 1996). For example, major changes in soil resources (for example, through erosion or other mechanisms) can greatly affect productivity, recruitment opportunities, and competitive relationships of plants, and thus can cause significant change to the structure and functioning of plant communities and higher trophic levels. Changes in vegetation structure can affect the ecosystem's disturbance regime through altered fuel characteristics. These factors and processes in combination can result in an altered system which is fundamentally different from the original system in terms of structure, functioning, and dynamics.

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[3] *Functional groups* are groups of species that have similar effects on ecosystem processes (Chapin and others, 1996). This concept is generally synonymous with *functional types*.

[4] *Ecosystem health* is a metaphor pertaining to the assessment and monitoring of ecosystem structure, function, and resilience in relation to the notion of ecosystem *sustainability* (following Rapport, 1998, and Costanza and others, 1998). A healthy ecosystem is sustainable.

[5] *Ecological integrity* is a concept that expresses the degree to which the physical, chemical, and biological components (including composition, structure, and process) of an ecosystem and their relationships are present, functioning, and capable of self-renewal. Ecological integrity implies the presence of appropriate species, populations and communities and the occurrence of ecological processes at appropriate rates and scales as well as the environmental conditions that support these taxa and processes (*http://science.nature.nps.gov/im/monitor/Glossary.htm*).

General Model

Expanding on the framework of the Jenny–Chapin model, figure 4 serves as a general conceptual model describing structural components and functional relationships that characterize dryland ecosystems. Climatic and atmospheric conditions, soil resources, major functional groups, and disturbance regimes characteristic of dryland ecosystems are reviewed in this section. (Appendix table A provides a tabular supplement to fig. 4.)

Regional Climatic and Atmospheric Conditions

Precipitation Regime

Precipitation regime is the most important climatic factor defining the characteristics of dryland ecosystems because of the importance of precipitation inputs for driving water-limited ecological processes such as primary production, nutrient cycling, and plant reproduction (Noy-Meir, 1973; Comstock and Ehleringer, 1992; Whitford, 2002). Precipitation seasonality (that is, timing in relation to the annual cycle of potential evapotranspiration) and form (that is, snow versus rain) are particularly important attributes because they strongly control the partitioning of precipitation among various compartments of the hydrologic budget—evaporation, transpiration, runoff, drainage, and soil-water storage. Because of their effects on hydrologic partitioning, precipitation seasonality and form are major determinants of ecosystem dominance by different vegetative life forms and functional groups (Comstock and Ehleringer, 1992).

In the area encompassed by this report, precipitation seasonality varies regionally due to the influence of the Arizona monsoon (Mitchell, 1976; Peterson, 1994). The Arizona monsoon (also referred to as the "southwest monsoon" or the "Mexican monsoon") is recognized by climatologists as the northernmost part of an extensive summer monsoon region that extends to central Mexico and the western slopes of the Sierra Madre Occidental (Higgins and others, 1998). Areas affected by monsoon circulation receive greater amounts of summer precipitation from moist air masses derived from the Gulfs of Mexico and California. Notably, the mean northwestern extent of summer monsoon moisture is approximated by a band which cuts across the Colorado Plateau (fig. 1). Areas that are well northwest of this band are dominated by cool-season precipitation (for example, Golden Spike National Historic Site, Timpanogos Cave NM, and Fossil Butte NM), whereas areas that are southeast of this band (for example, Bandelier NM, El Malpais NM, and Salinas Pueblo Missions NM) receive higher amounts of summer monsoon precipitation from convective thunderstorms. Areas close to the band are generally characterized by a bimodal precipitation regime, with summer monsoon precipitation that is highly variable from year to year.

Ehleringer and others (1999) hypothesized that effects of global change on atmospheric circulation patterns and precipitation may be seen relatively early in the Colorado Plateau region because of the presence of this significant climatic
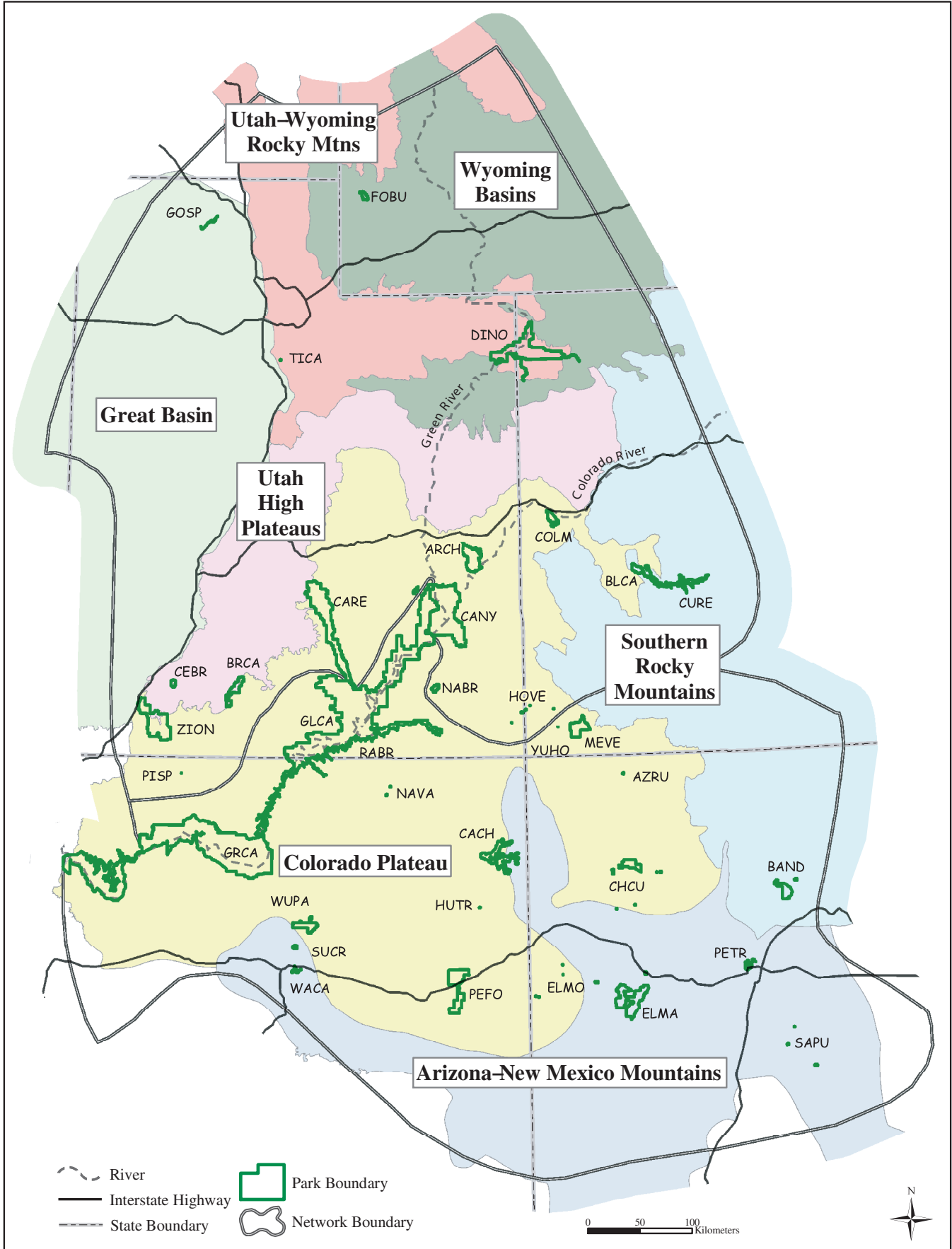
Utah–Wyoming Rocky Mtns

Wyoming Basins

FOBU

GOSP

Great Basin

TICA

DINO

Green River

Colorado River

Utah High Plateaus

ARCH

COLM

BLCA

CURE

CARE

CANY

Southern Rocky Mountains

CEBR   BRCA

NABR

HOVE

ZION

GLCA

MEVE

RABR

YUHO

AZRU

PISP

NAVA

CACH

GRCA   Colorado Plateau

BAND

CHCU

WUPA

HUTR

SUCR

PETR

WACA

PEFO   ELMO

ELMA

SAPU

Arizona–New Mexico Mountains

River

Park Boundary

Interstate Highway

State Boundary

Network Boundary

0   50   100
Kilometers

N

boundary. In an analysis of regional precipitation trends for the central Colorado Plateau, Spence (2001) found that there has been a weak trend towards increasing winter precipitation but no evidence for significant changes in monsoon precipitation patterns since the 1960's. Annual minimum temperatures were found to have increased significantly across the region during the same time period (Spence, 2001).

Regional precipitation patterns are affected by global-scale fluctuations in sea-surface temperatures, atmospheric pressure, and atmospheric circulation patterns that vary at two different time scales (Hereford and others, 2002). Short-term interannual variations in precipitation are related in part to the occurrence of El Niño and La Niña conditions—the two contrasting phases of the El Niño–Southern Oscillation (ENSO) phenomenon that is driven by variations in sea-surface temperatures (SSTs) in the eastern tropical Pacific Ocean (Hereford and Webb, 1992; Cayan and others, 1999; Hereford and others, 2002). Hereford and others (2002) recently reported their analyses of 20th century precipitation patterns on the Colorado Plateau in relation to ENSO phases. They found that the detailed relationships were complex, but that strong El Niño episodes generally increased the variability of warm-season precipitation or the frequency of above-normal cool-season precipitation. In contrast, strong La Niña episodes tended to cause normal, low-variability warm-season precipitation and below-normal cool-season precipitation. Whether characterized by dry or wet conditions, extreme years can have long-lasting consequences for ecosystem structure and functioning by causing episodes of plant mortality or establishment (Ehleringer and others, 1999).

Over decadal-scale time periods, spatial and temporal patterns in precipitation across the conterminous United States are related to phenomena known as the Pacific Decadal Oscillation (PDO) and the Atlantic Multidecadal Oscillation (AMO; Mantua and Hare, 2002; McCabe and others, 2004). The AMO is an index of SST variations over the North Atlantic Ocean, whereas the PDO reflects SST variations over the North Pacific Ocean (Mantua and Hare, 2002; McCabe and others, 2004). The PDO and AMO are quasiperiodic and may be caused by internal variations in oceanic circulation patterns and associated patterns of heat transport (McCabe and others, 2004). In their analyses of 20th-century data, McCabe and others (2004) found that 52 percent of the spatial and temporal variance in multidecadal drought frequency across the conterminous United States was attributable to variations in these two SST indices. Hereford and others (2002) analyzed 20th-century precipitation patterns on the Colorado Plateau and found evidence for three relatively distinct precipitation regimes that appeared to be in phase with the PDO. The first

of these was a period of relatively wet conditions from 1905 to 1941. Notably, the onset of this wet period corresponds well with the pulse of ponderosa pine establishment that was documented throughout much of the Southwest during the first decades of this century (Cooper, 1960; Savage, 1991). Following this wet period, two other distinctly recognizable precipitation regimes occurred from 1942 to 1977 (dry) and from 1978 to 1998 (wet). The marked shift to dry conditions that began in 1999 and continues through the present suggests a transition to the dry PDO phase that could continue for the next 2–3 decades (Hereford and others, 2002). This has important implications for ecosystem management and monitoring in the region due to the effects of precipitation patterns on disturbance regimes (Swetnam and Betancourt, 1998) and on the capacity of ecosystems to resist or recover from natural disturbances and human land use activities (Ehleringer and others, 1999; Whitford, 2002).

In addition to temporal variability, spatial variability is another defining attribute of dryland precipitation regimes (Noy-Meir, 1973; Whitford, 2002). Topography and storm type are two factors that control spatial variability in precipitation. On a local scale, precipitation tends to increase with increasing elevation due to orographic effects of topography (precipitation caused by adiabatic cooling of rising air masses), but rain shadows also can develop on the lee side of massive topographic features. Such rain-shadow effects can produce high-elevation zones of aridity like the Gunnison Basin in western Colorado. As for storm type, summer precipitation derived from convective thunderstorms is characterized by greater spatial variability than winter precipitation from frontal storms (Noy-Meir, 1973; Whitford, 2002).

The size of precipitation events also is an important attribute of dryland precipitation regimes (Noy-Meir, 1973; Sala and Lauenroth, 1982; Lauenroth and Sala, 1992; Ehleringer and others, 1999; Whitford, 2002; Austin and others, 2004; Loik and others, 2004). Event size and timing (seasonal, diurnal, and in relation to antecedent environmental conditions) in combination are important for determining ecological responses to precipitation due to effects on hydrologic partitioning. A significant characteristic of dryland precipitation regimes is the predominance of small events (for example, see fig. 5). Depending on environmental conditions, small events (< 5 mm) may trigger soil-surface processes such as nutrient mineralization/volatilization, whereas larger events may be required to initiate seed germination, plant physiological processes such as photosynthesis, and hydrologic processes such as soil-water recharge (Ehleringer and others, 1999). The capacity to respond to precipitation events of different sizes and timing is an important ecophysiological characteristic of plants that determines their ability to persist under particular precipitation regimes (Sala and Lauenroth, 1982; Ehleringer and others, 1999).

Precipitation intensity (amount per unit time period) also affects hydrologic partitioning of precipitation. Precipitation intensity, soil characteristics (for example, texture and antecedent moisture conditions), and soil-surface features (for
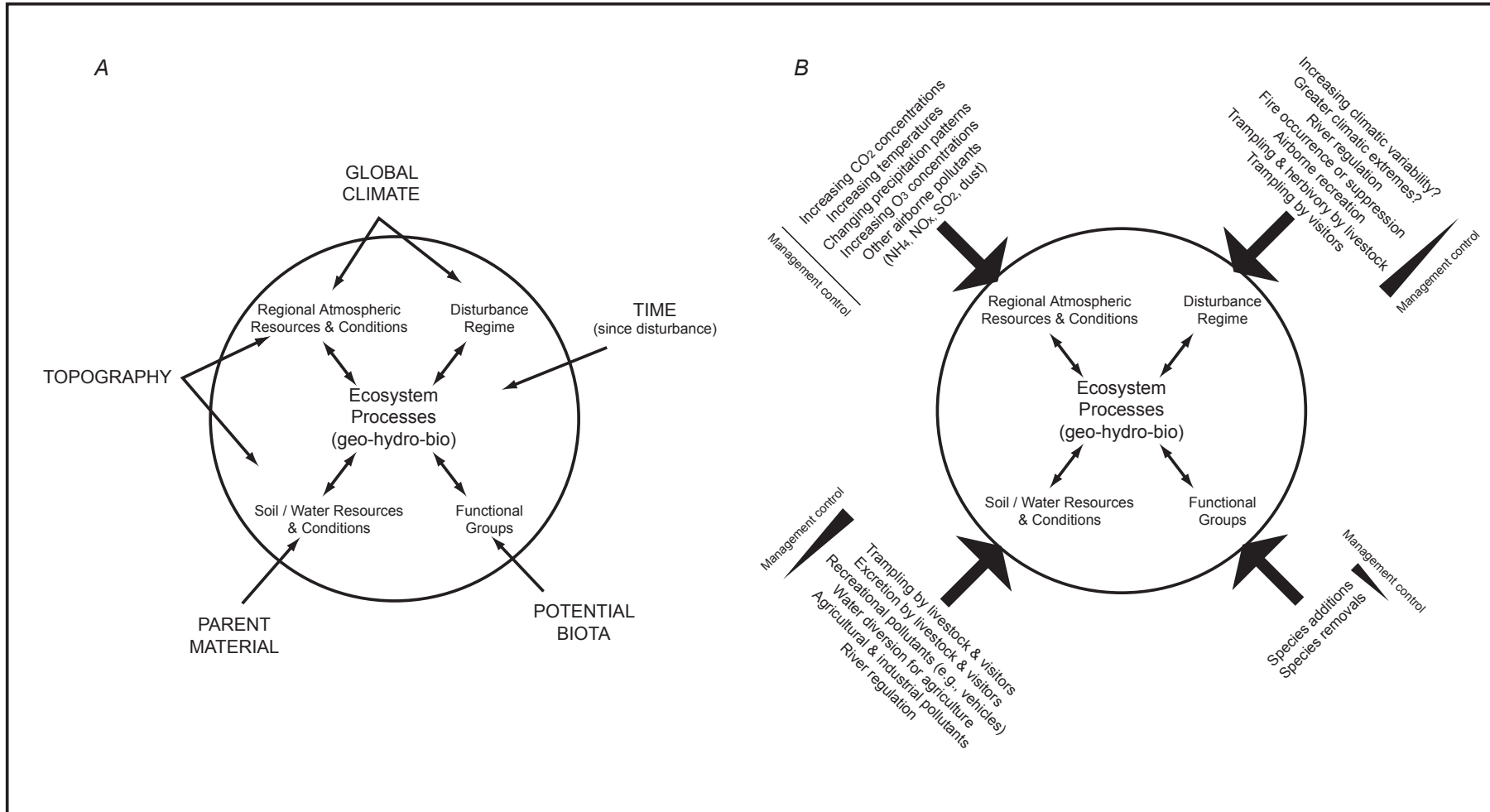
Figure 3. Modified version (*A*) of the Jenny-Chapin model that serves as the general ecosystem model for the SCPN and NCPN (redrawn with permission from *The American Naturalist* and The University of Chicago Press; Chapin and others, 1996) and (*B*) the array of stressors affecting SCPN/NCPN ecosystems arranged in the model in relation to their first-order effects. Complex, higher order effects occur as the four major controls interact via ecosystem processes. The circle represents the boundary of the ecosystem.
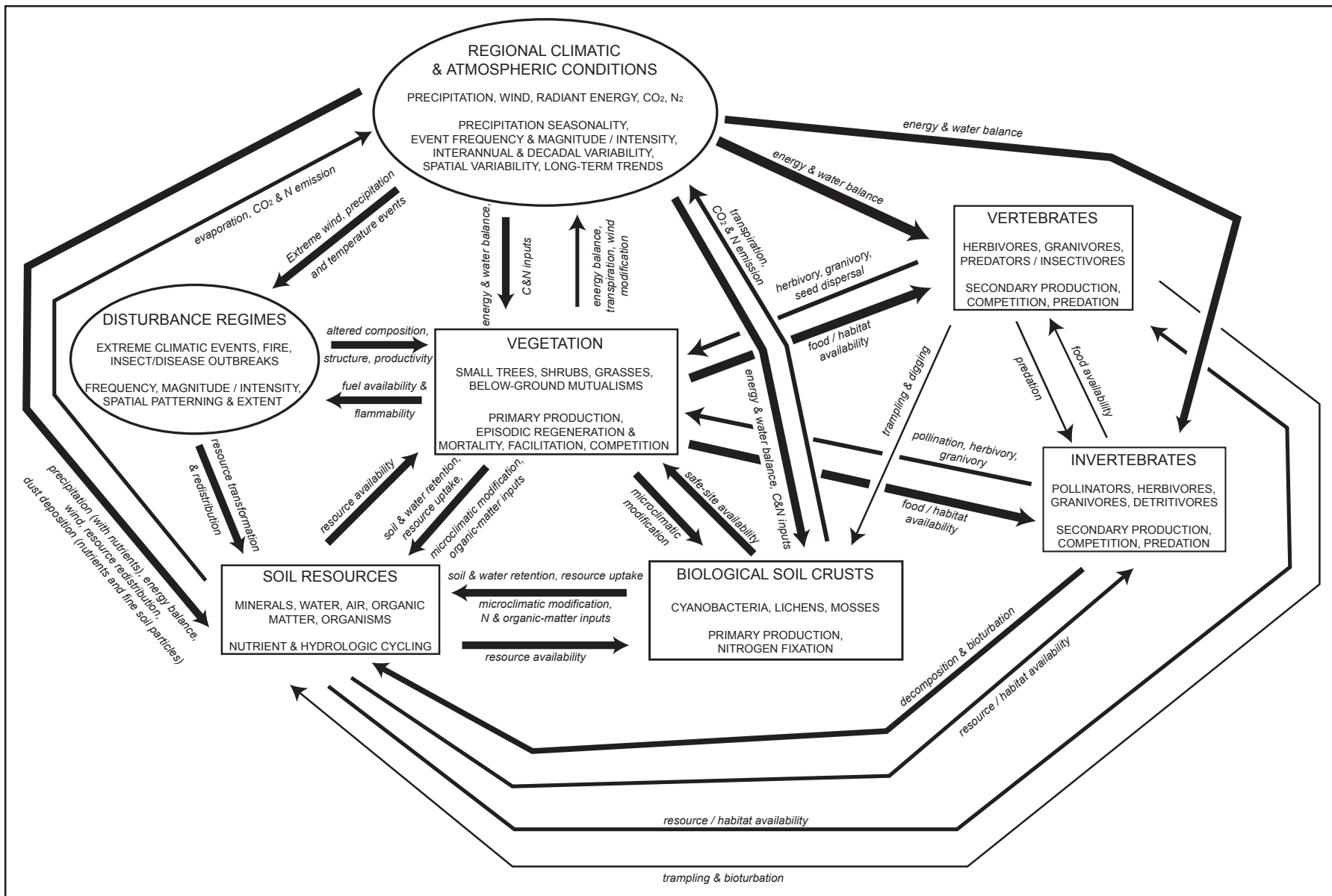
Figure 4. General conceptual model depicting the structure and functioning of dryland ecosystems. Ovals indicate major drivers of ecosystem change and temporal variability, as well as important attributes of drivers. Boxes indicate major structural components and important processes. Arrows indicate functional relationships among components, and line weights indicate relative importance of relationships. The model is constrained by global climatic and atmospheric conditions, topography, parent material, potential biota, and time.

USGS meteorological station established to monitor climate (temperature, precipitation, wind direction and strength) and geologic processes (erosion and deposition) for studies of land use and landscape change on the Colorado Plateau (USGS Earth Surface Dynamics Program, *http://climweb.cr.usgs.gov/info/sw/clim-met/*). San Juan County, Utah. Photograph by Rich Reynolds, USGS.

Summer rainstorm on the Colorado Plateau, Grand County, Utah. Photograph by Brad Wilcox, Texas A&M University.

example, soil-surface roughness; amount, type, and distribution of ground cover) together determine whether precipitation events result in infiltration or runoff (Whitford, 2002; Breshears and others, 2003). If precipitation intensity exceeds the soil infiltration rate, runoff will be generated—increasing the potential for soil erosion. In the Colorado Plateau region, precipitation intensity tends to increase with increasing elevation and decreasing latitude (fig. 6), because these variables together generally indicate relative exposure to high-intensity convective thunderstorms. Results of regression analyses indicate that about two-thirds of the variation in precipitation intensity[6] across the region can be explained by elevation and latitude ($F = 2, 29$; $R^2 = 0.66$, $p < 0.001$).

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[6] The intensity measure used in this analysis was the estimated maximum intensity of precipitation (mm/hr) expected to occur over a 5-minute period with 50 percent probability during any given year at NWS stations located at or near NCPN and SCPN units. Data were acquired in December 2003 from the National Oceanic and Atmospheric Administration's Precipitation Frequency Data Server (http://hdsc.nws.noaa.gov/hdsc/pfds/).

