Chapter 3: Subsystem Models for the Dry System

By M.E. Miller, S.P. Finn, and D.M. Miller

As described in the Dry System model, we partitioned the Great Basin dry system into vegetation zones for the creation of subsystem models to capture the importance of plant communities for ecosystem function. The subsystem models are ordered from low elevation, relatively dry zones to high elevation zones that are colder and have more moisture (figs. 1.3 and 2.13). We acknowledge that the following subsystem models are uneven in level of detail. We did not undertake a Salt Desert Scrub model due to time constraints and lesser management concern regarding this system. Models for Sagebrush Steppe and Pinyon-Juniper ecosystems are fairly detailed due to the broad extent of these biomes in the Great Basin and implications for many landscape-level land-management issues. The Conifer Forest models are less detailed partly because of lack of information. Aspen forests, although decreasing rapidly in parts of the Great Basin, were not modeled at this time. The alpine tundra has received relatively little study in the Great Basin, and the model is correspondingly brief.

Salt Desert Scrub

Salt desert scrub, or alkali desert scrub, vegetation consists of xerophytic and halophytic species such as shadscale (*Atriplex confertifolia*) and winterfat (*Krascheninnikovia lanata*), most of which are members of the Chenopodiaceae (West and Young, 2000). It is widespread on desert floors of Great Basin valleys, where it commonly grades downslope into phreatophytic communities dominated by species such as greasewood (*Sarcobatus vermiculatus*) or to dry playas, and upslope into sagebrush steppe ecosystems dominated by varieties of big sagebrush (*Artemisia tridentata*). Developing a specific set of conceptual models for this system is beyond the scope of this study.

Sagebrush Steppe and Pinyon-Juniper Ecosystems

By M.E. Miller

This section provides an overview of the structure, function, and dynamics of sagebrush steppe and pinyon-juniper ecosystems in the Great Basin. Many of the following generalizations about dryland structure and function also apply to salt desert scrub as well as to dryland ecosystems characteristic of the nearby Colorado Plateau (Miller, 2005) and Mojave Desert (Belnap and others, 2008). However, specific patterns of ecosystem dynamics vary widely among dryland ecosystems within and among the dryland regions of North America due to differences in environmental setting (climate and soil-geomorphic properties), structural and functional attributes of component species, and types and degrees of human land-use activities.

Distribution and Management Significance

As defined for this project, the Great Basin covers a spatial extent of about 61.7 million ha. Within this region, the three dominant types of low-elevation dryland ecosystems are salt desert scrub (10.4 million ha, or 17.0 percent of the region), sagebrush steppe (28.2 million ha, or 46.1 percent), and pinyon-juniper (coniferous) woodlands (8.1 million ha, or 13.2 percent). (Estimated spatial coverages are based on revisions to Küchler's [1970] map of potential natural vegetation types [U.S. Department of Agriculture, Forest Service, 2001] and do not consider land-cover alterations attributable to human land use.) In Great Basin landscapes, these three ecosystems typically are arrayed sequentially along a gradient of increasing soil moisture availability as controlled by soil properties, elevation, and geomorphic setting (see figs. 2.1 and 2.13; West and Young, 2000). Typical elevations for these systems range from 1,200 m in basins to 2,100 m on piedmont alluvial fans and mountain slopes. Pinyon-juniper and sagebrush steppe ecosystems occur as high as 2,500 m on south-facing slopes. These are the two primary types of upland ecosystems managed by the Bureau of Land Management (BLM) throughout the Great Basin; extensive areas dominated by pinyon-juniper woodlands also are managed by the U.S. Department of Agriculture (USDA) Forest Service. These dryland ecosystems support a tremendous diversity of plants, animals, and other organisms (for example, Rosentreter and Belnap, 2003; Welch, 2005). In addition, they provide livestock forage, watershed services, and wildland recreational opportunities. Pinyon-juniper ecosystems also provide substantial fuel-wood resources to local communities. Because of their spatial extent and the breadth of ecosystem services they provide, they have great significance for management and society.

Ecosystem Components and Processes

Climate and the Physical Template – Determinants of Site Potential

Dynamic and relatively static abiotic factors including regional climate, elevation, and soil-geomorphic setting determine the potential distribution, biotic structure, and dynamics of terrestrial ecosystems through their combined effects on environmental conditions and resources (Jenny, 1980; Stephenson, 1990; Monger and Bestelmeyer, 2006;