Studies conducted in some dryland ecosystems have found time lags in the response of above-ground net primary production (ANPP) to interannual variations in precipitation (Lauenroth and Sala, 1992; Oesterheld and others, 2001; Wiegand and others, 2004). For example, analyses of a 52-year-long data set from a short-grass steppe ecosystem in Colorado found that only 39 percent of the interannual variation in ANPP could be explained by current-year precipitation (Lauenroth and Sala, 1992). The best model, which accounted for 60 percent of ANPP variability, included precipitation from the current year *and* from the two previous years (Oesterheld and others, 2001). Due to this lag or carryover effect, ANPP fluctuations are buffered if wet and dry years alternate but amplified if multi-year sequences of dry and wet years occur (Oesterheld and others, 2001; Wiegand and others, 2004). Preliminary analyses of vegetation-monitoring data from Canyonlands NP suggest that production-precipitation lags also may occur in Colorado Plateau systems (J. Belnap, unpub. data, 2005).
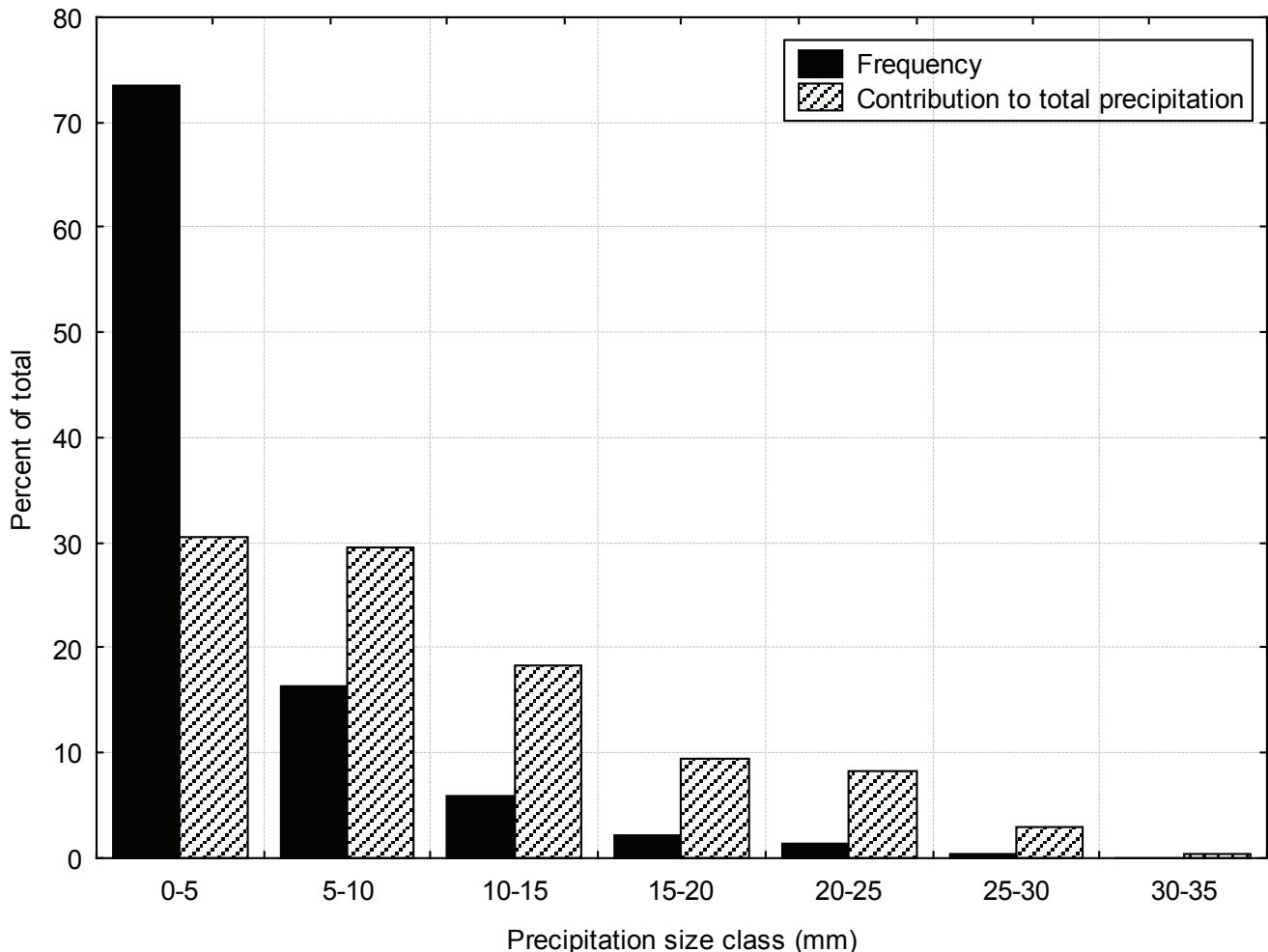
Figure 5. Distribution of precipitation events (based on daily values) by size class at the Needles District of Canyonlands National Park, 1965-1998.

Legend:

Precipitation Intensity Estimate, mm/hr

- Station, No Data
- 35.1 - 40.0
- 40.1 - 45.0
- 45.1 - 50.0
- 50.1 - 55.0
- 55.1 - 60.0
- 60.1 - 65.0
- 65.1 - 80.0
- 80.1 - 90.0

Map labels: FOBU, GOSP, TICA, DINO, Green River, Colorado River, COLM, ARCH, BLCA, CURE, CANY, CARE, GLCA, CEBR, BRCA, NABR, ZION, HOVE, MEVE, YUHO, GLCA, RABR, AZRU, PISP, NAVA, GRCA, CACH, CHCU, BAND, HUTR, WUPA, SUCR, ELMO, PETR, WACA, ELMA, PEFO, SAPU

Northern Colorado Plateau Network

Southern Colorado Plateau Network

N

0   50   100   200 Kilometers

—— Interstate Highway   Monsoon Northern Boundary

– – – State Boundary   Network Boundary

– ·· – River

Figure 6 (facing page).   Map depicting regional variations in the estimated maximum intensity of precipitation (mm/hr) that can be expected to occur over a 5-min period with 50 percent probability during any given year at NWS stations located at or near NCPN and SCPN units. Shaded zone approximates the mean northwestern extent of summer monsoon moisture (from Mitchell, 1976). Data were acquired from NOAA's Precipitation Frequency Data Server (see *http://hdsc.nws.noaa.gov/hdsc/pfds/*). See table 1 for key to four-letter park codes.

Wind

Wind is another atmospheric phenomenon that can have important effects on the structure and functioning of dryland ecosystems. As a driver of near-surface air circulation, wind strongly affects evapotranspiration rates and thus can modify the energy and water balances of plants and soils (Larcher, 1995). Like precipitation, wind also is an important force driving the redistribution of soil resources both within and among ecosystems (Whicker and others, 2002). In a recent comparison of wind- and water-driven erosion (off-site redistribution of soil resources) and horizontal transport (within-site redistribution of soil resources) in dryland ecosystems, Breshears and others (2003) estimated that wind erosion exceeded water erosion by about 33 times at a shrubland site and by about five times at a forest site. At a grassland site, the authors estimated that water erosion was about three times greater than wind erosion. Horizontal transport by wind was greater than that by water in all three systems, including a 2,200-fold difference in the shrubland. Soil texture, vegetation structure, and ground cover were important variables affecting among-site differences in the relative importance of wind and water erosion and transport. The frequency-intensity distributions of process-driving wind and precipitation events are climatic factors that also affect the importance of wind versus water erosion and transport on particular sites (Breshears and others, 2003). Finally, wind also interacts with topography to influence fire behavior and is a major factor determining whether a wildfire can be contained or whether it will spread explosively across the landscape (see Peters and others, 2004).

Soil Resources

Inherent Edaphic Heterogeneity

Soil resources, including mineral nutrients, organic matter (including litter), water, and soil biota, are fundamental determinants of ecosystem structure and function (Jenny, 1980; Vitousek, 1994b; Reynolds and others, 2003). A characteristic feature of soils in the Colorado Plateau region is tremendous spatial heterogeneity attributable to combined effects of geology, topography, and geomorphic processes (Brotherson and others, 1985; Norton and others, 2003). Due to low rates of weathering and pedogenic processes in dryland environments, the relative importance of parent material as

a factor determining soil properties generally increases with aridity (Jenny, 1941). Geologic and climatic features of Colorado Plateau drylands have produced weakly developed soils with physical and chemical characteristics that closely match the shales, sandstones, limestones, and igneous materials from which they were derived. Geomorphic processes, such as erosion and deposition, have built upon this geologic template to generate abrupt or gradational juxtapositions of landforms and soils differentiated on the basis of soil depth, particle-size distributions, mineralogy, and degree of profile development (Schimel and others, 1985; Daniels and Hammer, 1992; Birkeland, 1999; Norton and others, 2003). Effects of human activities (Amundson and Jenny, 1991) and aeolian dust inputs (Reynolds and others, 2001) are superimposed on this mosaic. Whereas disturbances such as fire often are the primary factors responsible for generating landscape patterns in comparatively mesic environments (Clark, 1991), inherent edaphic heterogeneity is a primary cause of landscape patterns in dryland parts of the Colorado Plateau region.

Soil Functions and Soil Quality

Soils perform several ecological functions pertinent to ecosystem management and monitoring. Soils regulate hydrologic processes and the cycling of mineral nutrients. As a medium for storage and delivery of water and nutrients, soils also sustain the existence and productivity of plant and animal populations. The capacity of a specific kind of soil to perform these functions is described by the concept of *soil quality* (Karlen and others, 1997; Herrick and others, 2002; Norfleet and others, 2003). Soil quality and soil functioning are determined by relatively static soil properties, such as texture, depth, and mineralogy, and by relatively dynamic soil properties, such as organic-matter content, aggregate stability, soil-surface roughness, and structure (Seybold and others, 1999). Compared with soil properties that are relatively static over management time frames, dynamic soil properties are more subject to change under the influence of climatic fluctuations, land use activities, natural disturbances, and management actions. But even soil properties such as depth and texture can change as a consequence of erosion (Neff and others, 2005).

Within a given climatic region, soil is the most important factor affecting the structure of terrestrial ecosystems because of its role in mediating the bioavailability of water and mineral nutrients (Whitford, 2002). This is particularly true of dryland ecosystems because small differences in soil physical and chemical traits can have relatively large effects on water and nutrient bioavailability (Comstock and Ehleringer, 1992; McAuliffe, 2003).

Resource Limitations

In general, water has been described as the soil resource that most commonly limits the productivity of dryland ecosystems (Noy-Meir, 1973; Ehleringer and others, 1999). But there is increasing recognition that nutrients also can limit

Wind-driven erosion of unstable soils. San Juan County, Utah. Photograph by Jason Neff, USGS.

dryland productivity, particularly during periods when water is abundant relative to evapotranspirational demands (Havstad and others, 2000; Archer and Bowman, 2002; Whitford, 2002; James and others, 2005). Water and nutrient uptake are not independent (Barber, 1995; Marschner, 1995), and Chapin (1991) has argued that the effects of low soil moisture on nutrient availability to plants may be as significant as the direct effects of water stress on plant performance. Following a review of fertilization experiments in dryland ecosystems, Hooper and Johnson (1999) concluded that there was no evidence for a shift from water to nutrient limitation along a geographic gradient of increasing water availability. Instead, their review supported the hypothesis that water and nitrogen (N) generally are co-limiting in dryland ecosystems. In addition to N, field studies on the Colorado Plateau suggest important roles for phosphorus (Miller and others, 2001; J.C. Neff, unpublished data, 2005) and potassium (Belnap and Phillips, 2001) in structuring dryland ecosystems of the region.

The retention of water and nutrient resources is essential for sustaining the structure and functioning of dryland ecosystems (Ludwig and Tongway, 1997, 2000; Whitford, 2002). Dynamic soil properties important for water and nutrient retention include soil structure, infiltration capacity, soil-surface roughness, organic-matter content, soil aggregate stability, and soil biotic activity (Herrick and others, 2002). Other ecosystem components that promote the capture and retention of soil resources include vegetation, biological soil crusts, and other soil-stabilizing features such as litter and rocks (Warren, 2003; Whitford, 2002).

Plant-Soil Feedbacks

Coupled spatial patterning of vegetation and soil resources is a common characteristic of dryland ecosystems because of strong interactions between plants and soils (Charley and West, 1975; Schlesinger and others, 1990, 1996). Vegetation affects the spatial distribution of soil resources because of processes such as nutrient uptake, above- and below-ground litter deposition, and microclimatic modification, as well as vegetation interactions with hydrologic processes and

Oblique aerial photograph of the Escalante River drainage in Grand Staircase-Escalante National Monument showing heterogeneous patterns of soil and vegetation attributable to effects of geology, topography, and geomorphic processes. Garfield County, Utah. BLM aerial photograph.

water- and wind-driven erosional processes (Whitford, 2002). Vegetation patterns in turn are strongly influenced by spatial patterns of resource availability, resulting in a classic positive-feedback relationship (Aguiar and Sala, 1999). Because the spatial patterning of soil resources is so closely linked with several important biotic and abiotic processes, changes in resource distributions both within (canopy vs. interspace) and among ecosystems can indicate significant changes in ecosystem functioning (Ludwig and Tongway, 1997, 2000). Some workers have suggested that indices of soil-resource patterning may prove useful as early warning indicators of ecosystem degradation in dryland environments (Herrick and Whitford, 1995; Havstad and others, 2000).

Major Functional Groups

Background

Chapin and others (1996) identified biotic functional groups (hereafter described as *functional types*) as one of the four interactive controls of ecosystem sustainability because of the capacity of dominant functional types to shape the structure and functioning of whole ecosystems. Associated with efforts to model ecological consequences of global change, a vast literature has developed concerning different approaches to deriving or classifying functional types—particularly with respect to vegetation (for example, Smith and others, 1997). Identification and use of a particular functional-type scheme

depend on the level or scale of analysis and on the function(s) of interest. For example, within a taxonomic group such as nematodes, different functional types may be identified on the basis of feeding preferences (Coleman and Crossley, 1996). The emphasis in this report is on broadly defined ecosystem-level functional types. Several workers have proposed that the most important functions in dryland ecosystems are those that control the retention of water and nutrient resources because productivity and diversity cannot be sustained in systems that fail to retain resources (Ludwig and Tongway, 1997; Whisenant, 1999; Whitford, 2002). Functions affecting the cycling and retention of water and nutrient resources will be emphasized here, but other functions will not be excluded. For purposes of this report, it is less important to adopt a specific functional-type classification scheme than it is to take a broad functional perspective when considering the biotic components of dryland ecosystems.

Without adopting a particular classification scheme, it remains useful to identify two general categories of functional types that are equally important for ecosystem dynamics. These are (1) *functional effect types*—organisms with similar effects on ecosystem functions such as primary production, nutrient cycling, and soil stabilization, and (2) *functional response types*—organisms with similar responses to environmental factors such as climate, resource availability, natural disturbances, and land use activities (Walker, 1997; Walker and others, 1999; Díaz and Cabido, 2001; Díaz and others, 2002). The distinction between these two types is important for considering how biotic composition affects the resistance and resilience[7] of ecosystems to climatic fluctuations and changes, natural disturbances, and anthropogenic stressors (Walker and others, 1999). *Redundancy* among organisms in terms of their *effects* on ecosystem processes, and *diversity* among organisms in terms of their *responses* to environmental factors, both can contribute to the buffering of ecosystem functioning in relation to changing environmental conditions (Díaz and Cabido, 2001). Although some workers have emphasized the importance of overall functional diversity for sustaining ecosystem processes (Tilman and others, 1997), the functional effect-response distinction suggests that the long-term persistence of ecosystem functioning may be most likely when different functional response types are nested within the same functional effect type (Walker and others, 1999; Díaz and Cabido, 2001). Detailed consideration of functional effect types and functional response types probably is most useful to ecosystem managers when applied on a relatively site- or system-specific basis. Because of the generality of this report,

the functional effect-response distinction is not carried forth through the following discussion of biotic functional types.

Vegetation

Broadly speaking, vegetation generally is recognized as *the* dominant functional type in terrestrial ecosystems. In addition to conducting photosynthesis, above-ground structures of vascular plants protect soils from erosive raindrops, obstruct erosive wind and overland water flow, and enhance the capture and retention of soil resources. Litter from plants further reduces the erosive impacts of rainfall on soil surfaces and provides inputs to soil organic matter for soil stabilization and nutrient cycling. Plants and litter intercept solar radiation and precipitation, thereby mediating spatial and temporal patterns of soil water content and temperature (Breshears and others, 1997), and strongly affecting soil-resource conditions experienced by other organisms. Roots stabilize soils, are conduits for resource acquisition and redistribution, and provide organic-matter inputs to soil food webs. Vegetation also provides fuel for fire, as well as resources and habitat structure for below-ground and above-ground organisms ranging from fungi and bacteria to birds and large mammals (Whitford, 2002; Wardle, 2002). Finally, carbon storage and the mediation of earth-atmosphere energy/water balances are additional vegetation functions that are increasingly emphasized by researchers investigating global-change processes (Breshears and Allen, 2002; Asner and others, 2003).

A large number of vegetation attributes affects the manner and extent to which these many functions are performed. Size, biomass, photosynthetic rate, relative and absolute growth rates, tissue chemistry, basal cover, canopy cover, canopy structure, spatial arrangement and contiguity, leaf area, leaf longevity, and life span are some of the more important vegetation attributes for ecosystem functioning (Chapin, 1993). Root distribution, photosynthetic pathway, and phenology are additional functional attributes of vegetation that are particularly important in dryland ecosystems (Ehleringer and others, 1999; Whitford, 2002). With respect to disturbance interactions, important functional attributes include palatability, flammability, and mode of post-disturbance regeneration.

Small trees, shrubs, dwarf shrubs, and perennial grasses are the vegetative life forms with the greatest effects on the structure and functioning of dryland ecosystems (Whitford, 2002). In some dryland systems, annual grasses (typically exotic) also can have significant effects on ecosystem structure and function (for example, Billings, 1990; Belnap and Phillips, 2001; Evans and others, 2001). The two most important tree genera in drylands of this region are *Juniperus* and *Pinus*. Important genera of shrubs and dwarf shrubs include members of the Asteraceae (*Artemisia, Chrysothamnus, Ericameria, Gutierrezia, Tetradymia*, and *Xylorhiza*), the Chenopodiaceae (*Atriplex, Grayia, Sarcobatus,* and *Krascheninnikovia*), the Rosaceae (*Cercocarpus, Purshia, Coleogyne*, and *Fallugia*), the Fagaceae (*Quercus*), and the Ephedraceae (*Ephedra*). Important genera of perennial grasses include those

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[7] *Resistance* refers to the capacity of a particular ecosystem attribute or process to remain essentially unchanged from its reference state or dynamic despite exposure to a disturbance and/or stressor. *Resilience* refers to the capacity of a particular ecosystem attribute or process to recover to its former reference state or dynamic after exposure to a temporary disturbance and/or stressor (adapted from Grimm and Wissel, 1997). *Resistance* and *resilience* are dynamic properties that vary in relation to environmental conditions (Scheffer and others, 2001).

characterized by the C$_4$ photosynthetic pathway (*Bouteloua, Muhlenbergia, Aristida, Pleuraphis*, and *Sporobolus*) and the C$_3$ photosynthetic pathway (*Acnatherum, Hesperostipa, Poa*, and *Festuca*). In general, the relative importance of C$_3$ versus C$_4$ perennial grasses in dryland ecosystems increases regionally with latitude and locally with elevation. Genera of annual grasses include *Bromus, Festuca*, and *Schismus*.

Many of the functional attributes described above differ greatly among vegetative life forms.[8] For example, there are relatively large differences among dryland trees, shrubs, and perennial grasses in terms of canopy architecture and spatial arrangement, as well as in their responses to climate, fire, and herbivory. As a consequence, ecosystems characterized by different proportions and spatial patterns of trees, shrubs, and grasses can be expected to differ greatly in terms of associated ecosystem processes including nutrient cycles, hydrologic cycles, disturbance regimes, and wildlife-habitat relationships. Likewise, temporal shifts in the relative abundance and spatial configuration of vegetative life forms can significantly affect the functioning of numerous ecosystem processes.

Soil Biota

Soil biota represent another broadly defined group of organisms that is a major contributor to the structure and functioning of dryland ecosystems. Most of the ecosystem processes described above in relation to soil resources (that is, nutrient cycling, water infiltration and storage, soil aggregate stability) are mediated by soil organisms (Skujins, 1984; Whitford, 1996, 2002; Lavelle, 1997; Wardle, 2002). Although the general significance of soil biota for ecosystem processes (particularly nutrient cycling) has long been acknowledged, there is increasing recognition that this diverse group of organisms must be considered much more explicitly in order to develop a better understanding of the structure and functioning of terrestrial ecosystems (Bever and others, 1997; Wardle, 2002; Reynolds and others, 2003). Because of their intimate association with other components of dryland ecosystems, soil biota in figure 4 are included in components identified as soil resources, vegetation, biological soil crusts, and invertebrates.

Wardle (2002) noted that most terrestrial species occur in soil and that the tremendous (and poorly understood) diversity of this group has added to the logistical difficulties posed by studying below-ground organisms and processes. Soil biota include microfloral components (bacteria, algae, and fungi), microfaunal components (nematodes, microarthropods, and protozoans), and macrofaunal components (earthworms, ants, termites, and larval stages of several insect families) that are involved in a variety of processes essential for litter decomposition and nutrient cycling. Functioning of these below-ground processes is dependent on the amounts and types of organic-matter inputs from vegetation and on soil conditions such as moisture availability, soil structure, soil aeration, and soil

temperature (Coleman and Crossley, 1996; Whitford, 1996, 2002; Wardle, 2002).

Soil biota also include mycorrhizal fungi that form symbiotic associations with roots of many plant species. The mycorrhizal symbiosis is one in which the fungal partner provides nutritional benefits to the host plant, and the plant provides carbohydrates to the fungi (Smith and Read, 1997). Roots colonized by mycorrhizal fungi acquire phosphorus, zinc, and possibly copper and N more efficiently than uncolonized roots. There is also evidence that mycorrhizae can increase water uptake in plants due to the greater soil volume accessed by colonized roots (Smith and Read, 1997). Due to their role in enhancing resource availability to colonized plants, mycorrhizae have been found to mediate competitive relations between plants with differing responses to mycorrhizal colonization (Allen and Allen, 1990; Marler and others, 1999). Recent work also has shown that the diversity of mycorrhizal fungi can determine the diversity and productivity of vascular plant communities (van der Heijden and others, 1998).

Some species in most of the plant families common to dryland ecosystems have been identified as mycorrhizal when inspected by botanists (Trappe, 1981). Families with a high frequency of mycorrhizal colonization among inspected species include the Asteraceae, Fabaceae, Rosaceae, Poaceae, and Solanaceae. Frequency of colonization among inspected species in the Chenopodiaceae and Cactaceae is much lower, although mycorrhizal species have been found. The Brassicaceae stands out as a common dryland plant family in which most inspected species are nonmycorrhizal (Trappe, 1981).

Another important symbiotic relationship involving soil biota is that between plants and N-fixing bacteria. Several shrubs that are locally common or abundant throughout the Colorado Plateau region are capable of forming a symbiotic association with N-fixing actinomycetes in the genus *Frankia*. Actinorhizal shrub genera of the region include *Cercocarpus* and *Purshia* (Rosaceae), *Shepherdia* (Elaeagnaceae), and *Ceanothus* (Rhamnaceae; Baker and Schwintzer, 1990; cited by Schwencke and Carú, 2001). The frequency of actual actinorhizal colonization in these genera and the overall contributions of this relationship to dryland N cycling are poorly understood. However, it is significant that all of the actinorhizal shrub genera in the region are important forage resources both for wild herbivores and for domestic livestock, suggesting that the actinorhizal relationship may be a factor affecting forage preferences.

Biological Soil Crusts

Biological soil crusts (BSCs) are biotic communities composed of cyanobacteria, algae, microfungi, mosses, and lichens that occur on and within the upper few millimeters of the soil surface (Belnap, Büdel, and Lange, 2003). These diverse communities are characteristic biotic components of ecosystems where environmental conditions limit the development of closed-canopy vascular plant communities or thick layers of surface litter (Belnap, Büdel, and Lange, 2003). They are particularly prominent features in drylands of the

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[8] There also is significant functional variation *within* each of these life forms that must be considered with respect to the structure and functioning of specific ecosystems on a site-specific basis.

Colorado Plateau vegetation consisting of shrubs (*Artemisia tridentata* and *Krascheninnikovia lanata*), perennial grasses (*Acnatherum hymenoides* and *Hesperostipa comata*), and juniper (*Juniperus osteosperma*). The La Sal Mountains are in the background. San Juan County, Utah. Photograph by Mark Miller, USGS.

Colorado Plateau region where much pioneering work has been conducted concerning their environmental relationships, disturbance responses, and ecological functions (for example, Rosentreter and Belnap, 2003; Belnap, 2002; Bowker and others, 2002).

In addition to their major contributions to biological diversity, BSCs perform several functions in dryland ecosystems. The presence and physiological activity of BSC organisms aggregate soil particles, thereby increasing soil stability and reducing the susceptibility of soil to erosion by wind and water (Williams and others, 1995a,b). Surface characteristics and stability of BSCs also favor the capture and retention of aeolian sediments that can be significant sources of mineral nutrients in dryland ecosystems (Belnap, Prasse, and Harper, 2003; Reynolds and others, 2001). BSCs similarly can capture and enhance ecosystem retention of windborne and waterborne organic matter and seeds (Belnap, Prasse, and Harper, 2003).

Hydrologic effects of BSCs are complex, with few generalizations possible due to variations in relation both to soil factors and BSC factors. [The following synthesis is mostly drawn from the recent review by Warren (2003).] Aboveground structures of BSCs intercept rainfall, thereby reducing raindrop impact and erosivity and reducing the detachment of soil particles that can clog soil pores and inhibit infiltration. In this function, cyanobacteria and algae are less effective than mosses and lichens. Based on available evidence, BSCs on sandy soils (> 80 percent sand content) with inherently high infiltration capacities tend to *reduce* infiltration relative to soils of similar texture without BSCs because BSC organisms block pore spaces near the soil surface. However, adverse effects of BSCs on infiltration in sandy soils may be mitigated by effects of BSCs on soil-surface roughness. In cool-desert regions such as the Colorado Plateau, frost heaving can result in BSCs with pinnacled or rolling soil-surface microtopography (Belnap, 2003a). Where these microtopographic features significantly enhance soil-surface roughness, the velocity of overland flow may be reduced, thereby increasing the residence time of runoff on hillslopes, enhancing slope retention of water and waterborne sediment, and facilitating water infiltration (Belnap, 2003a).

On relatively fine-textured soils, BSC effects on hydrologic processes can differ from those found on sandy soils—although the soil-roughness hypothesis still applies (Warren, 2003). Compared with sandy soils, soils with a significant percentage of clay-size particles are characterized by lower porosity and lower inherent infiltration capacities. Organic carbon produced by BSC organisms can contribute to the formation of stable soil aggregates that increase the ratio of macropores to micropores and thus enhance infiltration. Due to enhanced soil aggregate stability, fine-textured soils with BSCs are likely to

Biological soil crusts fill the interspaces among perennial grasses (*Hesperostipa comata*), shrubs (*Atriplex canescens* and *Ephedra viridis*) and cacti (*Opuntia* sp.) in Canyonlands National Park, San Juan County, Utah. Photograph by USGS.

have higher infiltration rates than soils of similar texture without BSCs. However, in silty soils where a *vesicular A horizon*[9] subtends the BSC layer and controls soil infiltration capacity, the presence of BSC organisms is unlikely to enhance infiltration except through the hypothesized soil-roughness effect (for example, Dobrowolski, 1994).

In addition to enhancing soil stability and the retention of nutrients in sediment and organic matter, BSCs contribute to dryland nutrient cycles in other ways. Mosses, cyanobacteria, green algae, and lichens all are photosynthetic and thus are significant sources of carbon in dryland ecosystems, particularly in interspaces among vascular plants where soil crusts can attain 100 percent cover (Lange, 2003). Cyanobacteria (for example, *Microcoleus, Nostoc*, and *Scytonema*) and cyanolichens (for example, *Collema* and *Peltigera*) also are capable of fixing atmospheric N into a mineral form that can be used by vascular plants (Evans and Lange, 2003; Belnap, 2002). Although actinorhizal shrubs also are likely contribu-

tors to N cycles in the region (see above), the ubiquity of BSCs relative to actinorhizal shrubs suggests that BSCs are the major N contributors in the region (Evans and Ehleringer, 1993; Belnap, 2002). Soil-crust organisms are significant food sources for other soil biota, particularly enhancing the activity of soil food webs in interspaces among vascular plants (Belnap, 2003b). BSCs also affect the nutrient cycling activities of soil food webs through their effects on near-surface moisture availability, soil structure, soil aeration, and soil temperature (Belnap, 2003b).

BSCs influence vascular plants in a variety of ways. Effects of BSCs on soil-surface stability and roughness result in seed-bed characteristics that differ greatly from those of soils without BSCs. Seed catchment and retention are generally enhanced by the presence of BSCs. Belnap, Prasse, and Harper (2003) reviewed the literature concerning effects of BSCs on plant establishment and found that research results varied depending on BSC characteristics, the plant species investigated, methods of study, and environmental conditions. BSCs are best viewed as environmental sieves that favor or discourage plant establishment, depending on environmental conditions and on species-specific attributes such as propagule morphology and germination requirements. If a generalization

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[9] Vesicular A horizons as much as several mm thick are common at the surface of silty desert soils. Vesicular structure is characterized by a large volume of spherical soil voids that appear to form when soil air is entrapped in wetted soil. Presence of a vesicular horizon greatly reduces soil hydraulic conductivity (Hillel, 1998; Birkeland,1999).

Grains of sand held by cyanobacterial filaments found in biological soil crusts. San Juan County, Utah. Photograph by Mark Miller, USGS.

is possible, it is that BSCs tend to inhibit establishment of annuals and species without specialized burial mechanisms such as twisting awns (Belnap, Prasse, and Harper, 2003). In southeastern Utah, Howell (1998) found that BSCs inhibited establishment of the exotic grass *Bromus tectorum*. Following the establishment phase, plants growing in soils with BSCs generally have been found to have greater biomass and lower root:shoot ratios than comparable plants growing in soils without BSCs, suggesting greater availability of soil resources in the presence of BSCs (Belnap, Prasse, and Harper, 2003). Relative to plants growing in soils without BSCs, plants growing in association with N-fixing cyanobacteria and cyanolichens consistently have greater N concentrations in tissues and usually have higher concentrations of the plant-essential nutrients potassium, magnesium, copper, and zinc (Harper and Belnap, 2001). In contrast, plants growing in soils with BSCs commonly have lower concentrations of phosphorus and iron than plants growing in soils without BSCs, suggesting that plants and BSCs may compete for these elements. Nutritional differences between plants grown in soils with and without BSCs are greatest in shallow-rooted herbaceous species, probably because they are rooted in near-surface soils that are most directly influenced by BSCs (Harper and Belnap, 2001).

Invertebrate and Vertebrate Consumers

Vertebrate and invertebrate consumers are significant contributors to the biological diversity of dryland ecosystems in the region (for example, Nelson, 1994; Griswold and others, 1997; Hanna and Graham, 2003; San Miguel and Colyer, 2003). There are numerous ways in which above-ground consumers can directly or indirectly affect the structure and functioning of dryland ecosystems (Whitford, 2002). Activities associated with granivory and herbivory are among those that have the greatest ecosystem-level consequences because of their many effects on vegetation structure and soil processes. Processes of competition and predation likewise can have important ecosystem-level consequences by altering the structure of consumer food webs, but these processes are not reviewed here.

Granivory is one of the most-studied processes in dryland ecosystems, although most research on this topic has been conducted outside the region encompassed by this report. Organisms that can be important granivores in dryland ecosystems of the region include harvester ants, beetles, rodents, frugivorous mammals, and birds (Chambers and others, 1999; Whitford, 2002). Through selective harvesting, consumption, and dispersal via caching and defecation, granivores can have

strong effects on the abundance, composition, and spatial distribution of the seed bank (Whitford, 2002). Through time, these seed-bank effects can be reflected in the composition and spatial structure of plant communities. For example, seed hoarding and caching behaviors of corvids such as Steller's jays (*Cyanocitta stelleri*) and Clark's nutcrackers (*Nucifraga columbiana*) have been implicated in the upslope migration of piñon in the Southwest (Chambers and others, 1999). In desert grasslands of southeastern Arizona, Brown and Heske (1990) proposed that selective seed harvesting and soil disturbance by kangaroo rats (*Dipodomys* sp.) were responsible for major changes observed in vegetation structure over a 12-year period. However, on the basis of subsequent studies, Whitford (2002) questioned whether the hypothesized mechanisms were sufficient to explain the observed vegetation changes. Whitford (2002) also suggested that effects of granivorous rodents and ants on soils (that is, resource enrichment through excretion and soil disturbance through burrowing) could have greater impacts on dryland vegetation structure than granivory itself.

Like granivory, herbivory can have numerous direct and indirect effects on ecosystem properties. Native herbivores in dryland ecosystems of the region include insects (grasshoppers, moth and butterfly larvae, bark beetles, and many others) and mammals such as woodrats (*Neotoma* spp.), desert cottontails (*Sylvilagus audubonii*), black-tailed jackrabbits (*Lepus californicus*), bighorn sheep (*Ovis canadensis*), pronghorn (*Antilocapra americana*), and mule deer (*Odocoileus hemionus*). In some locations, elk (*Cervus elaphus*) use of dryland systems also can be significant, particularly in winter (Allen, 1989). Herbivorous insects and small to medium-size mammals can have significant effects on vegetation structure and ecosystem processes such as nutrient cycling. With the exception of infrequent insect outbreaks (discussed below as a disturbance), the greatest ecosystem-level consequences of herbivory are those that can be caused by high densities of large-bodied browsers and grazers such as mule deer, elk, and domestic livestock.

Large herbivores can affect individual plants both directly and indirectly through a variety of mechanisms. Direct impacts include altered physiological function and morphology attributable to defoliation and trampling (Briske, 1991; Briske and Richards, 1995). Defoliation and trampling by large herbivores may indirectly influence plant performance as a consequence of altered microenvironmental conditions, soil properties (Thurow, 1991), mycorrhizal relations (Bethlenfalvay and Dakessian, 1984), competitive relations, and through effects on ecosystem processes such as nutrient cycling and hydrology. Seed dispersal is yet another indirect mechanism by which large herbivores and other animals may affect vegetation structure. Through time, combined direct and indirect impacts can result in altered plant population dynamics (for example, altered rates of reproduction, recruitment, and mortality) and consequent changes in plant community composition, structure, and distribution (Crawley, 1983; Archer and Smeins, 1991; Archer, 1994; Miller and others, 1994; Bich and others, 1995). Because of strong interactions of vegetation with nutrient cycling, hydrologic processes, disturbance

regimes, and geomorphic processes, herbivore-driven changes in vegetation structure can have cascading effects on multiple ecosystem processes and properties.

Considerable debate has occurred concerning the consequences of herbivory for plant productivity (for example, McNaughton, 1983, 1986, 1993; Belsky, 1986, 1987; Painter and Belsky, 1993; Dyer and others, 1993). This debate has centered on the phenomenon of "compensatory growth" in defoliated plants. Compensatory growth generally is defined as a positive response of plants to injury by defoliation (Belsky, 1986). McNaughton (1983, p. 329) described the phenomenon as follows:

"Compensatory growth in plants subjected to herbivory may alleviate the potential deleterious effects of tissue damage, whether to vegetative or reproductive organs. Tissue destruction is rarely, if ever, translated monotonically into a proportional reduction of final yield. Internal mechanisms of compensation involve modifications of plant metabolism; external mechanisms of compensation involve modifications of the plant environment that are favorable to plant growth and yield."

Belsky (1986) clarified the discussion by subdividing the term "compensation" into three separate terms defined by the productivity of a defoliated plant in relation to that of an undefoliated plant (see table 2).

Numerous physiological (internal) and/or microenvironmental (external) mechanisms may contribute to the occurrence of compensatory growth in plants (Crawley, 1997). For example, remaining foliage may experience increased relative growth rates due to diminished shading and increased light levels following grazing (a microenvironmental mechanism), or remaining foliage of a grazed plant may experience greater above-ground growth due to the reallocation of resources from root growth (a physiological mechanism). In general, the potential for and significance of compensatory growth is believed to vary in relation to the timing of herbivory in relation to plant phenology, the frequency and intensity of herbivory, the availability of resources both within the plant and in the surrounding soil environment (water and mineral nutrients), as well as the presence and competitive ability of neighboring plants (Briske and Richards, 1994, 1995; Crawley, 1997). Given the importance of resource availability for the occurrence and significance of compensatory growth, DeAngelis and Huston (1993) and Bartolome (1993) reasoned that overcompensation was most likely to occur in productive, intensively managed systems rather than in resource-poor environments characteristic of dryland ecosystems. In a review concerning the physiological responses of plants to grazing, Briske and Richards (1994, p. 169) concluded that (1) compensatory mechanisms only infrequently increase the total growth of defoliated plants above that of undefoliated plants (that is, "overcompensation" is rare), and (2) application of the concept to management of wildland vegetation is unwarranted because the phenomenon is so complex and poorly understood.

Table 2.   Compensatory growth of plants in response to tissue removal (modified from Belsky 1986).

Possible Plant Responses to Defoliation	Productivity of Defoliated Plant in Relation to that of Undefoliated Plant	Growth Compensation (%)
1. Overcompensation	Defoliated > Undefoliated	>100
2. Exact compensation	Defoliated = Undefoliated	100
3. Undercompensation	Defoliated < Undefoliated	<100
a. Partial compensation	Defoliated < Undefoliated	1-99
b. No compensation	Defoliated < Undefoliated	0
c. Damage	Defoliated < Undefoliated	<0

   Although compensatory growth of individual plants may occur, alteration of competitive relations among defoliated or differentially defoliated plants is of greater consequence for plant populations and communities (Briske, 1991; Archer and Smeins, 1991; Briske and Richards, 1994; Crawley, 1997). Plants that possess a greater capacity for regrowth following defoliation experience a competitive advantage over defoliated competitors that possess a lesser capacity for regrowth. Similarly, plants that are defoliated less frequently or less intensively experience a competitive advantage relative to plants that are defoliated more frequently or more intensively due to relative differences in accessibility or palatability. For an individual plant, the most significant benefit arising from herbivory is the relative advantage gained when a neighboring plant has been reduced in size and competitive ability by an herbivore (for example, Caldwell and others, 1987). Through time, altered competitive relations eventually can be expressed in population dynamics and plant community structure (Briske, 1991).

   Large herbivores also can affect the productivity and composition of plant communities through numerous indirect and direct effects on nutrient cycling (Archer and Smeins, 1991). Herbivore-driven shifts in plant community structure can affect nutrient cycles by altering the capacity of vegetation to capture and retain soil and water resources (Whitford, 2002) and by altering the quantity and quality of organic-matter inputs (Bardgett and Wardle, 2003; Reeder and others, 2004). Herbivory removes foliage and directly diverts nutrients from litter and physiological processes of intra-plant cycling. Nutrients acquired from foliage may be incorporated in animal biomass or spatially redistributed across the landscape in urine and dung. Where excreta are deposited, productivity may be enhanced if nutrients contained in the excreta are accessible to nearby plants. In other portions of the landscape, productivity may be reduced due to the removal of nutrients in foliage.

   Significant losses of nutrients from ecosystems may occur as a consequence of herbivory (Archer and Smeins, 1991; West 1991). A significant proportion of the N consumed in foliage is lost to the atmosphere in gaseous products of digestion and through volatilization of ammonia from dung and urine. In ecosystems where dung beetles are not present to bury feces and cycle nutrients through soil food webs (including much of the Colorado Plateau region), as much as 80 percent of fecal N may be lost to volatilization, with greatest losses expected from sandy, high-pH soils (Woodmansee, 1979). Schimel and others (1986) found lower rates of N loss from cattle urine, possibly because urine enters the soil more readily than dung. These researchers reported higher N losses from cattle urine in coarse soils (12–27 percent) than from fine-textured soils (0–2 percent). Nutrients incorporated in animal biomass are removed from the ecosystem entirely when livestock are removed.

   In dryland ecosystems where components of biological soil crusts are the predominant sources of N inputs, trampling by large herbivores also can have direct effects on nutrient cycling. Evans and Ehleringer (1993) found that N-fixing cyanobacteria and cyanolichens in biological soil crusts were the primary sources of N inputs to a piñon–juniper ecosystem in southern Utah. They hypothesized that trampling disturbance of biological soil crusts could eventually result in long-term ecosystem degradation due to diminished N inputs by damaged or eliminated N-fixing crust organisms. In southeastern Utah (Canyonlands NP), Evans and Belnap (1999) compared soil N dynamics between an ungrazed grassland and an adjacent grassland that experienced intermittent winter grazing by livestock prior to 30 years ago. Cover of N-fixing cyanolichens was 5.5 percent in the ungrazed grassland and less than 1 percent in the formerly grazed grassland. Compared with the formerly grazed grassland, the ungrazed grassland was characterized by soil-crust N fixation rates that were 2.5 times greater and soil N content that was 1.35–2.5 times greater. The authors concluded that soil disturbance had resulted in long-term consequences for N cycling and storage in the dryland ecosystem they studied. Thus, although some plants may benefit from localized resource enrichment attributable to herbivore excreta, the literature suggests that the long-term consequence of herbivory and trampling by large ungulates in dryland ecosystems could be a gradual ecosystem-level decline in N

USGS geologist measuring soil magnetic properties to support studies relating vegetation patterns to geomorphic processes affected by climate and land use. San Juan County, Utah. Photograph by Mark Miller, USGS.

Magnetic susceptibility meter used for measuring magnetic properties of soils and rocks. San Juan County, Utah. Photograph by Mark Miller, USGS.
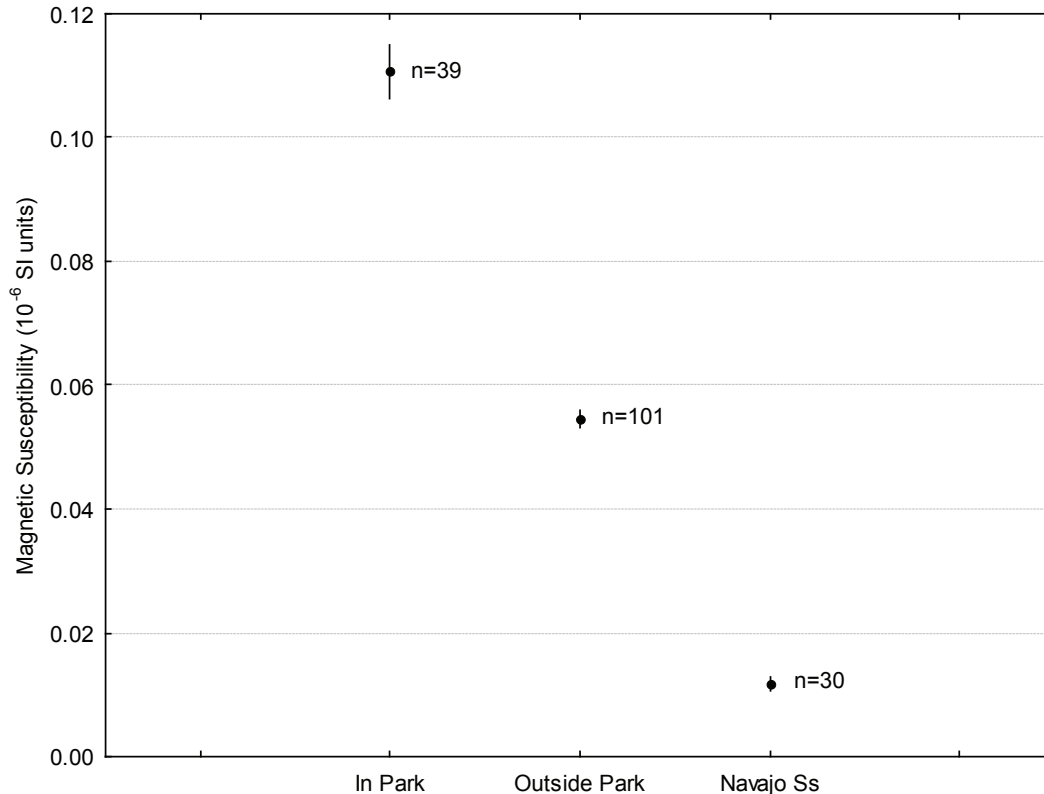
Figure 7.   Magnetic susceptibility (mean ± 1 SE) of surficial sediments at a formerly grazed grassland site in the Island in the Sky District of Canyonlands National Park (ungrazed for 30 years), a currently grazed grassland site outside the Park, and of Navajo Sandstone bedrock—the principal parent material for soils at both sites. Surface soils at both sites are classified as Begay fine sandy loams (coarse-loamy, mixed, mesic Ustollic Camborthid). The higher magnetic susceptibility value for soils at the formerly grazed site indicates greater soil content of dust-borne magnetite, clay- and silt-size soil particles, and rock-derived mineral nutrients relative to soils at the currently grazed site outside of the park, thus suggesting loss of accumulated nutrients at the grazed site. The value for Navajo Sandstone indicates a baseline measure of surficial sediments without aeolian magnetite.

fertility. Following a review of mechanisms by which above-ground and below-ground herbivores affect nutrient cycling, Bardgett and Wardle (2003) concluded that positive effects of herbivory on soil processes and soil biota are most common in ecosystems with high soil fertility and relatively high consumption rates, whereas adverse effects are most common in low-fertility ecosystems with relatively low consumption rates.

In addition to impacts of trampling on N inputs where biological soil crusts are present, repeated trampling by large herbivores can destabilize soils and result in the depletion of rock-derived nutrients through the aeolian loss of fine soil particles. For example, Neff and others (2005) found lower contents of fine soil particles and rock-derived nutrients at two formerly grazed sites relative to an ungrazed site at the Needles District of Canyonlands NP. On the basis of soil magnetic properties which indicate the presence of far-traveled aeolian dust in these sandstone-derived soils, the authors attributed

soil differences between the ungrazed and grazed sites to accelerated wind erosion caused by destabilizing effects of repeated trampling at the grazed sites. Because of the strong positive relationship between soil magnetic susceptibility and several lab-based measures pertaining to the bioavailability of rock-derived nutrients in sandstone-derived soils (for example, cation exchange capacity, silt content, phosphorus and potassium bioavailability), magnetic susceptibility shows promise as an indicator of long-term soil-surface stability in some Colorado Plateau landscapes (for example, fig. 7).

Some workers have hypothesized that trampling by large herbivores has beneficial impacts on infiltration (Savory and Parsons, 1980; Savory, 1988). However, an extensive amount of hydrologic research has failed to support this hypothesis (Spaeth and others, 1996; Holechek and others, 2000), indicating instead that trampling tends to result in lower infiltration rates where it destroys stable

soil aggregates and leads to a deterioration of soil structure (Thurow, 1991). Hydrologic impacts of trampling by large herbivores vary in relation to soil type (for example, texture and the presence of a vesicular A horizon), soil water content, seasonal climatic conditions, vegetation type, and the magnitude of trampling (Thurow, 1991).

Natural Disturbance Regimes

Background

A *disturbance* is "...any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (White and Pickett, 1985, p. 7). For purposes of ecosystem management and monitoring, disturbances are considered to be ecological factors that are within the range of conditions naturally experienced by the ecosystem (for example, drought). These are differentiated from *stressors*, which may fit the definition of disturbance but are outside the range of disturbances naturally experienced by the ecosystem and typically are anthropogenic in origin (Whitford, 2002). Implicit in the "natural" aspect of these definitions is the need to identify ecosystem-specific reference conditions which are framed with respect to a particular time period and place (White and Walker, 1997; Landres and others, 1999). In addition to these temporal and spatial bounds, ecosystem managers should explicitly identify associated goals, assumptions, and value judgments when adopting a particular set of reference conditions as the "natural" standard for management and monitoring (Truett, 1996; Landres and others, 1999). Late-Holocene, pre-European conditions often are identified as the standard for defining natural disturbance regimes, although it is important to recognize the potentially important role of pre-European human populations in shaping disturbance regimes and ecosystem conditions found at the time of European contact (Betancourt and Van Devender, 1981; White and others, 1999).

In addition to climatic fluctuations, disturbances are major drivers of ecosystem change and variability. Disturbance is a factor affecting the spatial and temporal dynamics of all ecosystems, but disturbances differ greatly among ecosystems in relation to climate, topography, substrate, and ecosystem attributes such as vegetation structure. Disturbances can be differentiated on the basis of several descriptors which, taken in combination, characterize the *disturbance regime*. Descriptors of disturbance regimes include the kind of disturbance (for example, surface fire versus windthrow), spatial characteristics (for example, patch size, spatial extent and patterning), temporal characteristics (for example, frequency, timing, return interval), specificity (for example, selective effects by species, age class, or landscape unit), magnitude (for example, intensity, severity), and synergisms (for example, interactions with other disturbances ; Sousa, 1984; White and Pickett, 1985; White and others, 1999). Most ecosystems experience more than one type of disturbance, and interactions among disturbances commonly occur because particular disturbance events can affect

the capacity of ecosystem components or processes to resist or recover from subsequent disturbances. Similarly, interactions can occur between natural disturbances and anthropogenic stressors (White and others, 1999; Archer and Stokes, 2000). Because disturbances play such an important role in shaping the structure and functioning of ecosystems (strongly interacting with soil resources and vegetation structure), disturbance-regime alteration is one of the most common ways by which human activities affect the functioning and sustainability of ecosystems (Chapin and others, 1996).

Extreme Climatic Events

Episodic severe climatic events are major disturbances in dryland ecosystems (Walker, 1993; Whitford, 2002). Drought, extreme precipitation events and floods, and wind storms can induce long-term changes in ecosystem structure and function by causing widespread mortality or enabling establishment of long-lived plants that are structural dominants. The erosive energy of extreme precipitation and wind events also can result in massive transport and redistribution of soil resources, potentially inducing geomorphic changes that fundamentally alter site conditions. Event sequencing (for example, timing of flooding in relation to drought) is an important factor that can affect ecosystem resistance and resilience to episodic climatic events. Although episodic, event-driven change is an important feature of many ecosystems (Holling, 1996; Scheffer and others, 2001), it is particularly characteristic of dryland ecosystems (Whitford, 2002). Examples from this region include the 1950's drought that affected the structure of piñon–juniper woodlands throughout much of the Southwest (Betancourt and others, 1993; Allen and Breshears, 1998), as well as the recent severe drought (the "early 21st century drought" of Webb and others, 2004) that has caused region-wide mortality in piñon (USDA Forest Service, 2003) and sagebrush (*Artemisia* spp.). Climatic conditions and events can affect ecosystem susceptibility to other disturbances such as fire and insect outbreaks (Swetnam and Betancourt, 1998), as well as affect ecosystem resistance and resilience to anthropogenic stressors (Archer and Stokes, 2000; Scheffer and others, 2001).

Fire

Fire is another type of natural disturbance that can have many direct and indirect effects on the structure and functioning of dryland ecosystems. One of the most significant direct effects of fire is the alteration of vegetation composition and structure due to the selective damaging or elimination of fire-intolerant life forms or age classes (Whelan, 1995). Specific effects of fire on vegetation structure vary in relation to fire-regime characteristics (for example, frequency, intensity, seasonality, and spatial patterning) and fire responses of dominant vegetative life forms. Fire-regime characteristics are strongly influenced by the vegetation itself, as well as by preceding and coincident weather conditions that affect fuel availability, fuel flammability, and fire behavior. In some

Soils susceptible to erosion following fire in a piñon-juniper woodland, Dinosaur National Monument, Moffat County, Colorado. Photograph by Mark Miller, USGS.

dryland ecosystems, low-intensity surface fires play a role in thinning or eliminating fire-intolerant woody vegetation and favoring the relative dominance of relatively fire-tolerant graminoids (Jameson, 1962; Wright, 1980). In systems where repeated surface fires are required to maintain grassland- or savanna-like physiognomic structure, the necessary fire frequency depends on the amount of time needed for predominant woody taxa to (1) develop features that confer resistance to surface fires (for example, thick bark and elevated canopies) or (2) competitively exclude herbaceous taxa that provide fine fuels to support surface fires. Most effects of fire on wildlife also are mediated through effects on vegetation structure and nutritional quality of forage (Smith, 2000).