fig. 3.1). Climate was described in Chapter 2. Great Basin landscapes are characterized by a diversity of parent materials, landforms, and soils that contribute to the physical template and thus the characteristics of sagebrush steppe and pinyon-juniper ecosystems. Geologic parent materials range from Tertiary basalt and andesite on volcanic plateaus to Mesozoic and Paleozoic igneous rocks and marine and continental sedimentary rocks in uplifted fault-block mountain ranges (Hunt, 1974; U.S. Department of Agriculture, Natural Resources Conservation Service, 2006). Piedmont slopes are
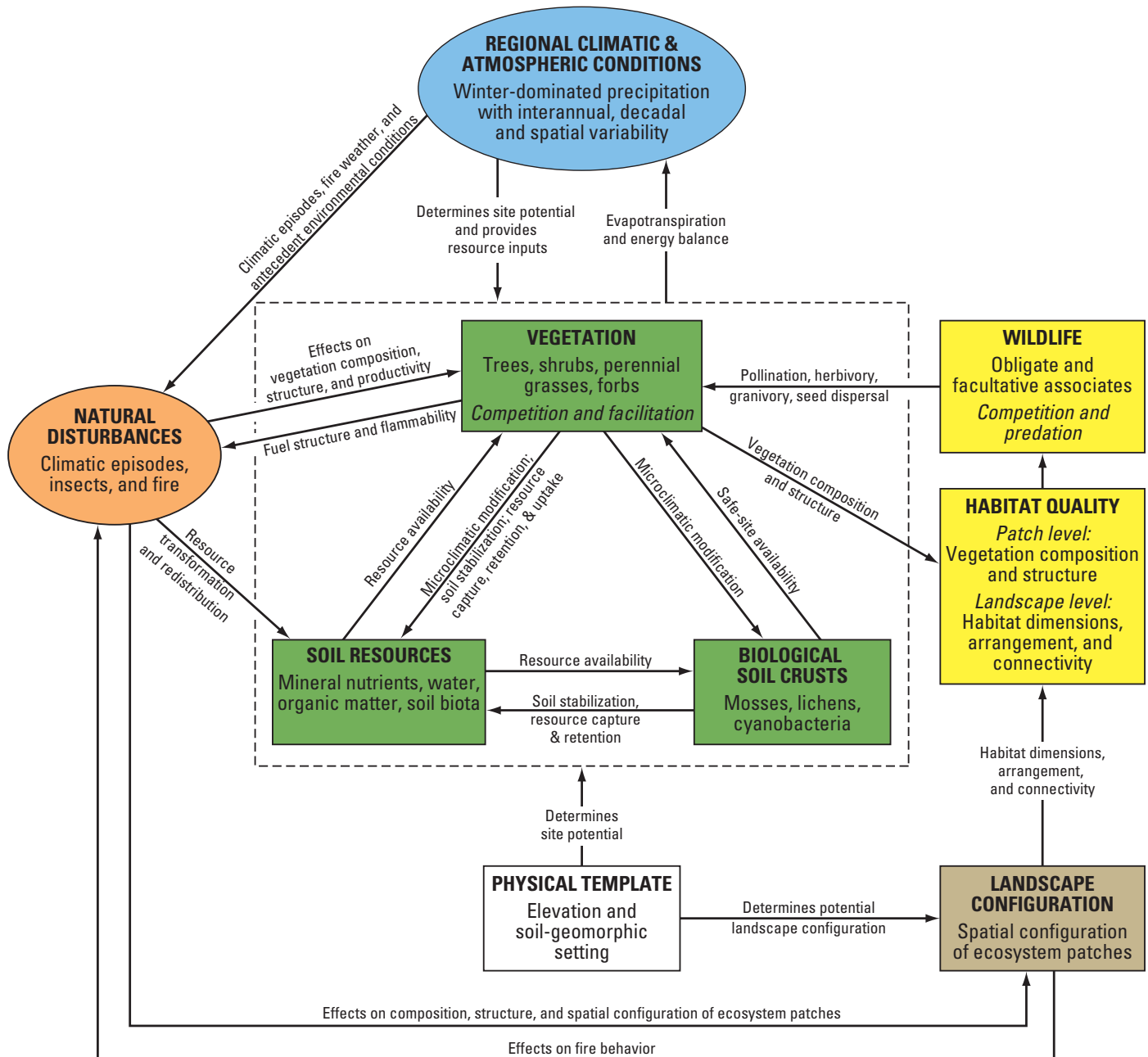
Figure 3.1.   Diagram showing control model illustrating key components (rectangles), natural drivers of temporal change and variability (ovals), and functional relations (arrows) of Great Basin sagebrush steppe and pinyon-juniper ecosystems, excluding major human influences. The dashed box bounding vegetation, soil resources, and biological soil crusts emphasizes strong feedbacks among these three components that together form the foundation of dryland ecosystems. (Adapted from Miller, 2005.)

mantled and intermontane basins are filled with Quaternary alluvium and other deposits with physical and mineralogical properties inherited from these parent materials and modified by geomorphic processes and soil formation. In basins formerly occupied by pluvial lakes, basin-floor soils are formed in lacustrine sediments as well as alluvium. Deposits and resultant soils generally become progressively deeper and finer in texture downslope from mountain fronts to basin floors. Although these are useful generalizations, spatial patterning of key soil properties such as depth, particle-size distribution, and degree of profile development are far more complex in actual Great Basin landscapes (Peterson, 1981). This spatial complexity is attributable to differences in the origins and ages of major types of landforms (for example, mountain-valley fans, alluvial fans, fan piedmonts, alluvial flats, and alluvial plains) that comprise piedmont slopes and basin floors (Peterson, 1981). In the Great Basin, these landforms developed primarily during or before the late Pleistocene, and since that time have been repeatedly modified during recurrent periods of erosion and deposition as well as by soil formation during periods of greater landscape stability (Peterson, 1981). As a consequence, different types of soils (that is, in terms of depth, particle size, and degree of development) and ecosystems (that is, in terms of structure and dynamics) tend to be associated with different landforms as well as with finer-scale components and elements of landforms (Peterson, 1981; Monger and Bestelmeyer, 2006). Aridisols, Mollisols, and Entisols generally are the dominant soil orders associated with sagebrush steppe and pinyon-juniper ecosystems in the Great Basin (U.S. Department of Agriculture Natural Resources Conservation Service, 2006).

Vegetation, Biological Soil Crusts, and Soil Resources— The Foundation for Sagebrush Steppe and Pinyon-Juniper Ecosystems
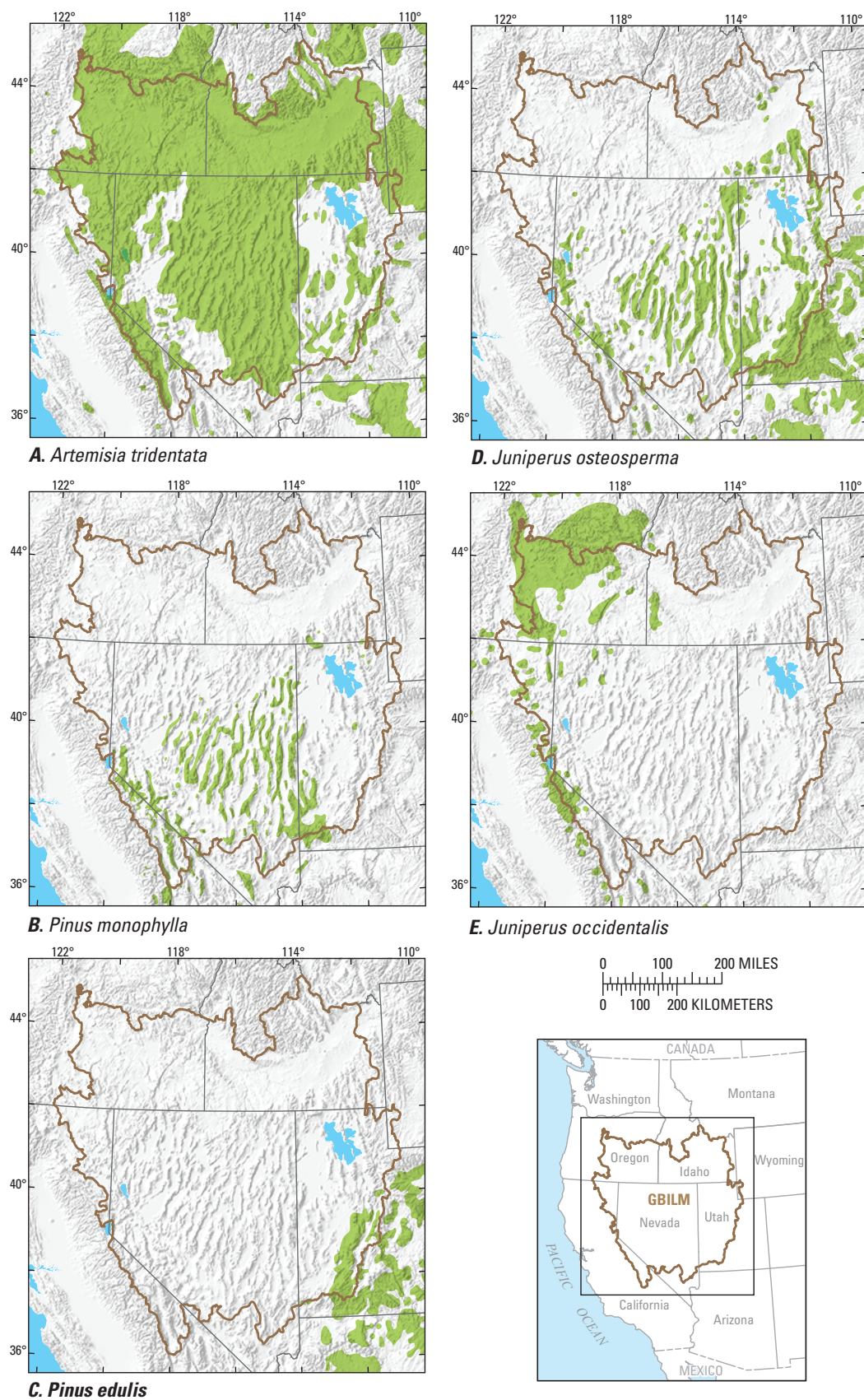
Vegetation.—Vegetation, biological soil crusts, and soil resources are tightly coupled components of dryland ecosystems in the Great Basin (fig. 3.1; Whitford, 2002)— including those dominated by big sagebrush, pinyon, and juniper. Big sagebrush is widely distributed across the Great Basin (fig. 3.2; Little, 1976) and is perhaps the single plant species that best characterizes the region. Three of five known varieties of big sagebrush are prevalent throughout the region (West and Young, 2000). These three taxa— Wyoming big sagebrush (*A. t.* var. *wyomingensis*), basin big sagebrush (*A. t.* var. *tridentata*), and mountain big sagebrush (*A. t.* var. *vaseyana*)—generally shift in relative abundance along gradients of decreasing soil temperature and increasing soil moisture (West and Young, 2000). Of these three, Wyoming big sagebrush has the most extensive distribution as a shrubsteppe dominant in deep, salt-free soils below the elevation of pinyon-juniper woodlands. Basin big sagebrush commonly is restricted to deep alluvial soils along