Effects of fire on vegetation structure have multiple ecosystem-level consequences because of strong vegetation interactions with soil, hydrology, and geomorphic processes. Fire-caused reductions in ground cover and vegetation structure can result in significant erosional losses of soils, nutrients, and organic matter by water and wind (Johansen and others, 2001; Whicker and others, 2002). Soil hydrophobicity caused by fire is another factor which can result in accelerated water-driven erosion because of decreased infiltration and increased runoff (Johansen and others, 2001; MacDonald and Huffman, 2004). In a study conducted in burned and unburned Chihuahuan desert shrublands, Whicker and others (2002) found that aeolian soil movement measured by passive soil collectors was 70 times greater at the burned site relative to the unburned site

during high-velocity wind events shortly after fire occurrence and was 3 times greater over the entire 8-month study period.

Fire also has significant ecosystem-level consequences due to effects on nutrient cycles (Raison, 1979; Blank and others, 1994a, b). Depending on the type and intensity of fire events, fire can (1) increase nutrient *bioavailability* on a short-term basis due to ash deposition and accelerated rates of nutrient cycling, and (2) deplete total nutrient *stocks* due to gaseous losses (particularly N) and off-site transfers of ash (Raison, 1979). Nutrient losses in gases and ash are generally proportional to heat generated and organic-matter consumed by fire (Raison, 1979; Schlesinger, 1997). Depending on fire severity, other soil characteristics can be affected by fire, including pH (typically increased by ash deposition), cation exchange capacity and infiltration capacity (both typically decreased by organic-matter losses and transformations; Raison, 1979), and erodibility (Whicker and others, 2002).

Natural fire regimes vary greatly among dryland ecosystems of the Colorado Plateau region. Fire generally is insignificant as a natural disturbance in sparse desert shrublands dominated by taxa such as *Atriplex confertifolia, A. corrugata, Coleogyne ramosissima,* and *Sarcobatus vermiculatus*, as well as in semidesert grasslands dominated by taxa such as *Acnatherum hymenoides, Hesperostipa comata, Aristida* spp., *Sporobolus* spp., and *Pleuraphis jamesii*. These grasslands have been described as "galleta—three-awn shrub steppe" (Küchler, 1964; West and Young, 2000) and are characteristic

Prior to a prescribed fire conducted by NPS resource managers, vegetation on Iron Springs Bench in Dinosaur National Monument was dominated by Wyoming big sagebrush (*Artemisia tridentata ssp. wyomingensis*). Post-fire vegetation is dominated by native grasses including western wheatgrass (*Pascopyrum smithii*), bluebunch wheatgrass (*Pseudoroegneria spicata*), muttongrass (*Poa fendleriana*), and needle-and-thread grass (*Hesperostipa comata*). Dinosaur National Monument, Moffat County, Colorado. Photograph by Mark Miller, USGS.

of Canyonlands NP, Capitol Reef NP, Arches NP, Glen Canyon NRA, and Chaco Culture National Historic Park.

In contrast to these fuel-limited systems where fire is of minimal importance, fire is a significant natural disturbance in several other dryland ecosystems of the region. These include sagebrush shrublands and shrub steppe (for example, Dinosaur NM, Fossil Butte NM, and Black Canyon of the Gunnison NP), relatively productive semidesert grasslands and juniper savannas (for example, Wupatki NM; Jameson, 1962; Johnsen, 1962), and piñon–juniper woodlands and forests (for example, Mesa Verde NP and Zion NP). Miller and others (1994) estimated that natural fire-return intervals in sagebrush steppe varied from 20–30 years in mountain big sagebrush systems (*Artemisia tridentata* ssp. *vaseyana*) to 50–100 years in Wyoming big sagebrush systems (*A. tridentata* ssp. *wyomingensis*) prior to the introduction of livestock and effective

fire suppression. However, caution is warranted regarding generalizing from these estimates since they were derived from observations made in Great Basin ecosystems rather than Colorado Plateau ecosystems. Fire-history studies in sagebrush systems also are hampered by the absence of plant species that record fires by means of datable scars.

Natural fire regimes in ecosystems vegetated by various species of piñon and juniper are poorly understood. Contributing factors include the tremendous structural and functional diversity of systems broadly categorized as piñon–juniper vegetation types (for example, Harper and others, 2003) and the relative lack of area-specific fire-regime studies conducted in such systems across the region (Baker and Shinneman, 2004). In a systematic review of the natural role of fire in piñon–juniper ecosystems, Baker and Shinneman (2004) concluded that (1) spreading, low-severity surface fires probably were

uncommon in such ecosystems prior to EuroAmerican settlement, and (2) much additional area-specific research is urgently needed to provide a foundation for science-based management and restoration efforts. In this latter conclusion, they are in agreement with other workers who have warned ecosystem managers not to rely uncritically on fire-regime generalizations derived from studies conducted elsewhere (for example, Veblen, 2003; Romme, Floyd-Hanna, and Hanna, 2003).

Some of the most extensive work on piñon–juniper fire regimes on the Colorado Plateau has been conducted at Mesa Verde NP. Floyd and others (2000, 2004) recently estimated that the natural fire rotation time (amount of time required to burn an area equal in size to the entire area under consideration) in piñon–juniper ecosystems at Mesa Verde NP is approximately 400 years (Floyd and others, 2000, 2004; Floyd, Romme, and Hanna, 2003; Romme, Floyd-Hanna, and Hanna, 2003). No fire scars indicative of surface-fire occurrence have been located at Mesa Verde NP despite extensive searching. Instead, minimum stand ages ranging from 200 to over 400 years indicate that the natural piñon–juniper fire regime at Mesa Verde NP is one characterized by infrequent, stand-replacing canopy fires. In a study conducted on the Uncompahgre Plateau north of Mesa Verde NP, Eisenhart (2004) also concluded that (1) there was no evidence to support the idea that frequent, low-severity surface fires were common in any piñon-juniper ecosystems in her study area, and (2) the predominant natural disturbance regime in these ecosystems is infrequent, stand-replacing canopy fires.

In an attempt to clarify issues associated with piñon-juniper fire regimes, Romme, Floyd-Hanna, and Hanna (2003) proposed a framework describing a set of hypotheses concerning variations in piñon-juniper structure, function, and status (see table 3 on p. 41). They identified three types of piñon–juniper systems that are fundamentally different in these respects. Of the three types, the authors hypothesized that only the *piñon–juniper grass savanna* is characterized by a natural fire regime consisting of frequent, low-severity surface fires (table 3). Grasslands and juniper savannas found in and around Wupatki NM exemplify this type of system (Jameson, 1962; Johnsen, 1962), as did significant proportions of the landscape at Bandelier NM prior to the introduction of livestock in the 19th century (Allen, 1989). The *piñon–juniper shrub woodland* is a vegetation type with a natural disturbance regime that involves moderately frequent stand-replacing fire carried by shrub and tree canopies (table 3; Romme, Floyd-Hanna, and Hanna, 2003). The authors hypothesize that the natural post-fire successional sequence in this type proceeds from herb dominance, to shrub dominance, to a mixed shrub-tree community (with young trees) before the sequence is reset by a stand-replacing fire. Evidence exists to suggest that this type of dynamic may be naturally characteristic of some sagebrush ecosystems on the Colorado Plateau (for example, Rowlands and Brian, 2001; Harris and others, 2003). Finally, the studies conducted at Mesa Verde NP (Floyd and others, 2004) and on the Uncompahgre

Plateau (Eisenhart, 2004) provide evidence for the third type of system—*piñon–juniper forests*—which is characterized by infrequent, stand-replacing fires carried by tree canopies.

Insect and Disease Outbreaks

The roles of insect and disease outbreaks in dryland ecosystems are poorly understood. In montane and boreal forests, insects are recognized as major agents of disturbance (for example, Veblen and others, 1991; Logan and others, 2003). It is believed that the occurrence of insect outbreaks in tree-dominated ecosystems is linked with climatic conditions that diminish the vigor and insect resistance of host plants and/or affect life cycles and dispersal patterns of insect herbivores (Swetnam and Betancourt, 1998; Logan and others, 2003). In piñon–juniper ecosystems, outbreaks of the bark beetle *Ips confusus* (piñon ips) can be triggered by drought conditions that weaken host-tree populations (Leatherman and Kondratieff, 2003). Drought and ips beetle outbreaks in combination can act as broad-scale disturbances in these systems, as reflected by the massive mortality that has occurred recently in piñon populations across the southern Colorado Plateau region in response to the early 21st century drought (USDA Forest Service, 2003). As with fire, insect outbreaks thus can interact with climate to generate long-term changes in vegetation structure (Allen and Breshears, 1998). Insect- or pathogen-generated changes in vegetation structure can have multiple ecosystem-level consequences due to vegetation interactions with nutrient cycles, hydrologic processes, and geomorphic processes.

Herbivory and Trampling

Herbivory and trampling are additional natural disturbances in dryland ecosystems of the region. Potential ecosystem-level effects of herbivory and trampling were discussed above, but actual effects will vary in relation to ecosystem characteristics (for example, climatic conditions, soil properties, and vegetation structure and composition) and disturbance characteristics. Similar to other disturbances such as fire, a key consideration for ecosystem management and monitoring is the *regime* of herbivory and trampling that is considered natural for particular ecosystems.

Predominant types of herbivores and the spatial patterning, temporal patterning, magnitude, selectivity, and synergistic relationships of herbivory and trampling likely varied among dryland ecosystems prior to European settlement. At the time of contact, large native ungulates such as elk and bison (*Bison bison*) were uncommon in most dryland ecosystems of the Intermountain West in comparison with the Great Plains region east of the Rocky Mountains (Mack and Thompson, 1982; Grayson, 1994). Probable factors affecting regional-scale variations include landscape characteristics (for example, availability of forage and perennial water, presence and extent of topographic barriers, proximity to other favorable habitats), nonhuman predation, and hunting activities of pre-European human populations (Truett, 1996). Truett (1996) proposed that water scarcity and hunting by pre-European peoples were primary factors explaining low numbers of large

Gallery of a cedar bark beetle (*Phoeosinus* sp.) on Utah juniper (*Juniperus osteosperma*) that subsequently was burned in a wildfire, Mesa Verde National Park, Colorado. Photograph by Mark Miller, USGS.

ungulate herbivores encountered by early Europeans throughout much of the American Southwest (see Allen, 1996). Archaeological findings suggest that small numbers of bison may have been present occasionally in some dryland locations on the Colorado Plateau during late-Holocene times (for example, Mead and others, 1991). But overall, herbivory and trampling by large ungulates probably were relatively minor disturbances in most dryland ecosystems of the region during the period prior to European settlement.

Landscape-Level Relationships

This report has focused on functional relationships among components of dryland ecosystems, but for purposes of ecosystem management and monitoring it also is important to recognize functional relationships among ecosystems in landscapes (Wiens and others, 2002). A *landscape* is a spatially structured mosaic of different types of ecosystems interconnected by ecological flows of materials (for example, water, sediments), energy, and organisms. Included in this definition is the notion that some of these flows may represent disturbances or stressors (fig. 8). A landscape perspective is essential for management and monitoring of bounded reserves such as NPS units where ecosystems within parks can be significantly affected

by activities occurring well outside park boundaries. Consideration of landscape-level processes also can be important for assessing whether ecological conditions or events in one park location might generate ecological consequences elsewhere within the park (Reiners and Driese, 2001).

Several aspects of landscape structure must be considered when assessing functional relationships among ecosystems in landscapes. These include ecosystem (or patch) type, ecosystem context, ecosystem condition, and ecosystem size (Groves and others, 2002; Wiens and others, 2002). Ecosystem *context* refers to the spatial configuration and connectivity of ecosystems (fig. 8). Connectivity is the degree to which ecological flows can occur between ecosystems in a landscape. Connectivity depends on spatial configuration, but it also is strongly dependent on the process of interest and the degree of contrast between ecosystems. For example, two adjacent ecosystems may be connected hydrologically due to their location within a particular watershed, but differences in vegetation structure may cause the same two adjacent ecosystems to be disconnected with respect to the movement patterns of particular organisms or the transmission of disturbances such as fire. In this example, the degree of cross-boundary contrast does not affect hydrologic connectivity but it strongly affects boundary permeability to
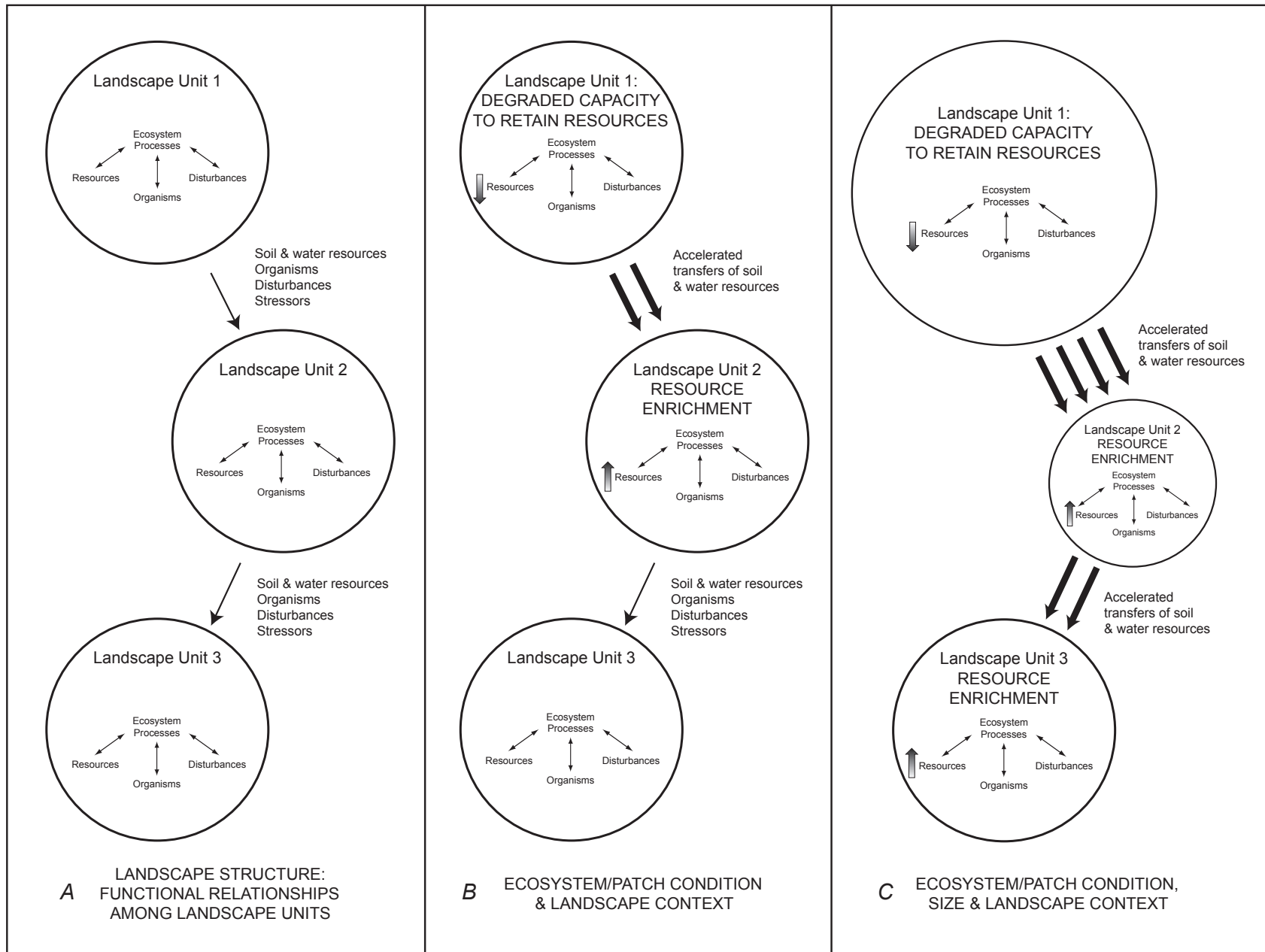
Figure 8. Examples of landscape-level processes and attributes important for ecosystem monitoring. In *A*, landscape units are functionally connected by flows of soil and water resources, organisms, disturbances, and stressors. In *B*, degraded conditions in Unit 1 are shown to cause resource enrichment in Unit 2—illustrating the importance of landscape context. In *C*, degraded conditions in Unit 1 are propagated to Unit 3 due to increased size of Unit 1 and decreased size of Unit 2.

organisms and disturbance. From an ecosystem perspective, *condition* refers to the functioning of ecological processes required to sustain ecosystem characteristics including abiotic and biotic structure, productivity, rates of biogeochemical cycling, and natural disturbance regimes. The condition of ecosystems in the landscape can affect among-system flows and the ecological consequences of among-system flows. For example, a diminished capacity for soil and water retention in one ecosystem can result in accelerated resource transfers to connected ecosystems (fig. 8*B*). Consequences of resource enrichment in the receiving ecosystem are dependent on conditions there. If invasive species are present in the receiving ecosystem, resource enrichment may result in rapid population expansion (Davis and others, 2000; With, 2002). When considered with respect to individual species, ecosystem condition is equivalent to the notion of habitat quality (Wiens and others, 2002).

The meaning of ecosystem *size* is intuitive, and ecosystem size (or changes in ecosystem size) can affect the type, magnitude, and consequences of among-system flows (fig. 8*C*). For ecosystems characterized by large-scale disturbance regimes (for example, extensive fire), it may be necessary to expand the notion of ecosystem size to encompass the amount of area required for the ecosystem to persist under the influence of characteristic large-scale disturbances. This area has been referred to as the *minimum dynamic area* (Pickett and Thompson, 1978; Peters and others, 1997; Groves and others, 2002).

Predominant Anthropogenic Stressors

This section briefly describes predominant anthropogenic stressors affecting the structure and functioning of dryland ecosystems in SCPN and NCPN units. Additional information on the significance of these stressors in particular parks can be found in associated NPS reports (Evenden and others, 2002; Thomas and others, 2003; Miller and others, 2003). Details concerning potential ecological effects of these stressors are summarized in tabular format in appendix table B and in conceptual models presented in the subsequent section of this report.

Visitor Use

Park use by terrestrial recreationists has been identified as a primary stressor of concern in many NCPN units and, to a lesser degree, in some SCPN units. Most parks experienced rapid growth in the number of annual recreational visits between the mid-1980's and the mid-1990's (Evenden and others, 2002; Thomas and others, 2003). These changes are exemplified by visitation patterns at Canyonlands NP, which averaged 16 percent annual growth in visitation between 1985 and 1995. During the year 2000, Canyonlands received seven times the number of recreational visits that it received in 1980. Zion NP—the most visited park in the NCPN—recorded

over two million recreational visits in 2000, twice the number recorded in 1980. Grand Canyon NP, consistently the most-visited SCPN park, has recorded over four million visitors every year since 1992 (Thomas and others, 2003). Potential resource impacts associated with terrestrial recreational activities include trampling of soils and vegetation (for example, Cole, 1990), dispersal of invasive exotic species, direct interactions with and disturbances of wildlife, and increased levels of water and air pollutants.

Livestock and Other Large Herbivores

Livestock use is permitted in parts of one SCPN park (Glen Canyon NRA) and four NCPN parks (Dinosaur NM, Capitol Reef NP, Curecanti NRA, and Black Canyon of the Gunnison NP). Seasonal livestock trailing is permitted in Fossil Butte NM and Bryce Canyon NP, and several other parks repeatedly experience trespass livestock. Most other parks were grazed by domestic livestock at one time, and contemporary soil and vegetation conditions in many parks reflect persistent legacies of past livestock grazing and livestock-management practices (for example, Sydoriak and others, 2000; Neff and others, 2005). Herbivory and trampling by elk (Bandelier NM; Allen, 1996), bison (Capitol Reef NP and Grand Canyon NP), and feral burros (Grand Canyon NP) also occur.

Fire-Regime Alteration

Ecological legacies of altered fire regimes are significant resource-management issues in many parks (Evenden and others, 2002; Thomas and others, 2003). Altered fire regimes attributable to past livestock grazing (fuel removal) and fire-suppression efforts have caused significant changes in vegetation structure and functioning of associated ecosystem processes. Mediated by changes in vegetation structure, ecosystem-level consequences of altered fire regimes can include diminished hydrologic functioning and increased erosion rates (for example, Wilcox and others, 2003; Davenport and others, 1998; Jacobs and Gatewood, 1999), as well as increased ecosystem susceptibility to drought and other disturbances and/or stressors.

Invasive Exotic Plants

Invasive exotic plants are recognized as an important component of global environmental change (Vitousek, 1994a; Mooney and Hofgaard, 1999), and they represent a significant resource-management challenge in the Colorado Plateau region. For example, NPS staff have estimated that approximately 24 percent of the total land area of Glen Canyon NRA may be infested with invasive plant species (Thomas and others, 2003). Significant proportions of grasslands found in Canyonlands NP and Arches NP have been converted to dominance by cheatgrass (*Bromus tectorum*; Evenden and others, 2002), and cheatgrass constitutes approximately 85 percent

of the dominant understory vegetation at Yucca House NM (Thomas and others, 2003).

Ecological effects of exotic species invasions vary depending on the characteristics of the invader and the invaded ecosystem, but they can include major changes in community composition (Bock and others, 1986), competitive displacement of native species, and alterations of ecosystem-level properties such as disturbance regimes (D'Antonio and Vitousek, 1992; Mack and D'Antonio, 1998) and soil-resource regimes (Vitousek, 1990; Evans and others, 2001). Many invasive plant species also possess physiological traits that will enable them to benefit from aspects of global change such as increased levels of atmospheric CO_2 and warmer minimum temperatures during winter (Alward and others, 1999; Dukes and Mooney, 1999; Smith and others, 2000).

Adjacent Land use Activities

Ecological effects of adjacent land use activities also represent a uniform concern among SCPN and NCPN units (Evenden and others, 2002; Thomas and others, 2003). Particular activities of concern include livestock grazing, forest management, urban/exurban development, and emissions of industrial and agricultural pollutants. Potential resource issues associated with adjacent land use activities include altered habitat structure for wide-ranging wildlife species; increased transfers of soil and water resources; emissions of airborne and waterborne pollutants; introductions of exotic plant and animal species; diminished quality of soundscapes, nightskies, and viewsheds; and water diversion and/or regulation.

Air Pollutants

Airborne particulates, tropospheric ozone, and nitrogen deposition are concerns at several SCPN and NCPN parks (Evenden and others, 2002; Thomas and others, 2003). Acid deposition may be an issue at Mesa Verde NP (Romme, Oliva, and Floyd, 2003). Nitrogen deposition in particular has potential implications for numerous ecological patterns and processes including ecosystem susceptibility to exotic species invasions (Asner and others, 1997; Galloway and others, 2003; Fenn, Baron, and others, 2003). Although current rates of N deposition generally are low across most of the western United States, there is very little information available for areas immediately downwind of emissions sources (Fenn, Haeuber, and others, 2003; Fenn, Baron, and others, 2003). Notably, modeling indicates potential "hot spots" of N deposition in the vicinity of Mesa Verde NP and Zion NP (Fenn, Haeuber, and others, 2003).

Global Atmospheric Changes

Global atmospheric changes attributable to anthropogenic emissions of CO_2 and other greenhouse gases are expected to have significant environmental consequences during this century (Houghton and others, 2001). Increasing levels of

USGS geologists investigating soil properties responsible for spatial patterns of sagebrush (*Artemisia tridentata*; shrubs in background) and invasive cheatgrass (*Bromus tectorum*; reddish grass in foreground). San Juan County, Utah. Photograph by Mark Miller, USGS.