stream courses, although it is a shrubsteppe dominant in some settings. Mountain big sagebrush typically occurs as a shrubsteppe dominant in forest clearings and meadows above or in more mesic topographic settings than pinyon-juniper woodlands. In their treatment of vegetation communities of the Intermountain West, West and Young (2000) differentiated sagebrush steppe from Great Basin sagebrush—with the former type having a greater proportion of perennial grass cover and a more northerly distribution in the sagebrush biome relative to the latter type. In this report, we do not retain this coarse-scale distinction because community composition and especially the shrub:grass ratio also varies widely with soil—geomorphic properties, climatic conditions, and disturbance history at finer spatial scales. These factors as well as regional biogeographical patterns together result in considerable variability in the composition, structure, and dynamics of sagebrush steppe ecosystems across the Great Basin. Depending on these many factors, a large variety of shrubs (for example, *Ericameria nauseosa*, *Ephedra viridis*, *Krascheninnikovia lanata*, and *Purshia tridentata*), perennial bunchgrasses (for example, *Pseudoroegneria spicata*, *Pascopyrum smithii*, *Poa secunda*, and *Festuca idahoensis*), perennial forbs (for example, *Astragalus spp.*, *Balsamorhiza sagittata*, *Eriogonum spp.*, and *Phlox spp.*), and annuals can be important components of sagebrush steppe (Holmgren, 1972). The issue of variability is a particularly important one for monitoring and management, and it is addressed later in this section.

Like sagebrush steppe, pinyon-juniper woodlands are extremely variable across the broad range of this general vegetation type. In the Great Basin, singleleaf pinyon (*Pinus monophylla*) and Utah juniper (*Juniperus osteosperma*) are the most widely distributed woodland species (fig. 3.2*B* and 3.2*D*). Western juniper (*Juniperus occidentalis*) occurs along the western margin and particularly in the northwestern corner of the Great Basin (fig. 3.2*E*), whereas Colorado pinyon (*P. edulis*) is restricted to the southeastern corner of the region (fig. 3.2*C*). In large areas of the region, junipers occur in the absence of pinyon. In landscapes where they co-occur, juniper tends to dominate at lower and upper ends of elevational gradients, whereas pinyon dominates middle elevation due to lesser tolerance for dry (low elevation) and cold (high elevation) conditions (West, 1999). As with sagebrush steppe ecosystems, the composition and structure of understory shrub and herbaceous communities varies greatly in relation to woodland structure and successional stage, soil-geomorphic setting, climatic conditions, and disturbance history (West, 1999).

Interspecific competition and facilitation are important types of plant interactions in dryland ecosystems (Archer and Bowman, 2002). Much research has focused on the importance of competition as a process affecting plant community structure in drylands (Fowler, 1986; Reichenberger and Pyke, 1990; Booth and others, 2003),

A. *Artemisia tridentata*

B. *Pinus monophylla*

C. Pinus edulis

D. *Juniperus osteosperma*

E. *Juniperus occidentalis*

Figure 3.2.   Distribution of (*A*) *Artemisia tridentata*, (*B*) *Pinus monophylla*, (*C*) *Pinus edulis*, (*D*) *Juniperus osteosperma*, and (*E*) *Juniperus occidentalis* in the Great Basin (derived from Little, 1971,1976; U.S. Geological Survey, 1999).

with particular emphasis on interactions between woody plants and perennial grasses (Archer, 1994; West and Young, 2000). But there is increasing recognition that facilitation also can be an important process in drylands due to ameliorating effects of overstory plants on environmental conditions or herbivory experienced by understory plants (Callaway, 1995; Archer and Bowman, 2002; Brooker and others, 2008). For example, sagebrush has been determined to facilitate establishment and persistence of perennial grasses under some conditions (Davies and others, 2007). The tendency for pinyons to establish beneath junipers (Chambers, 2001) also indicates an important role for facilitation in woodlands. The relative importance of competition versus facilitation can vary depending on characteristics of interacting species, environmental conditions such as aridity, and other factors such as grazing intensity (Brooker and others, 2008). Recent work also indicates that greater consideration of facilitative interactions between plants could enhance restoration success in the context of harsh environmental conditions (Pueyo and others, 2008).

Biological Soil Crusts.—Biological soil crusts (BSCs) play important functional roles in sagebrush and pinyon-juniper ecosystems of the Great Basin (fig. 3.1). BSCs are biotic communities composed of cyanobacteria, algae, microfungi, mosses, and lichens that occur on and within a few millimeters of the soil surface (Belnap 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 and Lange, 2003; Rosentreter and Belnap, 2003). In addition to their contributions to biological diversity, BSCs are major contributors to soil stability because they aggregate soil particles, thereby reducing the susceptibility of soil to erosion by wind and water (Williams and others, 1995a, 1995b). BSCs also roughen the soil surface, thereby facilitating the capture and retention of wind-blown dust that can be a significant source of mineral nutrients in dryland ecosystems (Reynolds and others, 2001; Belnap and Lange, 2003). BSCs similarly can capture and enhance ecosystem retention of windborne and waterborne organic matter and seeds (Belnap and Lange, 2003).

Hydrologic effects of BSCs are complex. Regardless of crust or soil type, BSCs stabilize soils and reduce water erosion by reducing the detachment of soil particles by erosive raindrops and overland water flow. In this function, cyanobacteria and algae are less effective than mosses and lichens. However, BSC organisms also can clog soil pores and inhibit infiltration. In undisturbed settings of the Great Basin, BSCs typically are characterized by a rolling surface morphology (Rosentreter and Belnap, 2003). Where BSCs roughen the soil surface in this way, they increase the residence time of runoff on hillslopes, thereby increasing infiltration and offsetting the inhibitive effects of BSCs on infiltration (Belnap, 2006). Organic carbon produced by BSC organisms also contributes to the formation of stable soil aggregates that increase the ratio of macropores to micropores and thus enhance infiltration. The presence of heavy, shrink-swell clays overrides the local hydrologic effects of BSCs.

In addition to enhancing soil stability and nutrient retention, BSCs contribute to dryland nutrient cycles in other ways. Mosses, cyanobacteria, green algae, and lichens 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, *Nostoc* and *Scytonema spp.*) and cyanolichens (for example, *Collema* spp.) also are capable of fixing atmospheric nitrogen into a mineral form that can be used by vascular plants (Evans and Lange, 2003). Consequently, BSCs can be the dominant source of nitrogen in many dryland regions (Evans and Ehleringer, 1993; Belnap, 2002). BSC organisms are significant sources of carbon for other soil biota, which are more abundant and diverse beneath BSCs than beneath bare soils (Belnap, 2003). BSCs also increase nutrient cycling rates of soil food webs through their effects on near-surface moisture availability, soil structure, soil aeration, and soil temperature, thus increasing soil nutrient availability (Belnap, 2003).

BSCs have numerous effects on vascular plants. Where their presence results in roughened soil surfaces, BSCs generally enhance seed catchment and retention. Following seed catchment, BSC effects on plant establishment are dependent on crust composition and morphology, plant species (propagule morphology and germination requirements), and site conditions (Belnap and others, 2003; Escudero and others, 2007). Serpe and others (2006) determined that short mosses characteristic of the Great Basin reduced germination of four grasses (*Festuca idahoensis, Festuca ovina, Elymus wawawaiensis*, and *Bromus tectorum*) relative to bare soil. In contrast, tall mosses increased time to germination relative to bare soil but did not have an effect on final germination percentages for these same species. In a similar experiment, a lichen crust dominated by *Diploschistes muscorum* reduced germination of the exotic annual grass *Bromus tectorum* and the native annual grass *Vulpia microstachys* by two-thirds relative to bare soil (Deines and others, 2007). A mixed lichen-moss crust had no effects on germination relative to bare soil, with similar results for both grass species. Following the establishment phase, plants growing in soils with BSCs generally have greater biomass and lower root:shoot ratios than comparable plants growing in soils without BSCs, indicating greater availability of soil resources in the presence of BSCs (Belnap and others, 2003). Relative to plants growing in soils without BSCs, plants growing in association with nitrogen-fixing cyanobacteria and cyanolichens consistently have high nitrogen concentrations in tissues and usually have high 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 low concentrations of phosphorus and iron than plants growing in soils without BSCs, indicating 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 the plants are rooted in near-surface soils that are most directly influenced by BSCs (Harper and Belnap, 2001).