Invasive exotic plants can diminish ecosystem resilience to wildfire even in systems where fire is a natural disturbance process. Wildfire in this piñon–juniper woodland in Mesa Verde National Park led to significant increases in the relative abundance of invasive exotics including cheatgrass (*Bromus tectorum*) and musk thistle (*Carduus nutans*). Here these exotics surround Schmoll's milkvetch (*Astragalus schmolliae*; plant with cream-colored flowers in center of photograph), a rare endemic plant restricted solely to Mesa Verde National Park and the adjacent Ute Mountain Ute Tribal Park. Photograph by Mark Miller, USGS.
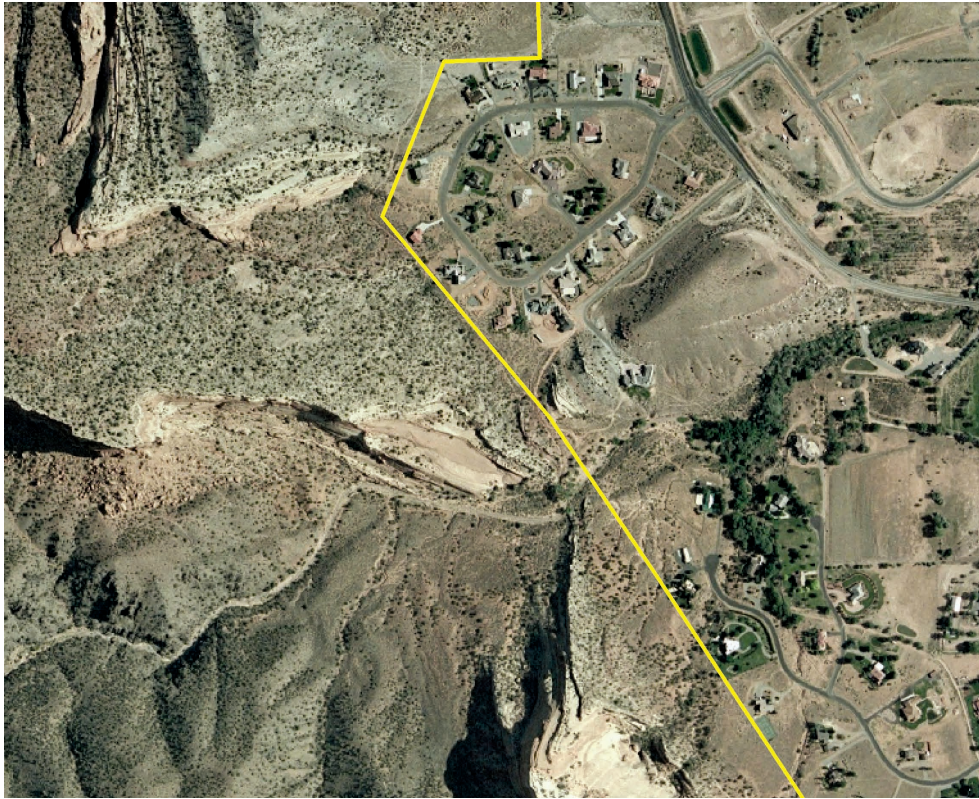
Urban development directly adjacent to the boundary of Colorado National Monument (represented by the heavy yellow line). Width of photograph is 1,400 m on the ground. Mesa County, Colorado. NPS aerial photograph.

Air-quality monitoring station at Bryce Canyon National Park, Garfield County, Utah. Photograph by Mark Miller, USGS.

atmospheric CO_2, increasing soil and air temperatures, and altered precipitation patterns (including a potential increase in the frequency of extreme events) are likely to affect physiological processes and competitive relationships of vascular plants, nutrient cycles, hydrologic processes, and disturbance regimes—all of which have the potential to greatly alter the structure and functioning of dryland ecosystems (for example, Alward and others, 1999; Ehleringer and others, 1999; Smith and others, 2000; Weltzin and others, 2003) and the sensitivity of these systems to other anthropogenic stressors. Despite modeling efforts, there is great uncertainty about how global atmospheric changes will affect temperature and precipitation patterns in particular regions such as the Colorado Plateau. Uncertainty regarding regional climatic consequences and ecological outcomes of global-change processes greatly compounds the challenges associated with ecosystem management and monitoring.

Ecosystem Dynamics

In this section, conceptual models are presented to describe hypotheses about how and why dryland ecosystems change through time. These models do not describe characteristic natural dynamics of the many specific dryland ecosystems found in the region (that is, dynamics driven solely by natural disturbances and short-term climatic fluctuations). Instead, they emphasize dynamics associated with a very generalized set of processes and pathways of degradation[10] that have been described for dryland ecosystems. The intent is that an emphasis on degradational dynamics will best highlight ecosystem attributes that should be monitored for purposes of sustaining ecosystem integrity. The models are intended to depict general ways in which natural drivers (for example, climate and disturbance) interact with stressors and/or management actions to affect the likelihood of these degradational changes. Because of the generalized nature of these models, they will require refinement for site-specific applications. Following the models, this section ends with a brief discussion of factors affecting the susceptibility of dryland ecosystems to change.

Background—Alternative Ecosystem States

Sustainable ecosystems, as defined by Chapin and others (1996), are persistent. Through the typical pattern of dynamics driven by natural disturbances and climatic fluctuations, such ecosystems maintain their characteristic diversity of major functional groups, productivity, and rates of biogeochemical cycling (Chapin and others, 1996). Inherent in the notions of ecosystem sustainability and persistence is the hypothesis that ecosystems can be caused to shift from one state to an alternative state.[11] Though capable of existing on the same site, these alternative ecosystem states are distinguished by relatively large differences in structure and in rates of ecological processes such as erosion, nutrient cycling, and disturbance regime. Such differences in structure and processes typically are matched by great differences in ecosystem dynamics. A transition from one state to an alternative state may occur gradually or relatively rapidly as the result of natural processes (for example, extreme climatic disturbances) or human actions (for example, land use activities). Frequently, human actions and natural processes interact to cause persistent transitions among states (Westoby and others, 1989; Bestelmeyer and others, 2003; Stringham and others, 2003; Bestelmeyer and others, 2004).

Although some transitions may be caused solely by natural processes, of greatest concern from a conservation perspective are anthropogenic transitions which result in degraded ecosystem states. Ecosystems that have been driven across thresholds of degradation generally cannot be restored to previous conditions simply by removing the stressor. Costly, manipulative restoration efforts are typically required (Hobbs and Norton, 1996; Whisenant, 1999; Sydoriak and others, 2000; Suding and others, 2004). The success of such restoration efforts usually is uncertain, and in some cases complete restoration may be impractical due to financial and technical constraints. Dryland ecosystems and aquatic ecosystems are the most frequently cited examples of systems characterized by multiple alternative states (Rapport and Whitford, 1999; Whitford, 2002; Scheffer and Carpenter, 2003).

Common Pathways and Processes of Dryland Degradation

The conceptual framework of alternative states is a useful one for identifying monitoring needs associated with goals of sustaining the health or integrity of dryland ecosystems. This alternative-state framework is depicted graphically in figure 9. In this framework, the reference state (state *A*, defined on a site-specific basis by climate, soil, and landscape setting) is represented by a dynamic ecosystem in which the characteristic abiotic and biotic components and processes are present and functioning within the natural range of variability, including processes that confer resistance and resilience to

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[10] For purposes of this report, *degradation* is defined as an anthropogenic reduction in the capacity of a particular ecosystem or ecosystem component to perform desired functions such as the conservation of soil and water resources or the maintenance of native biodiversity. Degradation also can be interpreted as an anthropogenic reduction in the capacity of a system to maintain itself within the natural range of variability or within the range of desired conditions specified by ecosystem managers.

[11] As applied here, *state* is a dynamic concept that (1) encompasses ecological processes such as natural disturbance and nutrient cycling, and (2) recognizes that plant community composition and structure on a particular site can vary spatially and temporally due to disturbance/successional processes and short-term climatic fluctuations. In contrast with these within-state dynamics, between-state dynamics reflect persistent changes in structure and processes that are not easily reversed through typical successional processes. For in-depth discussion of these topics, see Stringham and others (2003); Briske and others (2003); and Bestelmeyer and others (2003, 2004).

-- Global change?--

A. REFERENCE STATE/DYNAMIC

Major functional groups,
soil-resource conditions,
and ecological processes
(including natural disturbance
regime) are intact. System is
resistant/resilient to
disturbances & stressors.

**C. WOODY-DOMINATED
STATE/DYNAMIC**

Persistent increase in woody plants
and decrease / suppression of
herbaceous plants relative to reference
state -- representing a major shift in
functional-group structure. System
structure, functioning, & dynamics
(including disturbance regime)
significantly altered. System resistance
& resilience to disturbances/stressors
are diminished relative to reference state.

1

2

2

4

B. INVADED STATE/DYNAMIC

Major functional groups,
soil-resource conditions, and
ecological processes reasonably
intact, but system dynamics altered
by presence of functionally
significant plant invader. Resistance
& resilience of system to
disturbances/stressors (e.g.,
climatic fluctuations, fire, soil
disturbances) are somewhat
diminished relative to reference state.

3

3

6

**E. SEVERELY ERODED
STATE/DYNAMIC**

Significant loss (and/or redistribution)
of soil resources has occurred.
Functional-group diversity typically
reduced (often greatly). Site potential
is fundamentally altered due to
diminished resource availability, site
productivity, and capacity to support
characteristic functional groups.
Denuded sites (perhaps with sparse
& fluctuating populations of annuals)
represent extreme cases.

7

5

D. ANNUALIZED STATE/DYNAMIC

Persistent dominance by weedy annual
plants (typically exotic grasses),
representing major shift in
functional-group structure. System
structure, functioning, & dynamics
(including disturbance regime) significantly
altered. System resistance & resilience
to disturbances/stressors are diminished
relative to reference state.

TRANSITION	DEGRADATIONAL PROCESSES
1	Exotic plant invasion
2	Woody encroachment / thickening (fig. 10)
3	Soil erosion / redistribution (figs. 11 & 12)
4	Soil erosion / redistribution (figs. 14 & 15)
5	Exotic conversion (fig. 16)
6	Exotic conversion (fig. 17)
7	Soil erosion / redistribution (figs. 18 & 19)

Figure 9.   Conceptual model depicting major types of degraded alternative states (boxes *B* through *E*) that characterize dryland ecosystems of the region. Numbered arrows reflect general ecological processes responsible for transitions among states (see accompanying figures for detailed process models). Although not shown here, each state is characterized by a typical pattern of dynamic behavior. For state *A*, that pattern of behavior encompasses the "natural range of variability." Dashed boxes associated with state *A* reflect the likelihood that global-change processes (for example, altered atmospheric chemistry, temperatures and precipitation) will cause future patterns of variability to drift away from historic patterns.

natural disturbances and anthropogenic stressors. However, as a consequence of on-going global-change processes (for example, altered atmospheric chemistry, temperatures, and precipitation patterns), managers should recognize that future ecosystem characteristics are likely to drift away from historic patterns of variability even in the absence of local land use effects. Accordingly, the concept of the "reference state" should be sufficiently flexible to account for uncertain trajectories of global atmospheric change (for example, Currie, 2001; Shafer and others, 2001; Hannah and others, 2002; Walther and others, 2002) as well as factors such as altered landscape configurations and the introduction of invasive exotic species to regional and local species pools.

Despite uncertainties associated with future trajectories of change, four commonly observed types of degraded dryland states remain pertinent for purposes of ecosystem management and monitoring (fig. 9, boxes *B* through *E*). These are described here as follows:

- The invaded state (state *B*)—characterized by the presence of a functionally significant invasive exotic plant (for example, *Bromus tectorum*). System structure and functioning are somewhat altered relative to the reference state, but major functional groups and associated ecosystem processes generally remain intact. Presence of the invader may affect ecosystem resistance or resilience to natural disturbances or anthropogenic stressors.

- The woody-dominated state (state *C*)—characterized by a persistent increase in the ratio of woody plant biomass to herbaceous plant biomass relative to the reference state. Associated with this major structural change, ecosystem functioning (for example, disturbance regimes, rates of geomorphic and biogeochemical processes) is also significantly altered relative to the reference state.

- The annualized state (state *D*)—characterized by persistent ecosystem dominance by weedy annual plants—often including invasive exotics species such as *Bromus tectorum*. Associated with this major structural change, ecosystem functioning (for example, disturbance regimes, rates of geomorphic and biogeochemical processes) also is significantly altered relative to the reference state.

- The severely eroded state (state *E*)—characterized by severe loss or redistribution of soil resources. Site conditions have been fundamentally altered due to diminished (or persistently redistributed) resource availability, site productivity, and site capacity for supporting biotic functional groups characteristic of state *A*.

Depending on site-specific properties of particular ecosystems, there may be numerous expressions and intergradations of these four basic types of degraded states. In addition, there is tremendous variability among particular sites in their susceptibility to various transitions depicted in figure 9. Transition susceptibility varies as a function of (1) *ecosystem*

exposure to driving processes, and (2) *ecosystem resistance and resilience* to driving processes. These factors are discussed briefly at the end of this section.

The following are conceptual models describing degradational processes associated with transitions between states depicted in figure 9. As with figure 9, these process-based models are necessarily generalized and will require modification for site-specific applications. The relative significance of processes depicted in the models can be expected to vary widely among sites. The models are intended to assist managers in the consideration of ecosystem attributes to be included in long-term monitoring programs designed to support goals of sustaining the health or integrity of dryland ecosystems. The models are not meant to imply that ecosystem degradation is the certain outcome of particular factors or processes.

Transition 1—Exotic Plant Invasion

The transition from the desired state to the invaded state is caused by the establishment and spread of a functionally significant plant invader. Propagule dispersal clearly is an important factor in this transition, but resources also must be available if the introduced population is to reach a size sufficient for it to affect ecosystem functioning. Davis and others (2000) recently proposed a simple conceptual model illustrating their hypothesis that an ecosystem becomes more susceptible to invasion when there is an increase in the amount of resources that otherwise limit invasion. According to this model, factors that cause a pulse in resource supply (for example, precipitation events or fire) or a reduction in resource uptake (for example, episodic mortality of community dominants) may enable the rapid population expansion of responsive invaders that previously existed in the ecosystem at low levels. Other workers also have emphasized the importance of temporal and spatial patterns of resource availability as factors affecting ecosystem susceptibility to invasion (Johnstone, 1986; With, 2002). Consistent with the resource-based hypothesis of Davis and others (2000), there is increasing evidence that ecosystems or microsites that are rich in soil resources are particularly susceptible to invasion by exotic species (Stohlgren and others, 1999; Levine and D'Antonio, 1999; Búrquez–Montijo and others, 2002).

For example, the pulsed population expansion of *Bromus tectorum* in a relatively undisturbed grassland in Canyonlands NP was attributed to enhanced soil-moisture conditions resulting from an El Niño episode (Belnap and Phillips, 2001). Subsequent to this population expansion, community dynamics in relation to interannual climatic fluctuations were substantially different than prior to El Niño. In experimental studies, Smith and others (2000) found that the presence of the exotic annual grass red brome (*Bromus madritensis* ssp. *rubens*) in an otherwise intact Mojave Desert ecosystem affected ecosystem response to elevated concentrations of atmospheric CO_2. Similarly, the presence of invasive exotic plants can significantly degrade the resilience of dryland ecosystems to wildfire (Brooks and others, 2004), thereby increasing the likelihood

of a subsequent transition to a state dominated by an invader which promotes recurring fire (for example, transition 5 and state *D* in fig. 9).

Transition 2—Woody Plant Encroachment/Thickening

A persistent increase in the relative dominance of woody vegetation is perhaps the most widely documented transition in dryland ecosystems around the world (Archer, 1994; Archer and Stokes, 2000; see http://cnrit.tamu.edu/rlem/faculty/archer/bibliography.html). Factors proposed most commonly as explanatory mechanisms include excessive grazing and associated trampling by domestic livestock, active fire-suppression efforts, and climate (fig. 10). Elevated atmospheric CO_2 also has been suggested as a factor (Polley and others, 1996, 1997), although Archer and others (1995) argued that CO_2 enrichment is an insufficient explanation for observed patterns of vegetation dynamics. Climate plays an important role due to effects on population dynamics and competitive relations of herbaceous versus woody plants, but persistent overgrazing by domestic livestock generally has been implicated as the most important driver of transitions involving increasing dominance of unpalatable woody plants (Archer and others, 1995; Van Auken, 2000). Selective herbivory can affect the competitive relationships of plants, favoring the establishment and growth of unpalatable plants over those of palatable plants (Briske and Richards, 1994). The reduction of aboveground herbaceous biomass and litter by grazing also can reduce the availability of fine fuels required to support a regime of frequent surface fires.

Where such a fire regime is important for constraining the dominance of fire-intolerant woody vegetation, the removal of fine fuels by grazing may be more important than reduced herbaceous competition or active fire-suppression efforts as a driver of ecosystem change (Archer, 1994; Archer and others, 1995; Van Auken, 2000).

In this region, examples of persistent woody transitions outside the range of natural variability include juniper encroachment in grasslands of northern Arizona (Johnsen, 1962; Jameson, 1962) and thickening of juniper and piñon in grasslands and savannas of north-central New Mexico (for example, Bandelier NM; Allen, 1989). These examples correspond with the piñon-juniper grass savanna ecosystem (*sensu* Romme, Floyd–Hanna, and Hanna, 2003; table 3), which is characterized by a natural disturbance regime of frequent, low-severity surface fires. This model also may apply to former sagebrush steppe ecosystems and piñon–juniper shrub woodlands (Romme, Floyd–Hanna, and Hanna, 2003; table 3) where land use activities have altered ecosystem structure, lengthened fire-return intervals, and increased the range-wide proportion of systems that are shrub- or tree-dominated (Connelly and others, 2004). In some circumstances, transition to this woody-dominated state may increase the likelihood of subsequent transitions to eroded or annualized states (that is, transitions 4 and 6 to states *E* and *D* in fig. 9). It is important to recognize that this model does not apply to piñon–juniper forest ecosystems found at Mesa Verde NP (Romme, Floyd-Hanna, and Hannah, 2003) and possibly elsewhere. Nor does it apply to sparse desert shrublands or semidesert grasslands referred to as galleta—three-awn shrub steppe.
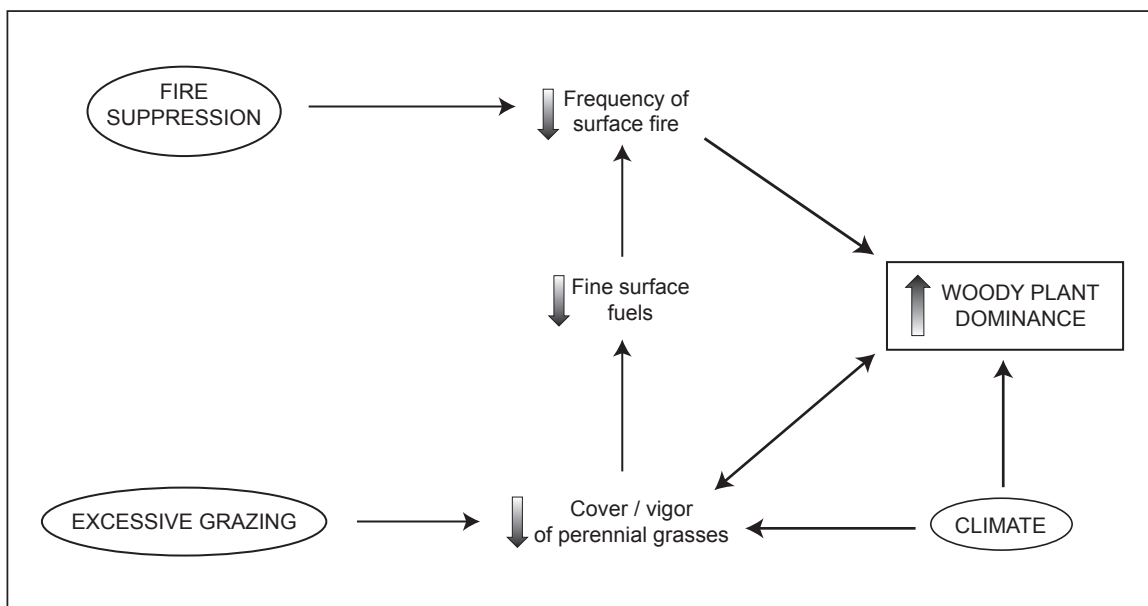

Figure 10.   Conceptual model illustrating the processes by which excessive grazing, fire suppression, and climate interactively can lead to increasing dominance by woody plants.

Table 3. Structure, disturbance dynamics, distribution patterns, current status, and restoration needs of three contrasting types of piñon–juniper ecosystems in western North America: A synthesis and set of hypotheses for further research. HRV = historic range of variability (from Romme, Floyd-Hanna, and Hanna, 2003, p. 346).

	Piñon-Juniper Grass Savanna	Piñon-Juniper Shrub Woodland	Piñon-Juniper Forest
Pre-1900 fire regime	Frequent, low-severity, surface fires carried by grasses	Moderately frequent, high-severity, crown fires carried by shrubs & trees	Very infrequent, very high-severity, crown fires carried by tree crowns
Pre-1900 stand structure	Sparse trees, few shrubs, dense grass, and other herbs	Sparse to moderately dense trees, sparse to very dense shrubs, moderately dense to sparse herbs, all depending on time since last fire	Dense trees, sparse to moderately dense shrubs, sparse herbs
Pre-1900 stand dynamics	Low tree density and high herbaceous biomass maintained in part by recurrent fire	Seral trend from herb to shrub to tree dominance, interrupted periodically by fire which returns a stand to early seral herb dominance	Stable/stationary tree age structure and little change in shrub or herbaceous layers during the long intervals without fire; very slow recovery after fire
Post-1900 changes in disturbance regime	Reduced fire frequency, great increase in fire severity	Reduced fire frequency, small increase in fire severity	Little change in fire frequency or fire severity
Post-1900 changes in structure	Increasing tree density, decreasing herbaceous biomass	Increasing tree density, decreasing shrubs and herbs	Little change in tree density or in shrubs or herbs
Overall current status	Outside HRV for disturbance regime, structure, & composition	Outside HRV for disturbance regime, structure, & composition	Still within HRV for disturbance regime, structure, & composition
Implications for restoration	Urgent need for active restoration	Urgent need for active restoration	No need for restoration, protect instead
Current stand age structure	Very old trees (> 300 years) present, but not numerous; young trees (< 150 years) dominate stands	Very old trees (> 300 years) absent or rare; young trees (< 150 years) dominate stands	Very old trees (> 300 years) numerous; stands with all-aged structure, including old & young trees
Distribution: soil characteristics	Deep, fine-textured soils	Deep, fine-textured soils	Shallow, rocky, or coarse-textured soils
Distribution: precipitation regime	Summer peak in precipitation	Winter peak in precipitation	Variable
Distribution: topographic characteristics	Gentle plains and broad valley bottoms, with few barriers to fire spread	Gentle plains and broad valley bottoms, with few barriers to fire spread	Rugged slopes, canyons, and mesa tops, with many barriers to fire spread
Distribution: adjacent vegetation types	Grasslands, ponderosa pine, or other types that burn frequently	Grasslands, big sagebrush, or other types that burn frequently	Desert scrub, "slickrock," or other types with sparse herbaceous vegetation that rarely burn
Geographic distribution	Most common in northern Mexico, southern New Mexico & Arizona, northern New Mexico, and possibly southeastern Colorado	Most common in the northern and central Great Basin and the Colorado Plateau	Scattered throughout the Colorado Plateau, Great Basin, central Oregon, southern Rocky Mountains, and southern California mountains
Examples	Jameson, 1962; Dwyer and Pieper, 1967; Allen, 1989; Segura and Snook, 1992; Dick-Peddie, 1993; Miller, 1999	Tausch and others, 1981; Koniak, 1985; Tausch and West, 1988; Miller and others, 1995; Miller and Tausch, 2001	Tausch and others, 1981; Tress and Klopatek, 1987; Kruse and Perry, 1995; Wangler and Minnich, 1996; Miller and others, 1999; Tausch and Nowak, 1999; Floyd and others, 2000; Waichler and others, 2001; Floyd and others, 2004

Although human land use activities frequently are implicated as primary drivers of woody transitions, it is important to recognize that increases in the relative dominance of woody vegetation also can occur in the absence of such activities. Between 1958 and 1996, juniper and piñon increased in sagebrush shrublands on a remote mesa in Grand Canyon NP that was unimpacted by human land use activities (Rowlands and Brian, 2001). Similarly, Harris and others (2003) found a significant increase in the dominance of woody vegetation on an ungrazed mesa in southern Utah between 1948 and 1993. In both cases, increases in the dominance of woody vegetation appear to be driven by natural successional processes. As indicated previously, area-specific research is necessary to evaluate natural disturbance regimes and processes responsible for observed dynamics.

Transition 3—Soil Erosion/Redistribution

Transition 3 (fig. 9) is associated with accelerated erosional processes that result in a significant and persistent decline in soil-resource availability, site productivity, and site capacity for supporting biotic functional groups characteristic of the reference state. Soil resources can be eroded and redistributed by aeolian processes (fig. 11), fluvial processes (fig. 12), or both. Whether wind or water is the driving force,

factors leading to accelerated rates of soil erosion and redistribution are similar. Trampling and other soil-surface disturbances can diminish soil stability by damaging biological soil crusts that protect and retain soils against erosive forces of wind, rain, and runoff (Williams, 1995b; Belnap and Gillette, 1998; Okin and others, 2001). Soil-surface disturbances also can disrupt stable soil aggregates that enhance soil stability and soil infiltration capacity (Thurow, 1991). By reducing herbaceous cover and organic-matter inputs from litter and roots, excessive grazing can diminish soil protection and soil aggregate stability (Thurow, 1991). Reductions in ground cover can result in accelerated erosion due to diminished capacity to obstruct wind and overland flow of water (Davenport and others, 1998; Reid and others, 1999; Ludwig and Tongway, 2000). Depending on site characteristics, such as soil texture, soil structure, and the vertical and horizontal structure of vegetation, reductions in ground cover may result in threshold-like increases in runoff and erosion (Davenport and others, 1998). Because of the complex and poorly understood effects of biological soil crusts on hydrologic processes, in figure 12 some uncertainty is indicated regarding effects of biological soil crusts on water and sediment capture and retention. Off-site conditions (that is, the functional status of adjacent landscape units; fig. 8) can contribute to accelerated rates of erosion. Examples are saltating soil particles that produce aeolian soil

Coppice dunes formed by wind-driven movement of unstable soil where most perennial grasses and shrubs have been removed. Dunes formed where persistent shrubs and exotic annual plants such as tumbleweed (*Salsola* sp.) captured sediment. Navajo County, Arizona. Photograph by Mark Miller, USGS.
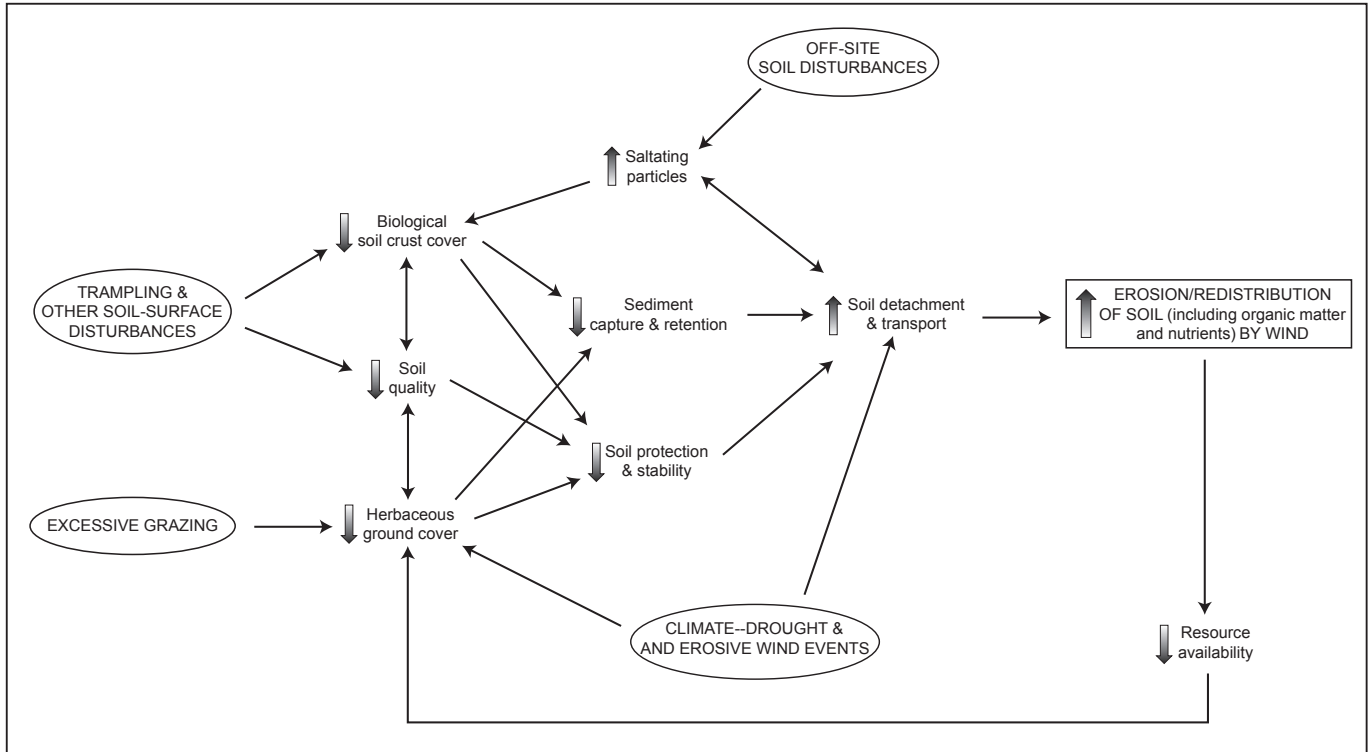
Figure 11. Conceptual model illustrating the processes by which excessive grazing, soil-surface disturbances, off-site soil-surface disturbances, and climate interactively can lead to accelerated erosion/redistribution of soil resources by wind.

Figure 12. Conceptual model illustrating the processes by which excessive grazing, soil-surface disturbances, off-site hydrologic function, and climate interactively can lead to accelerated erosion/redistribution of soil resources by water.
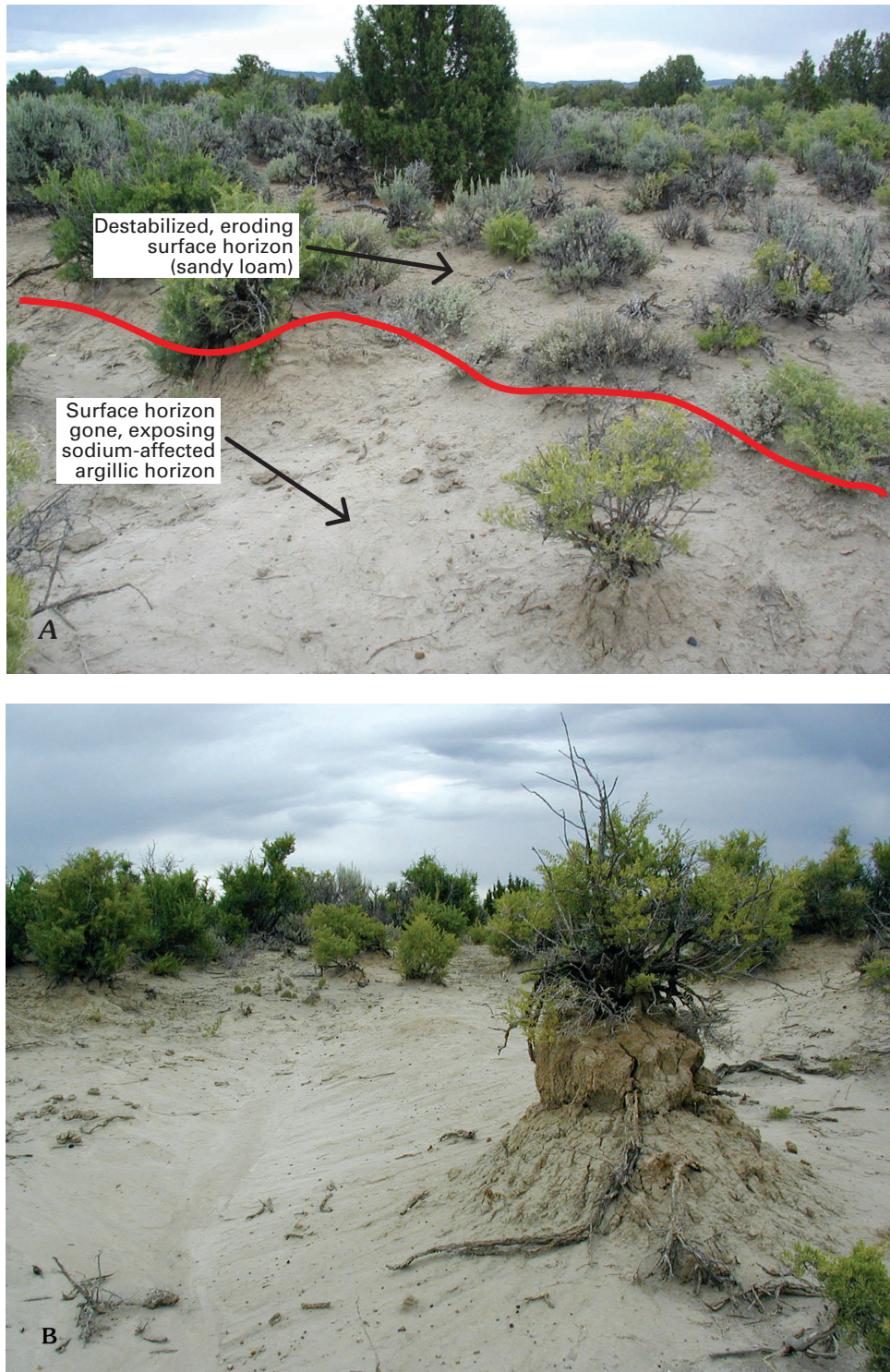
Figure 13. Example of site where accelerated erosion has led to the significant loss of soil resources and persistent alteration of ecosystem structure and functioning (BLM photos). In *A*, the area above the red line retains a sandy-loam surface horizon that, though unstable and eroding, facilitates water infiltration and provides conditions suitable for vascular-plant establishment. Where this thin surface horizon has been lost below the red line, soil physical and chemical properties inhibit plant establishment and facilitate water-driven erosion. Panel *B* illustrates extreme results of erosion at this site. Photographs are of a site in Headquarters Valley, Grand Staircase-Escalante National Monument, Utah. Soil is transitional between an Elias series (Natriargid) and a Barx series (Calciargid) (Kent Sutcliffe, pers. commun., 2004).

detachment (fig. 11; Toy and others, 2002) and runoff that causes fluvial soil detachment and transport (fig. 12; Thurow, 1991). Climate plays a role in this transition due to its effects on vegetative ground cover and the frequency of erosive wind and precipitation events (for example, fig. 5). As soil resources are lost due to erosional processes, declining resource availability generates a positive feedback facilitating further declines in vegetative ground cover and further increases in erosion (figs. 11 and 12; for example, Tongway and others, 2003; Friedel and others, 2003; Sparrow and others, 2003).

In the Colorado Plateau region, good examples of this transition can be found on stream-terrace soils that have been impacted by soil-surface disturbances (fig. 13). In this landscape setting, a typical intact soil profile consists of a thin (0–5 cm) surface horizon of fine sandy-loam texture that overlies a thick subsurface argillic (clay-rich) horizon with high sodium content caused by capillary rise of alluvial groundwater (for example, the Elias series—for the official series description see *http://ortho.ftw.nrcs.usda.gov/cgi-bin/osd/osdname. cgi*). Where unimpacted by land use activities, such sites are generally characterized by well-developed biological soil crust communities, productive stands of the C_4 bunchgrass *Sporobolus airoides* (alkali sacaton), and the shrub *Sarcobatus vermiculatus* (greasewood). Destabilization and loss of the surface horizon expose a horizon with physical and chemical

properties that tend to inhibit establishment of vascular plants and biological soil crusts, as well as enhance runoff and water-driven erosional processes. In all cases where this occurs, ecosystem structure and functioning are persistently altered; in extreme cases, erosion leads to the development of badland topography. Examples similar to those depicted in figure 13 can be found in Capitol Reef NP.

Transition 4—Soil Erosion/Redistribution

Erosional processes associated with transition 4 (figs. 14 and 15) are similar to those associated with transition 3 (figs. 11 and 12), but in the former, processes are modified due to an increase in the dominance of woody vegetation compared with the reference state. Relative to transition 3, within-site soil redistribution is more important in Transition 4 (figs. 14 and 15). Soil resources transported from interspaces may be captured and retained within the subcanopy environments of woody plants because of interactions of shrubs and trees with wind- and water-driven geomorphic processes. The redistribution of soil resources from intercanopy spaces to subcanopy environments contributes to a positive feedback favoring continued increases in the ratio of woody to herbaceous biomass. Regional examples of the positive-feedback linkage

Figure 14. Conceptual model illustrating the processes by which increasing woody-plant dominance, excessive grazing, soil-surface disturbances, off-site soil disturbances, and climate interactively can lead to accelerated erosion/redistribution of soil resources by wind.
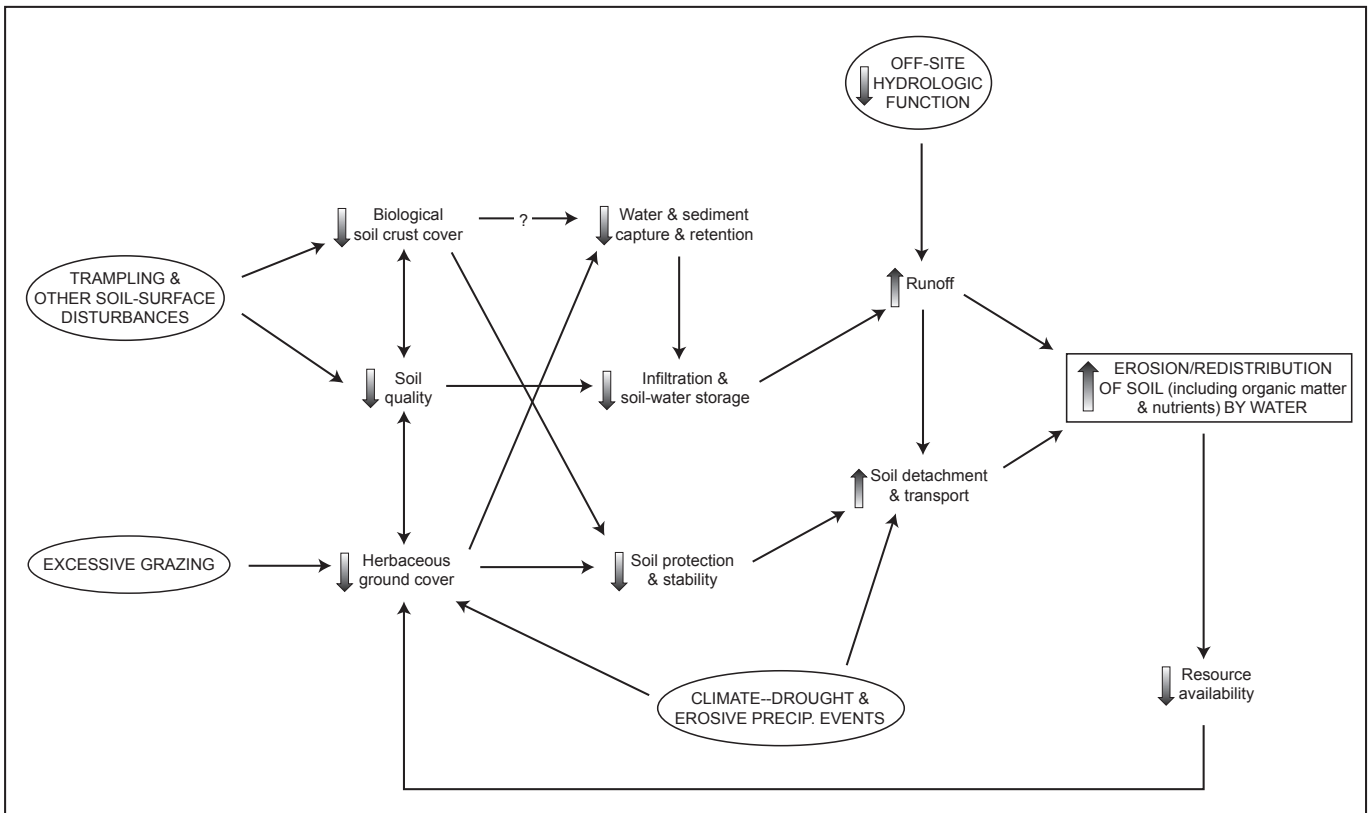
Figure 15.   Conceptual model illustrating the processes by which increasing woody-plant dominance, excessive grazing, soil-surface disturbances, off-site hydrologic function, and climate interactively can lead to accelerated erosion/redistribution of soil resources by water.
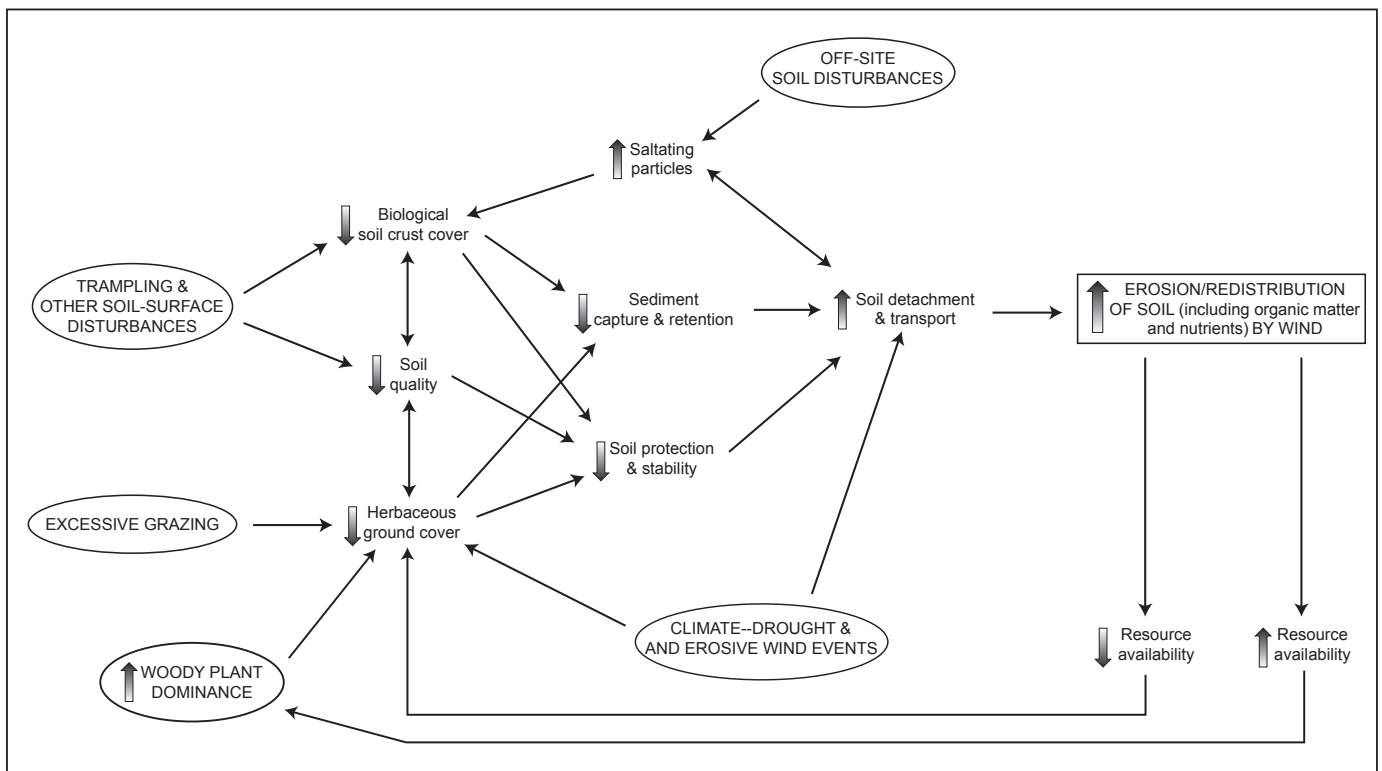
between soil redistribution and increasing dominance of woody vegetation include coppiced shrublands of Monument Valley (pers. obs.) and piñon–juniper rocklands of Bandelier NM where severe erosion has been facilitated by past grazing and fire-regime alterations that led to increased tree cover and diminished herbaceous cover (Allen, 1989; Wilcox and others, 2003; Davenport and others, 1998; Jacobs and Gatewood, 1999). This positive-feedback model has been proposed as a common pathway of dryland degradation or "desertification" (Schlesinger and others, 1990; Havstad and others, 2000).

Transition 5—Exotic Conversion

The persistent conversion of dryland ecosystems to dominance by exotic annuals is a widespread pathway of degradation (for example, Billings, 1990; Connelly and others, 2004). Many weedy annuals may be involved, but exotic annual grasses are the most common dominants. Several factors may contribute to processes associated with this transition to an "annualized" state (fig. 16), but all of them invariably affect the availability of resources that otherwise limit population growth in the exotic species (Davis and others, 2000). In this

context, resources may include safe sites for germination and establishment (Harper, 1977; Grubb, 1977), as well as water, mineral nutrients, and light. Soil-surface disturbances may facilitate establishment of ruderal exotic species if availability of safe-site opportunities is a limiting factor (Crawley, 1987). However, if soil-surface disturbances do not ameliorate resource limitations, then soil-surface disturbance alone will not facilitate a transition to exotic dominance (Hobbs, 1991). Excessive grazing can reduce the competitive abilities of native perennial grasses relative to exotic annuals if the former are preferentially grazed, thereby favoring population expansion of lesser grazed exotic annuals. Resource enrichment associated with climatic episodes, fire, resource transfers from adjacent sites, excreta from localized livestock concentrations, or atmospheric N deposition may facilitate population expansion and persistent conversion to dominance by exotic annuals—particularly if associated factors (for example, selective herbivory by livestock) simultaneously have an adverse effect on native competitors. Increasing dominance by exotic annuals can lead to a dramatic shift in fire regime where annuals drive increases in the abundance and continuity of fine fuels and in the frequency of surface fires (Brooks and others,
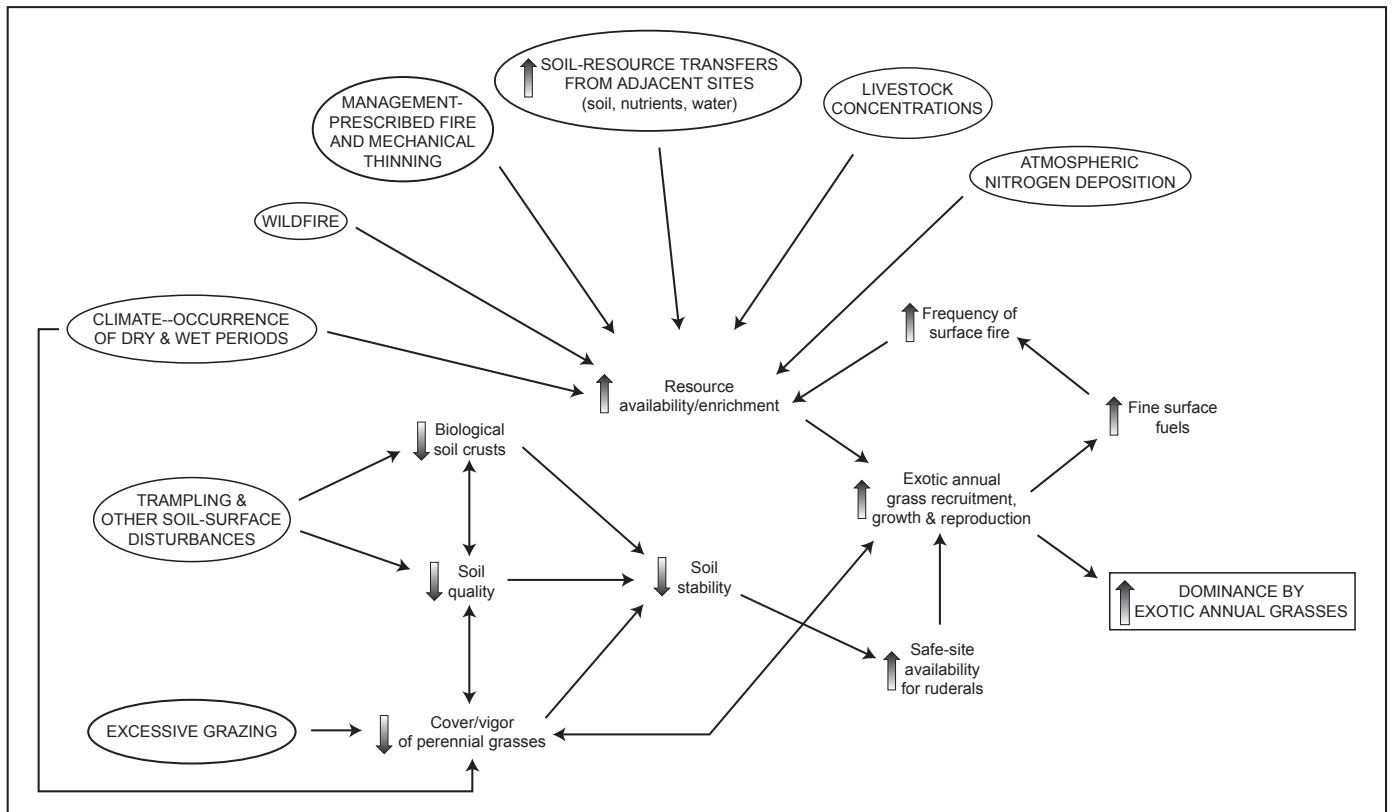
Figure 16. Conceptual model illustrating the processes by which excessive grazing, soil-surface disturbances, management-prescribed fire and mechanical thinning, wildfire, atmospheric nitrogen deposition, concentrated livestock activites, landscape-level soil-resource transfers, and climate interactively can lead to increasing dominance (and site conversion) by exotic annual grasses.

2004). Although a shift in fire regime does not always accompany ecosystem annualization, the positive-feedback linkage between exotic grasses and wildfire is sufficiently widespread to have been proposed as an important element of global change (D'Antonio and Vitousek, 1992). Fenn, Baron, and others (2003) suggested that, in some locations, atmospheric N deposition could trigger fire/exotic grass cycles by increasing resource availability for exotics. Experimental results from the Mojave Desert suggest that increasing levels of atmospheric CO_2 may have a similar triggering effect (Smith and others, 2000). Romme, Oliva, and Floyd (2003) expressed concern that invasive exotic species could respond to natural fires in piñon-juniper ecosystems of Mesa Verde NP and subsequently initiate a fire/exotic species cycle. Examples of annualized ecosystems are in several NPS units in the Colorado Plateau region, including Canyonlands NP, Arches NP, Golden Spike NHS, Zion NP, and Capitol Reef NP. In some circumstances, conversion to annuals may accelerate erosional processes that lead to further site degradation (for example, transition 7 to state *E* in fig. 9).