Soil Resources and Functions.—Soils are the third element constituting the foundation of dryland ecosystems because they are important for sustaining hydrologic processes, nutrient cycling, and plant establishment and growth, and erosion resistance in sagebrush steppe and pinyon-juniper. Key dynamic properties affecting these processes include organic matter content, aggregate stability, surface roughness, and structure. General soil characteristics and their importance to dryland ecosystems are discussed in Chapter 2.
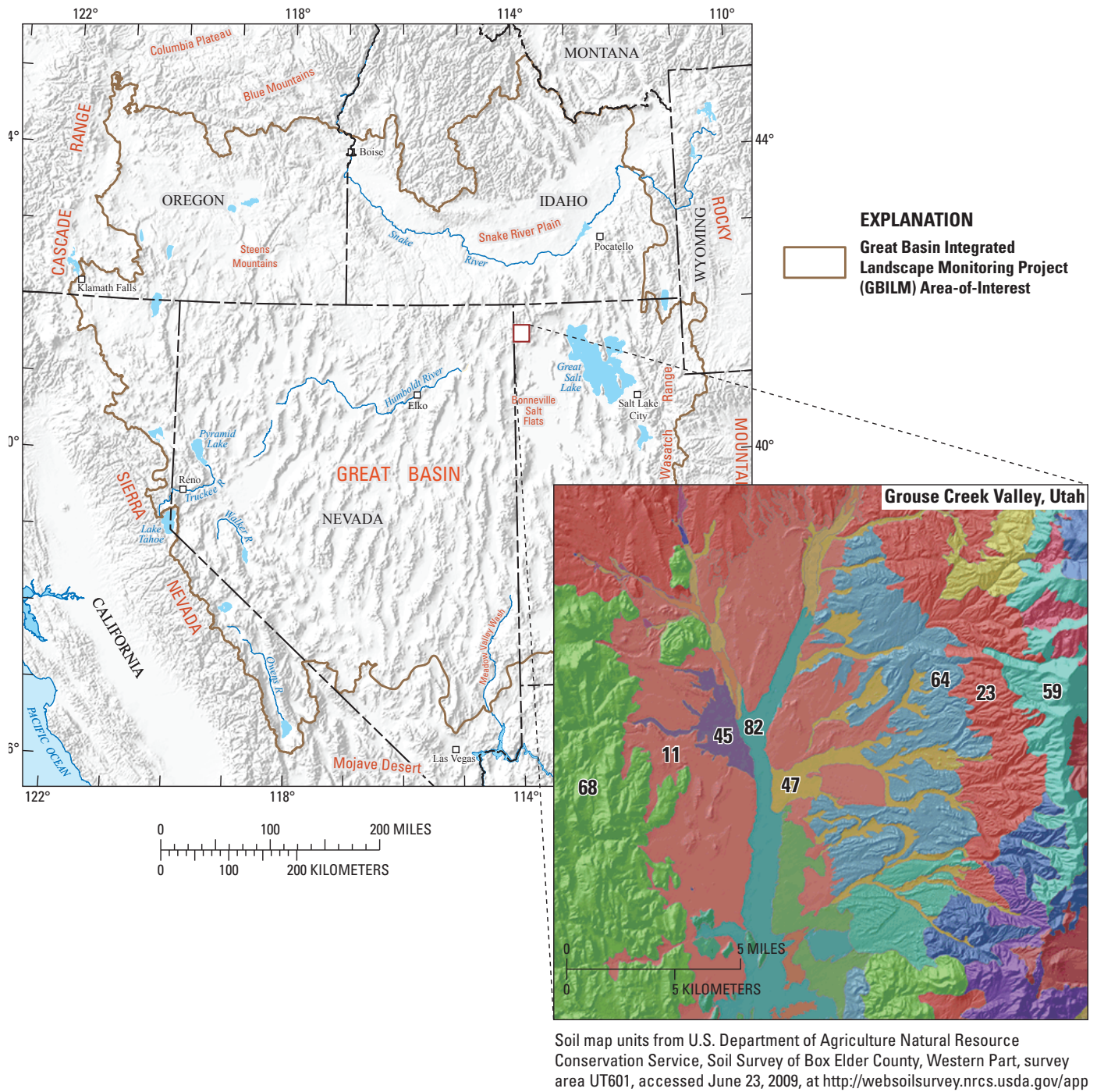
Because soils and their geomorphic, elevation, and climatic setting are fundamental to determining potential ecosystem structure and function, including many aspects of ecosystem resistance and resilience to drivers of change (Monger and Bestelmeyer, 2006), they can provide a basis for subdividing and classifying upland ecosystems into ecological land units for purposes of ecosystem management, assessment and monitoring, and associated research. One such system that has been widely applied in the Great Basin is the *ecological site* system developed and managed by NRCS. Ecological sites are land units that are delineated on the basis of soil properties (soil texture and mineralogy through the profile), climate (latitude, elevation, and aspect), and geomorphic setting (landform association and topographic / hillslope position; fig. 3.3; table 3.1). These units have potential to produce specific kinds and amounts of vegetation and distinct responses to management, climate, and other drivers of change (Society for Range Management Task Group on Unity in