Transition 6—Exotic Conversion

Similar to the concerns of Romme, Oliva, and Floyd (2003) regarding the potential for exotic conversion following wildfire in Mesa Verde NP ecosystems, West (1999) suggested that persistent increases in the dominance of woody vegetation could facilitate exotic conversion by increasing the likelihood of high-intensity fires (fig. 17). Due to increased levels of competition, unnaturally dense populations of woody plants also may be more susceptible to drought, insect infestations, or other disturbances/stressors. Whether mortality of woody dominants is triggered by fire or some other factor, the sudden pulse of resource availability and release from competitive suppression could enable rapid expansion of existing exotic-species populations. If the population expansion is sufficient to cause a persistent increase in the abundance and continuity of surface fuels, a self-maintaining fire–exotic species cycle could be initiated. This type of transition may be a concern in parks such as Bandelier NM where the early 21st century drought has triggered near-complete mortality in unnaturally dense piñon stands.

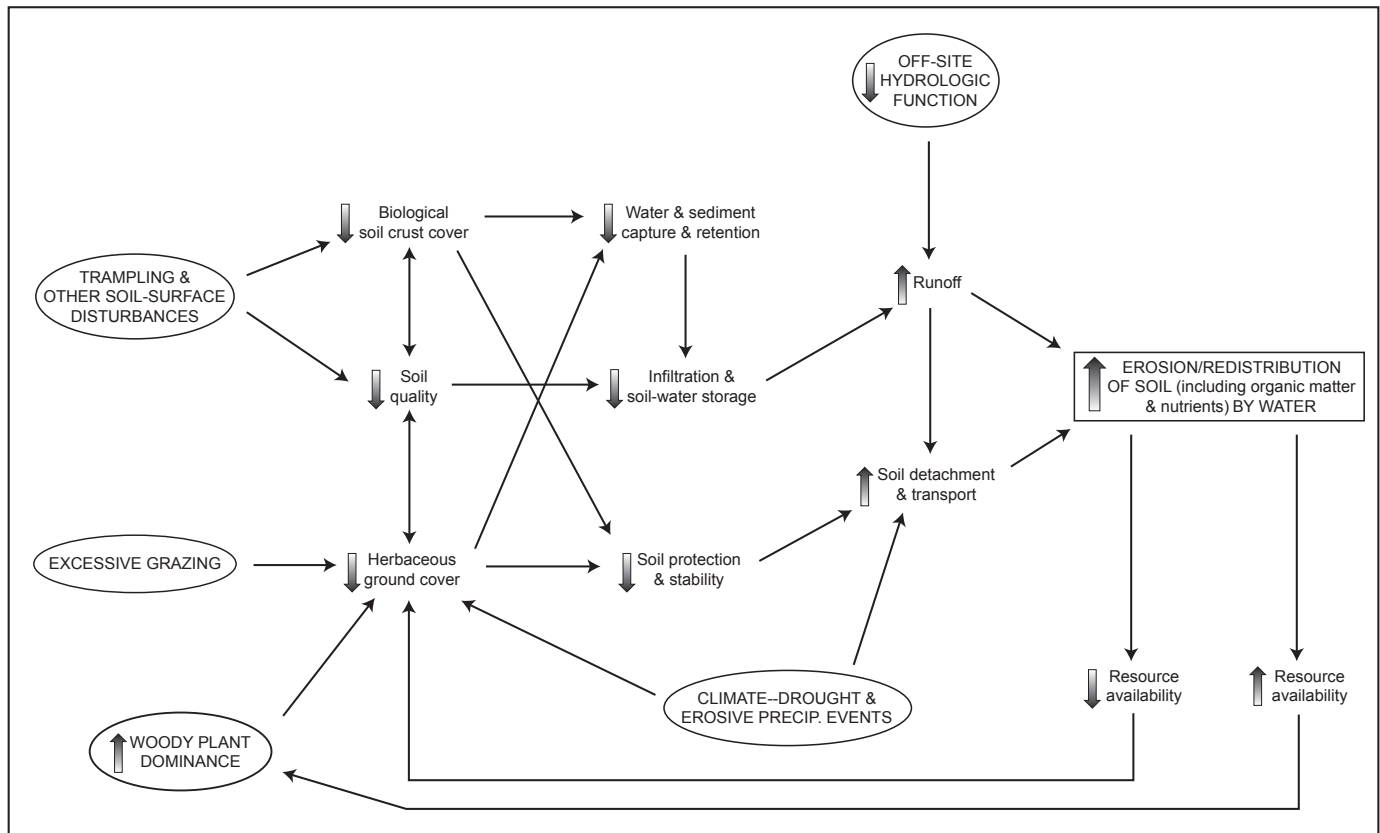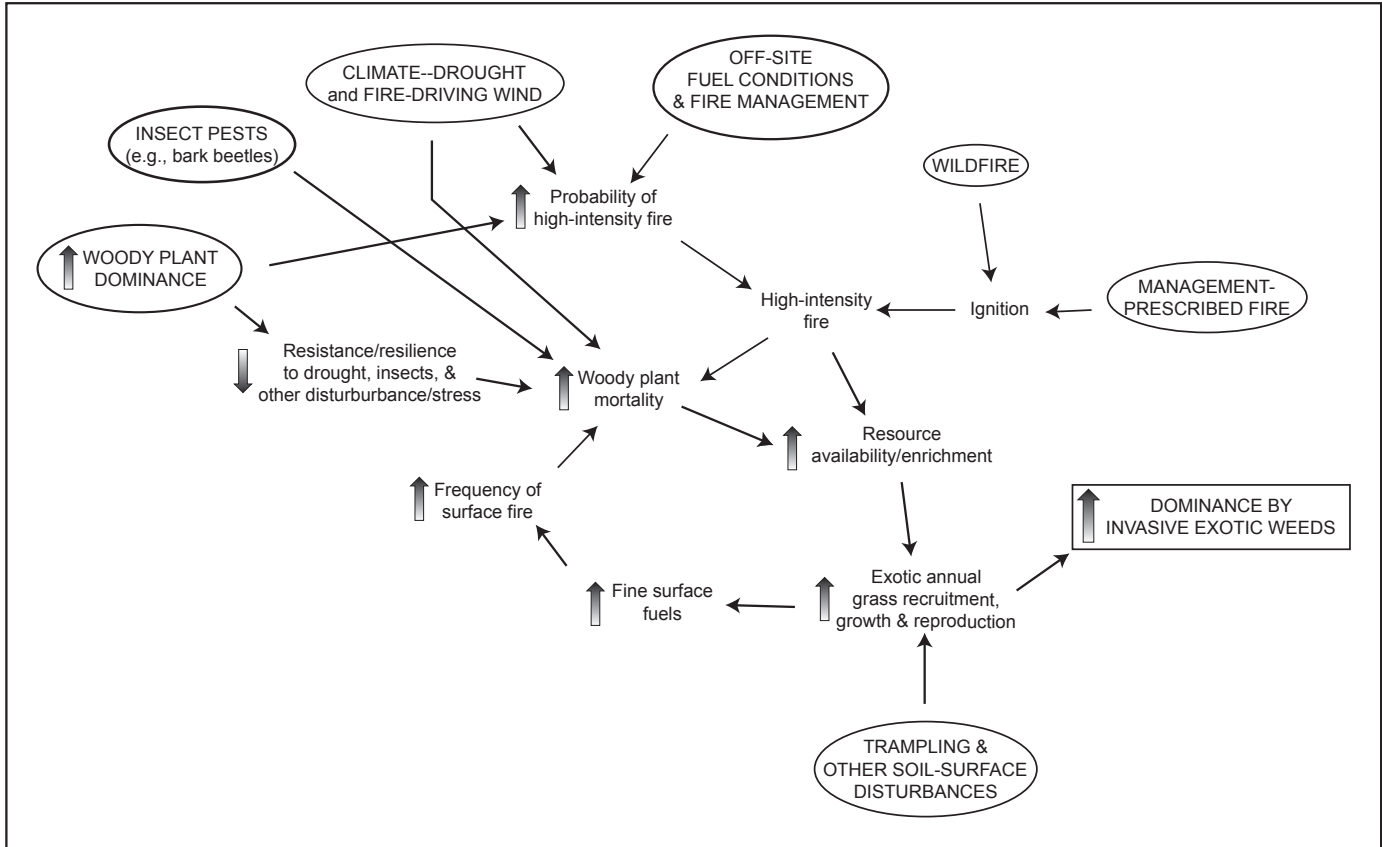**Figure 17.**   Conceptual model illustrating processes by which increasing woody-plant dominance, soil-surface disturbances, insect pests, climate, off-site fuel/fire conditions, wildfire, and management-prescribed fire interactively can lead to increasing dominance (and site conversion) by exotic annual grasses.

Transition 7—Soil Erosion/Redistribution

Severe erosion (transition to state *E* in fig. 9) may be more likely in ecosystems dominated by exotic annual plants than in ecosystems dominated by perennial species because of greater fluctuations in annual ground cover in relation to climate (figs. 18 and 19). Greater soil exposure to erosive forces during unfavorable climatic periods could trigger spiraling processes of degradation as soil losses cause decreased ground cover and even greater soil exposure to erosive forces. Examples of soil erosion in annualized ecosystems can be found in Arches NP (fig. 20) and Canyonlands NP.

Ecosystem Susceptibility to Change

As discussed previously, there is much variability among dryland ecosystems in their susceptibility to transitions depicted in figure 9. Transition susceptibility varies as a function of (1) *ecosystem exposure* to driving processes, and (2) *ecosystem resistance and resilience* to driving processes. Depending on the goals and objectives of a long-term monitoring program, factors affecting ecosystem exposure, resistance, and resilience may play a role in spatial and temporal aspects of the monitoring design.

Ecosystem Exposure

Ecosystem exposure to drivers of change—particularly those considered to be anthropogenic stressors—is an important factor influencing ecosystem susceptibility to change beyond the range of conditions represented by the reference state. For example, sites exposed to frequent soil-surface disturbances or excessive herbivory by large mammals will be more susceptible to transitions affected by those processes than sites that are not so exposed, all else being equal. Landscape configuration also must be considered when evaluating ecosystem exposure where stressors may be associated with ecological

Figure 18. Conceptual model illustrating processes by which increasing site dominance by exotic annual grasses, excessive grazing, soil-surface disturbances, off-site soil-surface disturbances, and climate interactively can lead to accelerated erosion/redistribution of soil resources by wind.

flows from connected landscape units (fig. 8). At a regional scale, there is variation in ecosystem exposure to climatic factors (for example, erosive, high-intensity precipitation events) that affect the probability of transitions caused by erosional processes (fig. 6). Ecosystem exposure is not a static property. It can change with changes in climate and atmospheric conditions, landscape configuration, management, magnitude of existing stressors, or emergence of novel stressors.

Ecosystem Resistance and Resilience

Persistent transitions to degraded states occur when ecosystem properties that confer resistance and resilience are damaged or otherwise exceeded (Archer and Stokes, 2000; Tongway and Hindley, 2000; Stringham and others, 2003). Ecosystem resistance and resilience are not static and can change in relation to varying climatic conditions and dynamic ecosystem properties affected by climate, land use, and management (Scheffer and others, 2001; Scheffer and Carpenter, 2003). Some aspects of resistance and resilience also are strongly controlled by ecosystem properties that are relatively stable through time. Examples of these inherent ecosystem properties include landscape position and soil characteristics

such as rock content, texture, mineralogy, profile development, and depth (for example, fig. 13).

A generalized description of factors affecting the resistance and resilience of dryland ecosystems is presented in appendix table C. Although generalizations can be useful, detailed considerations of resistance, resilience, and other aspects of system stability require that the variable of interest, benchmark conditions, spatial scale, temporal scale, and disturbance characteristics be clearly identified on a site-specific basis (Grimm and Wissel, 1997). Details matter—for example, the effects of soil properties on plant resistance and resilience to drought may vary with drought characteristics and among plant species in relation to particular ecophysiological traits.

Implications for Ecosystem Classification

Given the importance of ecosystem resistance and resilience in affecting probabilities of ecosystem change beyond the range of natural variability, an ideal ecosystem classification system to support ecosystem management and monitoring would be based on stable properties that influence ecosystem resistance and resilience. From the preceding discussion and appendix table C, general factors that most strongly affect resistance and resilience are climatic conditions, soil structure,
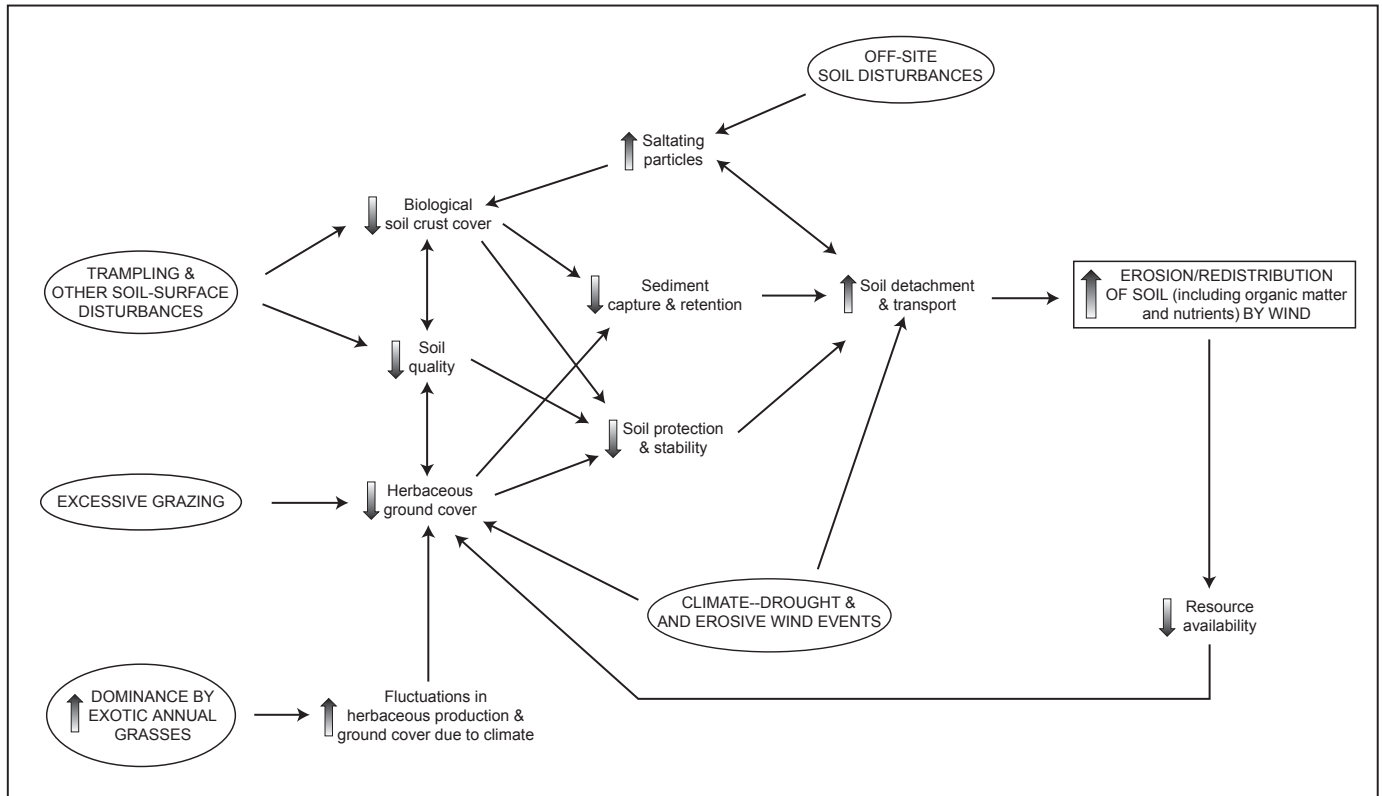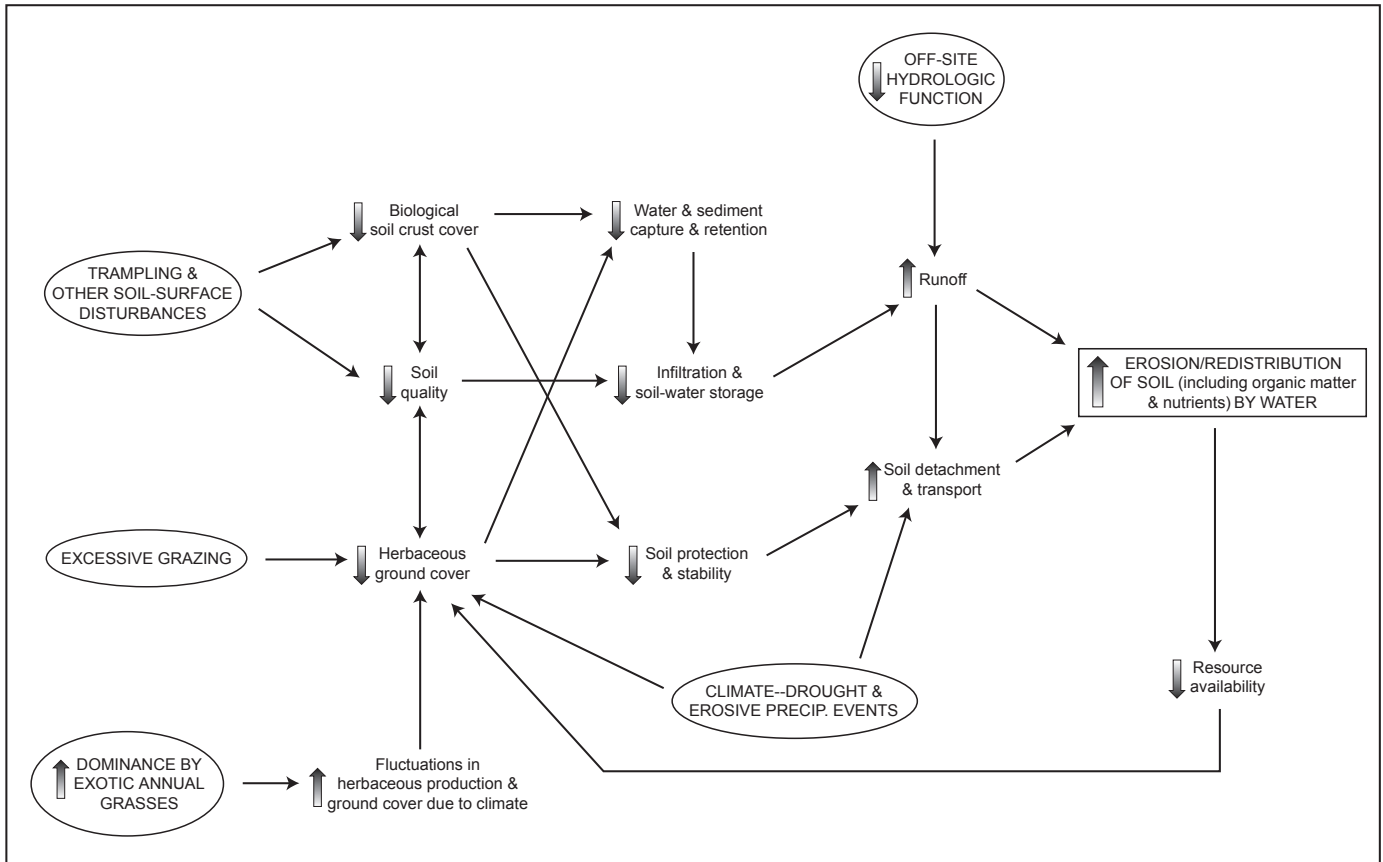
Figure 19. Conceptual model illustrating processes by which increasing site dominance by exotic annual grasses, grazing, soil-surface disturbances, off-site hydrologic function, and climate interactively can lead to accelerated erosion/redistribution of soil resources by water.

Figure 20. Example of an annualized ecosystem at Arches National Park where climate-driven fluctuations in ground cover and persistent soil instability likely contribute to accelerated rates of wind erosion. Photograph by Mark Miller, USGS.

vegetation structure, and inherent ecosystem properties described by substrate characteristics and landscape setting. Although climatic conditions themselves are not stable, latitude, elevation, and aspect are three invariant factors that are certain to affect climatic conditions irrespective of future global climate change. To support ecosystem management and monitoring, it is therefore recommended that ecosystems be classified in relation to invariant climatic zones, substrate characteristics, and landscape setting rather than by the current composition of biotic communities.

For dryland ecosystems, the most widely used classification scheme based on general climatic zones and inherent site properties is the *ecological site* system of the U.S. Department of Agriculture Natural Resources Conservation Service (USDA NRCS). In this classification system, an *ecological site* is defined as a kind of land with specific physical characteristics which differs from other kinds of land in its ability to produce distinctive kinds and amounts of vegetation and in its response to management (Society for Range Management Task Group on Unity in Concepts and Terminology 1995, p. 279; Creque and others, 1999). Soil surveys produced by NRCS match soil series with ecological sites, and many ecological site descriptions are available on-line.[12] These descriptions provide basic information on dynamics of soils and plant communities, and NRCS staff and cooperators currently are developing site-specific conceptual models that incorporate hypotheses regarding ecosystem resistance, resilience, and non-linear (threshold) responses in relation to land use and climate (USDA Natural Resources Conservation Service, 2003; Bestelmeyer and others, 2003, 2004). Challenges in the application of this scheme to planning, implementation, and interpretation of long-term monitoring may include lack of recent soil/ecological site mapping (older data may be less complete or accurate than recent data), complex map units (more than one soil series and ecological site per map unit), and inconsistent ecological site classifications across political boundaries. Alternative approaches to the classification of ecological land units for purposes of assessment and monitoring are provided by Bourgeron and others (2001a, b).

Conclusion

This report presents a literature review and a series of ecological conceptual models intended to inform policymakers and researchers in the selection of environmental attributes for long-term monitoring of dryland ecosystems of the Colorado Plateau. Climate and atmospheric conditions, soil-resource characteristics, major biotic functional groups, and typical natural disturbance regimes are reviewed because of their significance for ecosystem structure, functioning, and sustainability (Chapin and others, 1996). A generalized conceptual model describes (1) functional relationships among

key structural components of dryland ecosystems; (2) effects of climate, natural disturbances, and anthropogenic stressors on the functioning of selected ecosystem processes; and (3) how these drivers of ecosystem change can interact to produce particular patterns of ecosystem dynamics. Because a common goal of long-term monitoring is to provide managers with information needed to help sustain the health or integrity of ecosystems, additional models emphasize common processes and pathways of dryland degradation. Although developed to support the identification of long-term monitoring needs in NPS units, information in this report is broadly applicable well beyond NPS management boundaries and should be of use to other organizations or persons involved in management, conservation, and monitoring of dryland ecosystems in the Colorado Plateau or bordering ecoregions.

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[12] See the Electronic Field Office Technical Guide at http://www.nrcs.usda.gov/technical/efotg/.

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Appendix

Appendix Table A. Primary functions and attributes/measures associated with components of dryland ecosystems. Components are organized in relation to the four interactive controls of ecosystem structure and function.

INTERACTIVE CONTROLS*	COMPONENTS/PROCESSES		PRIMARY ECOSYSTEM FUNCTIONS	ATTRIBUTES/MEASURES
Regional climatic and atmospheric conditions	Precipitation		Water inputs; drives water-limited ecosystem and population processes (for example, nutrient cycling, C and N fixation, seed germination); erosive force for detachment, entrainment, and overland redistribution and export of soil, litter, and propagules; drives fire disturbances due to effects of interannual variability on fuel production and flammability; strongly affects ecosystem resistance and resilience to natural disturbances and anthropogenic stressors.	Seasonality, quantity, intensity (amount per event and per unit time), duration, temporal frequency, temporal variability (among seasons, within seasons, among years), spatial variability, form (rain vs. snow). Frequency, intensity, and duration of erosion-driving events.
	Wind		Drives the redistribution and export (transfer among patches and among systems) of soil, litter, and propagules; affects ecosystem-atmosphere gas-exchange (CO_2 intake and evapotranspiration); energy-balance modification (transfer of sensible and latent heat).	Average sustained and peak velocities and direction (and frequency-magnitude distributions of these by season), seasonal and diurnal variability, spatial variability. Frequency, intensity, and duration of erosion-driving events.
	Radiant energy		Energy inputs for photosynthesis and sensible heat; effects on ecosystem-atmosphere gas-exchange (CO_2 uptake and evapotranspiration) and energy balance; interacts with precipitation to affect resource availability and drive biotic processes through effects on timing and rate of metabolic activity.	Maximum, minimum, and average values by season (heat), spectral characteristics, intensity, temporal variability (seasonal and diurnal), spatial variability (horizontally and vertically).
	N_2 and CO_2		Nitrogen and carbon inputs (gaseous).	Atmospheric concentration.
	Dust & other airborne constituents		Mineral nutrient inputs.	Quantity, chemical composition, temporal distribution (seasonality), spatial distribution.
Disturbance regime	Episodic climatic events	Drought	Drives change in ecosystem structure and function (1) by altering competitive relations and inducing selective, potentially widespread mortality – resulting in persistent dominance shifts among vegetative functional groups; and (2) by affecting ecosystem resistance/resilience to other natural disturbances (for example, extreme precipitation events, wind storms, insect outbreaks, and/or fire) and anthropogenic stressors.	Seasonality, intensity, duration, frequency, extent, timing in relation to extreme precipitation and wind events.
		Extreme precipitation events/floods	Drives change in ecosystem structure and function (1) by inducing selective establishment episodes (or less commonly, selective mortality) of vegetative functional groups – resulting in persistent dominance shifts; and (2) due to extreme erosive forces for detachment, entrainment, and redistribution and export of soil and soil resources, potentially inducing geomorphic change.	Seasonality, intensity, duration, frequency, timing in relation to drought, and the amount of time required for biotic and biotically structured ecosystem components and functions to recover from drought.
		Wind storms	Drives change in ecosystem structure and function due to extreme erosive forces for detachment, entrainment, and redistribution and export of soil and soil resources.	Seasonality, intensity, duration, frequency, timing in relation to drought, and the amount of time required for biotic and biotically structured ecosystem components and functions to recover from drought.
		Extreme temperature events	Drives change in ecosystem structure and function by inducing selective mortality, potentially resulting in long-term shifts in dominants.	Intensity, duration, frequency, extent, timing in relation to other disturbances.