Table 3.1.   Dominant soil, ecological site, and generalized type of upland ecosystem associated with soil map units.

[Map units are ordered as they are encountered along a cross-valley transect from west to east (see fig. 3.3). Soil and ecological site information were compiled from U.S. Department of Agriculture Natural Resource Conservations Service, Soil Survey of Box Elder County, Western Part. **Dominant ecological site**: Descriptions of these ecological sites are available online at http://www.ut.nrcs.usda.gov/technical/technology/range/ecosites.html]

Soil map unit	Dominant soil		Dominant ecological site		Generalized type
	Taxonomic class	Landform	Name	No.	
68	Loamy-skeletal, mixed, frigid Lithic Haploxerolls	Hills	Upland Shallow Loam (Utah Juniper)	R025XY324UT	Pinyon-juniper
11	Loamy-skeletal, mixed, mesic Haploxerollic Durargids	Fan remnants	Semidesert Gravelly Loam (Wyoming Big Sagebrush) North	R028AY215UT	Sagebrush steppe
45	Coarse-loamy, mixed, mesic Durixerollic Calciorthids	Fan remnants	Semidesert Alkali Loam (Black Greasewood)	R028AY202UT	Salt desert scrub
82	Coarse-silty, mixed (calcareous), mesic Typic Torriorthents	Lake plains and terraces	Desert Loam (Shadscale)	R028AY124UT	Salt desert scrub
47	Coarse-loamy, mixed, superactive, mesic Xeric Argidurids	Fan remnants	Semidesert Loam (Wyoming Big Sagebrush)	R028AY220UT	Sagebrush steppe
64	Loamy, mixed (calcareous), mesic, shallow Xeric Torriorthents	Ridges on hillslopes	Semidesert Shallow Hardpan (8-10 " precip.)	R028AY231UT	Sagebrush steppe
23	Coarse-loamy, mixed, frigid Haploxerollic Durorthids	Hillslopes	Upland Juniper Savanna (Utah Juniper)	R025XY322UT	Pinyon-juniper
59	Loamy-skeletal, mixed Argic Pachic Cryoborolls	Mountain slopes	Mountain Gravelly Loam (Mountain Big Sagebrush)	R025XY4122UT	Sagebrush steppe

EXPLANATION

Great Basin Integrated Landscape Monitoring Project (GBILM) Area-of-Interest

Grouse Creek Valley, Utah

Soil map units from U.S. Department of Agriculture Natural Resource Conservation Service, Soil Survey of Box Elder County, Western Part, survey area UT601, accessed June 23, 2009, at http://websoilsurvey.nrcs.usda.gov/app

Figure 3.3. Soil map units in Grouse Creek Valley, Utah. A description of the eight numbered map units that occur along a cross-valley transect from west to east is shown in table 3.1.

Concepts and Terminology, 1995). In some cases, naming conventions for ecological sites include reference to one or more plant species that characterize the potential vegetation for the site (see table 3.1). Upland subsystems referred to in this report (for example, salt desert scrub, sagebrush steppe, and pinyon-juniper woodlands) represent coarse groupings

of ecological sites, which incorporate considerable variation in classification factors and ecosystem responses. A map of *actual* vegetation differs from a map of ecological sites because the former reflects disturbance and fire history rather than the potential to respond to climate or land-use activities.