INTERACTIVE CONTROLS*	COMPONENTS/PROCESSES	PRIMARY ECOSYSTEM FUNCTIONS	ATTRIBUTES/MEASURES
Disturbance regime (continued)	Fire	Drives change in ecosystem structure and function by (1) directly altering vegetation structure (differential resistance and resilience to fire), including spatial heterogeneity; (2) altering the forms, bioavailability, and spatiotemporal distribution of soil resources; and (3) increasing runoff and soil erosion. Over longer time scales, fire may decrease erosion and runoff due to increases in herbaceous ground cover.	Intensity, spatial extent and pattern, frequency, timing in relation to other disturbances such as extreme precipitation and wind events.
	Insect/disease outbreaks	Drives change in ecosystem structure and function by inducing selective and often widespread mortality, potentially resulting in long-term shifts among dominant functional groups. May reduce ecosystem resistance/resilience to other disturbances such as fire.	Intensity, duration, frequency, extent, timing in relation to other disturbances.
	Herbivory	Drives change in ecosystem structure and function by (1) altering competitive relations among palatable and unpalatable plant taxa; (2) altering vegetation resistance and resilience to drought, other disturbances, and stressors; and (3) potentially affecting primary productivity and litter deposition. In combination, these can alter functional group structure, including spatial heterogeneity, and ecosystem capacity to capture and retain soil resources. Excretion further alters the spatiotemporal distribution of resources.	Intensity, selectivity, spatial extent and pattern, frequency, timing in relation to other disturbances such as drought, and the amount of time required for biotic and biotically structured ecosystem components and functions to recover from drought.
	Digging/burrowing	Alters soil structure and function (creation of macropores potentially increases water capture and retention); alters spatiotemporal distribution of soil resources; generates patch structure/heterogeneity; potentially alters structure of vegetative functional groups due to resource alteration and creation of establishment opportunities.	Spatial distribution and extent, frequency, depth, timing in relation to other disturbances such as extreme wind and precipitation events.
	Trampling	Destabilizes soil and decreases resistance of soil to erosion and redistribution by wind and water; compacts soil (alters soil structure and function); alters structure and function of biological soil crusts; alters vegetation structure directly due to trampling of vegetation and indirectly due to effects on soil characteristics.	Intensity, spatial extent and pattern, frequency, timing in relation to other disturbances such as extreme wind and precipitation events, drought, and the amount of time required for biotic and biotically structured ecosystem components and functions to recover from drought.
Biotic functional groups	Predators	Regulation of (or response to) prey populations, including granivores and herbivores. May also impact ecosystem structure and function by digging/burrowing (see above).	Composition, quantity, population structure, and dynamics; physiological condition.
	Herbivores	See Herbivory, above. May also impact ecosystem structure and function by digging/burrowing (see above). [Potential agents of disturbance – see herbivory, above.]	Composition, quantity, population structure, and dynamics; physiological condition.
	Granivores	Alteration of vegetation structure (composition and spatial heterogeneity) due to selective collection, consumption, burial, and redistribution of propagules. May also impact ecosystem structure and function by digging/burrowing (see above).	Composition, quantity, population structure, and dynamics; physiological condition.

INTERACTIVE CONTROLS*	COMPONENTS/PROCESSES		PRIMARY ECOSYSTEM FUNCTIONS	ATTRIBUTES/MEASURES
Biotic functional groups (continued)	VEGETATION: Small trees Shrubs Dwarf shrubs Perennial grasses		Energy capture and conversion; biomass production; litter deposition (soil protection and inputs to nutrient cycles); nutrient retention (intraplant cycling); environmental modification (reducing soil temperatures and evaporative rates via shading and litter deposition; generating resource heterogeneity via uptake, litter deposition, and capture of waterborne and windborne materials); obstruction to wind and overland water flow (reducing erosive energy and enhancing capture and retention of soil resources); rainfall interception and redistribution via stemflow (reducing erosive energy and enhancing capture and retention of soil resources). In combination, these functions contribute to resistance/resilience of soil functions to disturbance by trampling and erosive forces of wind and water. Provide fuel for fire and habitat structure for vertebrates and invertebrates.	Composition, quantity (cover and biomass), population structure and dynamics, vertical structure, spatial distribution/heterogeneity, photosynthetic pathway, leaf longevity, litter quantity and quality (for example, C:N ratio), flammability, productivity, physiological activity and condition, resistance/resilience of structure and function to dominant natural disturbances and anthropogenic stressors.
	The Soil Continuum	Biological soil crusts (photoautotrophs)	Soil stabilization and soil-surface protection; energy capture and conversion; nutrient capture, retention, and cycling (N fixation, capture of airborne minerals in dust); obstruction to overland water flow (increased surface roughness enhances capture and retention of soil resources); environmental modification (albedo and soil temperature); soil-temperature increases (decreased albedo); habitat creation (due to long-term soil stabilization).	Composition, quantity (cover and biomass), spatial distribution and contiguity, microtopographic heterogeneity/surface roughness, physiological activity and condition, productivity, resistance/resilience of structure and function to dominant natural disturbances and anthropogenic stressors.
		The Soil Surface		
		Roots	Soil stabilization; nutrient and water acquisition and transport; water redistribution in soil profile; organic-matter inputs (exudates and tissues); macropore creation; rhizospere acidification (release CO_2 and organic acids).	Morphology, density, horizontal and vertical distribution, spatial and temporal patterns of physiological activity, productivity.
		Soil biota (heterotrophs)	Litter decomposition and nutrient cycling; N fixation; symbiotic relations with vascular plants (symbiotic enhancement of nutrient and water delivery to vascular plants may increase resistance/resilience of these plants to drought or other disturbances).	Composition, quantity (biomass), spatial distribution vertically and horizontally, temporal distribution, spatial and temporal patterns of physiological activity, productivity, resistance/resilience of structure and function to dominant natural disturbances and anthropogenic stressors.
Soil resources		Soil mineral matrix Soil organic matter Soil water Soil air	Nutrient storage, supply, and cycling; water storage and supply; medium for plant growth; habitat for soil biota involved in nutrient cycling; positive effects on resistance/resilience of vegetative functional groups to drought, herbivory, and trampling.	Inherent properties (relatively insensitive to change): Mineralogy and texture by depth, spatial heterogeneity in these properties, depth. Dynamic properties (subject to change): Aggregate stability and bulk density (structure), organic-matter quantity and quality (for example, C:N ratio), depth (often considered an inherent property, but subject to change over decadal time scales), erosion rate, infiltration rate, biotic activity, surface crusting (biotic or physicochemical), surface roughness, spatial heterogeneity of these properties, resistance/resilience of structure and function to dominant natural disturbances and anthropogenic stressors.
		Soil temperature	Regulates physiological activity of autotrophic and heterotrophic soil biota, including roots.	Maximum, minimum, and average values by season, temporal variability (seasonal and diurnal), spatial variability (horizontally and vertically).

Primary sources: Whitford (2002), Herrick and others (2002), Belnap and Lange (2003), Ehleringer and others (2000), Seybold and others (1999), Whisenant (1999), and Ludwig and others (1997).

* Interactive controls are constrained by the five state factors—(1) global/regional atmospheric resources and conditions, (2) topography, (3) parent material, (4) potential biota, and (5) time (Jenny, 1980; Chapin and others, 1996).

Appendix Table B. Potential effects of major anthropogenic stressors on structure and functioning of dryland ecosystems. Potential impacts of changing temperatures, atmospheric chemistry, and atmospheric circulation patterns (including precipitation) are excluded.

Stressors	Stress mechanisms	Potential effects on ecosystem components and functions (emphasizing effects on energy flow, nutrient capture and retention, and water capture and retention)
Park use by terrestrial recreationists	Trampling of soil and vegetation	Damaged biological soil crusts and vascular plants; decreased N fixation by biological crusts; decreased soil-surface roughness; enhanced recruitment opportunities for exotic plants favored by soil destabilization; altered vegetation structure; decreased soil protection by biological crusts; decreased soil aggregate stability; decreased soil stability; decreased resistance of soil to erosion by wind and water; increased bulk density; decreased infiltration; increased overland flow of water; decreased soil-water availability for plant growth, soil biotic activity, and nutrient cycling; decreased root growth and soil-organic-matter inputs; decreased plant growth; decreased resistance and resilience of plants to drought; increased redistribution and export of soil, litter, nutrients, and water; decreased capacity of ecosystem to capture and retain soil resources; multiple cascading effects due to feedbacks among soil functions, soil-resource retention, resource heterogeneity, and vegetation structure.
	Introduction of invasive exotic plants	See exotics, below.
Livestock & other large herbivores	Trampling of soil and vegetation	See trampling, above.
	Excessive herbivory	Altered competitive relations of plants; reduced plant canopy cover; reduced fine fuels and frequency of low-intensity surface fires; altered vegetation structure (for example, dominance shift from palatable plants to unpalatable plants or from herbaceous plants favored by fire to woody plants eliminated by fire); reduced plant-canopy protection of soil; reduced vegetative obstruction of wind and overland water flow; reduced capture and retention of soil resources; reduced litter deposition and litter-protection of soil; reduced soil-organic-matter inputs; reduced soil aggregate stability; decreased resistance and resilience of soil to trampling; decreased root growth; decreased resistance and resilience of grazed plants to drought; multiple cascading effects due to feedbacks among vegetation structure, soil-resource retention, resource heterogeneity, and soil functions.
	Excretion	Nutrient losses (N volatilization); nutrient immobilization in dung pats; increased spatial and temporal heterogeneity of nutrients; eventual alteration of vegetation structure; facilitation of exotic-plant invasion where nutrients are locally enriched (see exotics, below).
	Introduction of invasive exotic plants	See exotics, below.
Fire suppression	Altered fire regime	Decreased frequency and extent of fire; altered vegetation composition/structure (for example, dominance shift from herbaceous plants favored by fire to woody plants eliminated by fire); increased accumulation of coarse woody fuels; increased likelihood of high-intensity canopy fire; decreased ecosystem resistance/resilience to impacts from drought and insect outbreaks.
Invasive exotic plants	Competition with native plants	Altered vegetation composition/structure; eventual alteration of soil-resource dynamics and/or heterogeneity due to vegetation-soil feedbacks.
	Altered soil-resource dynamics	Altered nutrient dynamics (for example, exotic characterized by different tissue chemistry and/or by different spatiotemporal patterns of nutrient uptake and litter deposition than native plants); altered soil-water dynamics (for example, exotic characterized by different spatiotemporal patterns of water use than native plants); eventual alteration of vegetation composition/structure due to soil-vegetation feedbacks.
	Altered disturbance regime	Increased frequency and extent of fire (facilitated by increased quantity, flammability, and/or spatial continuity of fuels); eventual alterations of vegetation composition/structure and soil-resource availability due to strong feedbacks among fire, vegetation structure, and resource availability.
Adjacent land use activities	Trespass livestock	See livestock, above.
	Introduction of exotic plants	See exotics, above.
	Accelerated transfers of sediment, nutrients, and water	Soil-resource enrichment; eventual alteration of vegetation composition/structure; facilitation of exotic-plant invasion where resources are enriched (see exotics, above); increased overland water flow (increased erosive energy of water); increased redistribution and export of soil and nutrients.
	Fire from adjacent lands	Increased susceptibility to high-intensity fire and associated ecosystem changes.
	Altered landscape structure	Altered habitat structure, connectivity and habitat-use patterns of wildlife.
Air pollutants	Nitrogen deposition	Soil-resource enrichment; potential alteration of vegetation composition and structure--including facilitation of exotic-plant invasion (see exotics, above).
	Ozone	Altered competitive relations between ozone-sensitive and ozone-tolerant plants; altered vegetation composition & structure.

Appendix Table C. Climatic conditions, inherent ecosystem properties, and dynamic ecosystem properties hypothesized to confer resistance and resilience to selected ecosystem attributes in relation to particular disturbances or stressors. (BSC = biological soil crust; -- = not applicable)

Disturbance or stressor	Ecosystem attribute	Climatic conditions		Inherent ecosystem properties[1]		Dynamic ecosystem properties[2]	
		Resistance	Resilience	Resistance	Resilience	Resistance	Resilience
Drought	Native grass population structure	Coincident temperatures and winds that do not exacerbate evaporational demands	Antecedent moisture & temperature conditions favorable for seed production by native plants Subsequent moisture & temperature conditions favorable for plant growth & soil biotic activity; precipitation characterized by timing, intensity, and event size that maximize likelihood of infiltration and soil-water recharge	Deep sandy soil; run-on landscape position		Soil and vegetation structure that enhance site capacity to capture, retain, and cycle water and mineral nutrients; physiological condition of native grass populations unimpacted by other disturbances or stressors (for example, excessive herbivory)	Seed/propagule banks; soil and vegetation structure that enhance site capacity to capture, retain and cycle water and mineral nutrients; physiological condition of native plant populations unimpacted by other disturbances or stressors; absence of invasive exotic species capable of rapid population expansion and exclusion of native plant populations
	Shrub/tree population structure			Rocky soil (including rock outcrops with joints and fractures); run-on landscape position		Natural stand structure (that is, not overstocked); soil and vegetation structure that enhance site capacity to capture, retain, and cycle water and mineral nutrients; physiological condition of native shrub-tree populations unimpacted by other disturbances or stressors	
Insect outbreak (Here assumed to be triggered by drought stress)	Tree population structure	Antecedent and coincident moisture & temperature conditions favorable for tree growth	Antecedent moisture & temperature conditions favorable for seed production by native plants Subsequent moisture & temperature conditions favorable for tree growth	Rocky soil (including rock outcrops with joints and fractures); run-on landscape position		Natural stand structure (that is, not overstocked); soil and vegetation structure that enhance site capacity to capture, retain, and cycle water and mineral nutrients; physiological condition of native shrub-tree populations unimpacted by other disturbances or stressors	Seed/propagule banks; soil and vegetation structure that enhance site capacity to capture, retain, and cycle water and mineral nutrients; physiological condition of native plant populations unimpacted by other disturbances or stressors; absence of invasive exotic species capable of rapid population expansion and exclusion of native plant populations

[1]Inherent ecosystem properties are relatively insensitive to change in relation to land use, management, and climate (for example, soil texture, mineralogy, horizonation, and depth; landscape/topographic position).

[2]Dynamic ecosystem properties are sensitive to change in relation to land use, management, and climate (for example, soil structure, biotic activity, and vegetation composition and structure). Dynamic properties are generally mediated by biotic processes.

Disturbance or stressor	Ecosystem attribute	Climatic conditions		Inherent ecosystem properties		Dynamic ecosystem properties	
		Resistance	Resilience	Resistance	Resilience	Resistance	Resilience
Surface fire (As natural disturbance)	Native vegetation composition & structure	Antecedent moisture & temperature conditions that diminish fuel production and/or diminish fuel flammability; calm wind conditions	Subsequent moisture & temperature conditions favorable for plant growth & soil biotic activity	Natural landscape fragmentation (that is, sites potentially capable of supporting surface fire are discontinuously distributed in the landscape, separated by natural fuel breaks)	--	Abundance and spatial continuity of fine surface fuels inadequate to carry fire	Seed/propagule banks; soil and vegetation structure that enhance site capacity to capture, retain, and cycle water and mineral nutrients; physiological condition of native plant populations unimpacted by other disturbances or stressors; absence of invasive exotic species capable of rapid population expansion and exclusion of native plant populations through competition or alteration of fire regimes
Stand-replacing canopy fire (As natural disturbance)	Native vegetation composition & structure	Antecedent moisture & temperature conditions that diminish fuel production and/or diminish fuel flammability; calm wind conditions	Antecedent moisture & temperature conditions favorable for seed production by native plants Subsequent moisture & temperature conditions favorable for vegetative reproduction (for sprouters), plant establishment, plant growth, & soil biotic activity	Natural landscape fragmentation (that is, sites potentially capable of supporting high-intensity stand-replacing fire are discontinuously distributed in the landscape, separated by natural fuel breaks)	--	Abundance and spatial continuity of ladder and canopy fuels inadequate to carry fire	Seed/propagule banks; soil and vegetation structure that enhance site capacity to capture, retain, and cycle water and mineral nutrients; physiological condition of native plant populations unimpacted by other disturbances or stressors; absence of invasive exotic species capable of rapid population expansion and exclusion of native plant populations through competition or alteration of fire regimes

Disturbance or stressor	Ecosystem attribute	Climatic conditions		Inherent ecosystem properties		Dynamic ecosystem properties	
		Resistance	Resilience	Resistance	Resilience	Resistance	Resilience
Erosive wind events	Soil retention (Includes fine soil particles, litter, organic matter, nutrients)	Antecedent and coincident moisture & temperature conditions favorable for plant growth, BSC growth, soil biotic activity, maintenance of moist soil conditions, formation of stable soil aggregates, and/or formation of physical crust	Antecedent moisture & temperature conditions favorable for seed production by native plants Subsequent moisture & temperature conditions favorable for plant growth, BSC growth, soil biotic activity, maintenance of moist soil conditions, formation of stable soil aggregates, and/or formation of physical crust	Landscape setting that provides protection from erosive winds due to aspect, absence of wind-funneling landforms, minimal fetch exposure, etc.; soils with low erodibility by wind (for example, fine-textured soil not exposed to bombardment from saltating sand particles; soil surface covered by rock fragments) Soil physical and chemical properties and landscape setting (for example, north-facing aspect) that favor plant growth, BSC growth, soil biotic activity, and/or reformation of physical crust		Soil aggregate stability and ground cover of BSCs, stable litter, and/or other soil-stabilizing features at maximum levels relative to potential (that is, undiminished by other disturbances or stressors); vegetation structure that obstructs wind and reduces near-surface wind velocity (for example, tall, closely spaced vegetation)	Seed/propagule banks; unconstrained BSC growth, plant growth, litter accumulation, soil biotic activity, and soil aggregation; soil and vegetation structure that enhance site capacity to capture, retain, and cycle water and mineral nutrients
Erosive precipitation/ flood events	Soil & water retention (Includes fine soil particles, litter, organic matter, nutrients)	Antecedent moisture & temperature conditions favorable for plant growth, BSC growth, soil biotic activity, and formation of stable soil aggregates	Antecedent moisture & temperature conditions favorable for seed production by native plants Subsequent moisture & temperature conditions favorable for plant growth, BSC growth, soil biotic activity, and formation of stable soil aggregates	Deep sandy soil (high infiltration and storage capacity); soil surface covered by rock fragments; low slope gradient; short slope length; landscape position that does not receive runoff from upslope positions Soil physical and chemical properties and landscape setting (for example, north-facing aspect) that favor plant growth, BSC growth, and soil biotic activity		Soil aggregate stability and ground cover of BSCs, stable litter, and/or other soil-stabilizing features at maximum level relative to potential (that is, undiminished by other disturbances or stressors); vegetation structure that obstructs over-land water flow, increases flow tortuosity, and reduces flow velocity	Seed/propagule banks; unconstrained BSC growth, plant growth, litter accumulation, soil biotic activity, and soil aggregation; soil and vegetation structure that enhance site capacity to capture, retain, and cycle water and mineral nutrients
Trampling & other soil-surface disturbances	Soil stability (Susceptibility to wind erosion)	Antecedent moisture & temperature conditions favorable for plant growth, BSC growth, soil biotic activity, and formation of stable soil aggregates Coincident moisture & temperature conditions favorable for maintaining soils in moist or frozen state (frozen or dry in case of clay soils)	Antecedent moisture & temperature conditions favorable for seed production by native plants Subsequent moisture & temperature conditions favorable for plant growth, BSC growth, soil biotic activity, formation of stable soil aggregates, and/or formation of physical crust	Soil surface covered by rock or rock fragments Soil physical and chemical properties and landscape setting (for example, north-facing aspect) that favor plant growth, BSC growth, soil biotic activity, or reformation of physical crust		Maximum degree of soil stabilization provided by biotic features relatively unimpacted by trampling or other soil-surface disturbances, such as stable litter, continuous herbaceous ground cover, and continuous canopy cover. Soil stability in relation to wind erosion not dependent on integrity of sensitive biological or physical crusts.	Seed/propagule banks; unconstrained BSC growth, plant growth, litter accumulation, soil biotic activity, and soil aggregation; soil and vegetation structure that enhance site capacity to capture, retain, and cycle water and mineral nutrients

Disturbance or stressor	Ecosystem attribute	Climatic conditions		Inherent ecosystem properties		Dynamic ecosystem properties	
		Resistance	Resilience	Resistance	Resilience	Resistance	Resilience
Trampling & other soil-surface disturbances	Soil stability and infiltration capacity (Susceptibility to water erosion)	Antecedent moisture & temperature conditions favorable for plant growth, BSC growth, soil biotic activity, and formation of stable soil aggregates Coincident conditions: in presence of BSCs, moist or frozen soils; in absence of BSCs, frozen or dry soils	Antecedent moisture & temperature conditions favorable for seed production by native plants Subsequent moisture & temperature conditions favorable for plant growth, BSC growth, soil biotic activity, and formation of stable soil aggregates Occurrence of wet-dry or freeze-thaw cycles required to enhance recovery of compacted soils	Sandy soil or soil surface covered by rock or rock fragments Soil physical and chemical properties and landscape setting (for example, north-facing aspect) that favor plant growth, BSC growth, and soil biotic activity		Maximum degree of soil stabilization provided by biotic features relatively unimpacted by trampling or other soil-surface disturbances, such as stable litter, continuous herbaceous ground cover, and continuous canopy cover; site hydrologic functioning and soil stability in relation to water erosion not dependent on integrity of sensitive BSCs	Seed/propagule banks; unconstrained BSC growth, plant growth, litter accumulation, soil biotic activity, and soil aggregation; soil and vegetation structure that enhance site capacity to capture, retain, and cycle water and mineral nutrients
Excessive herbivory	Native vegetation composition & structure	Antecedent and coincident moisture & temperature conditions favorable for plant growth and soil biotic activity	Antecedent moisture & temperature conditions favorable for seed production by preferred forage species Subsequent moisture & temperature conditions favorable for soil biotic activity and regrowth, seed production, and germination/establishment of defoliated plants	Soil physical and chemical properties and landscape settings that DO NOT favor growth of plants that are palatable to predominant large-bodied herbivores Soil physical properties and landscape settings that DO NOT facilitate access or mobility of predominant large-bodied herbivores	Soil physical and chemical properties and landscape setting (for example, rich alluvial soils, riparian corridors) that favor vigorous plant growth and soil biotic activity	Plant communities with no plant species palatable to predominant large-bodied herbivores OR Plant communities in which all species are equally preferred by predominant large-bodied herbivores and exhibit similar physiological/morphological responses to defoliation (that is, preferential herbivory does not favor one species over another)	Seed/propagule banks; soil and vegetation structure that enhance site capacity to capture, retain, and cycle water and mineral nutrients; physiological condition of defoliated plant populations unimpacted by other disturbances or stressors; absence of unpalatable plants (woody or herbaceous, native or exotic) capable of rapid population expansion and exclusion of palatable native plant populations through competition or alteration of fire regimes
Invasive exotic plants	Native vegetation composition & structure	Conditions that favor native plant communities relative to invaders (will vary among communities and invaders); in general, conditions that constrain resource availability		Soil physical and chemical properties and landscape settings that present harsh resource constraints for vascular plants	--	Growth, competitive ability, and reproduction of native plant populations undiminished by other disturbances or stressors; soil-surface conditions that restrict safe-site opportunities for invasives	Growth, competitive ability, and reproduction of native plant populations undiminished by other disturbances or stressors