Wildlife and Habitat Quality

Wildlife (including vertebrates and invertebrates) are significant contributors to the biological diversity and functioning of sagebrush steppe and pinyon-juniper woodlands of the Great Basin. Bird species that have obligate habitat associations with sagebrush steppe include greater sage-grouse (*Centrocercus urophasianus*), sage thrasher (*Oreoscoptes montanus*), sage sparrow (*Amphispiza belli*), and Brewer's sparrow (*Spizella breweri*) (Knick and others, 2003; Welch, 2005). Welch (2005), citing a long list of other researchers, identified 91 additional bird species that are facultative associates of sagebrush steppe. Mammals considered to be sagebrush obligates include the pygmy rabbit (*Brachylagus idahoensis*) and the sagebrush vole (*Lagurus curtatus*) (Welch, 2005). At least 88 mammal taxa have been identified as facultative sagebrush associates, including pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and bighorn sheep (*Ovis canadensis*) (Welch, 2005). Depending on local habitat conditions, these same four species also have been determined to use pinyon-juniper woodlands on a facultative basis—with mule deer being the most important in terms of degree of woodland use for thermal cover and food (Frischknecht, 1975). In their study of pinyon-juniper woodlands in northeastern Utah (outside our Great Basin boundary), Paulin and others (1999) identified six bird species that they considered to be pinyon-juniper obligates—ash-throated flycatcher (*Myiarchus cinerascens*), blue-gray gnatcatcher (*Polioptila caerulea*), Bullock's oriole (*Icterus bullockii*), pinyon jay (*Gymnorhinus cyanocephalus*), western scrub-jay (*Aphelocoma coerulescens*), and Virginia's warbler (*Vermivora virginiae*). Periodic mast crops of pinyon and juniper seeds are particularly important resources for a wide range of birds and mammals (Frischknecht, 1975). Miller and others (2005) summarized the current understanding of habitat-use patterns of selected bird and mammal species in sagebrush steppe and western juniper woodlands in the northwestern Great Basin.

Vertebrates and invertebrates perform numerous functions (see Chapter 2, section "Wildlife and Habitat Quality") in sagebrush steppe and pinyon-juniper ecosystems, the most important of which is herbivory. Native herbivores in sagebrush steppe and pinyon-juniper 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, pronghorn, mule deer, and elk. 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 in section "Insect Outbreaks"), 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.

Herbivorous animals influence plant community composition and vigor through selective defoliation, transport of plant materials and seeds, caching, defecation, and trampling. Through time, these effects can lead to altered competitive relations among plants which then are expressed in population dynamics and plant community structure (Briske, 1991).

Drivers of Ecosystem Change

Natural Drivers

Climate Variability.—Climate variability and disturbance processes are the two natural factors that are most responsible for driving temporal patterns of change and variability in sagebrush steppe and pinyon juniper systems. With respect to climate, precipitation seasonality (that is, timing in relation to the annual cycle of potential evapotranspiration) and form (that is, snow versus rain) are major determinants of ecosystem dominance by different vegetative life forms and functional groups because these climatic attributes strongly control the partitioning of precipitation among various compartments of the hydrologic budget—evaporation, transpiration, runoff, drainage (recharge), and soil-water storage (Comstock and Ehleringer, 1992). In the Great Basin, winter precipitation is predominant, with greater summer precipitation in the east (see Chapter 2, section "Climate Patterns in the Great Basin"). The prevalence of cool-season precipitation results in effective soil-moisture recharge and relatively reliable growing conditions in spring (Caldwell, 1985; Comstock and Ehleringer, 1992; West and Young, 2000). Annual temperature extremes also influence plant species distributions and therefore contribute to landscape configuration; for example, the upper elevational limit of pinyon pine appears to be defined by minimum annual temperatures (West, 1999). Pinyon pine and the other plant species defining the sagebrush steppe and pinyon-juniper zones exhibit adaptations to climate conditions that promote their local dominance.

Natural Disturbance Regimes.—
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 ecologically significant 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. Episodic, event-driven change is an important

feature of many ecosystems (Holling, 1996; Scheffer and others, 2001), and is particularly characteristic of dryland ecosystems (Whitford, 2002). West and Young (2000) note that the occurrence of extremely wet springtime conditions or very cold winters without snow cover are climatic events that trigger sagebrush mortality and affect the ratio of shrubs to herbaceous species in sagebrush steppe ecosystems of the Great Basin. 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 drivers of change (Archer and Stokes, 2000; Scheffer and others, 2001).

Fire.—Wildfire is another type of natural disturbance that can have many direct and indirect effects on ecosystem structure and function, although there is considerable variability among dryland ecosystems in the specific characteristics of natural fire regimes. One of the most significant direct effects of fire is the alteration of vegetation composition and structure due to the selective reduction 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 vegetation composition and structure, as well as by preceding and coincident weather conditions that affect fuel availability, fuel flammability, and fire behavior. In describing fire regimes, fire intensity refers to how hot a fire burns (energy output; Whelan, 1995) whereas fire severity refers to the degree of mortality in overstory woody plants (Baker and Shinneman, 2004). High-severity fires in woodlands and forests result in near-complete mortality of overstory trees, whereas low-severity fires consume primarily herbaceous surface fuels, litter, fire-sensitive understory trees, and shrubs. Mixed-severity fires result in a mosaic of high-severity and low-severity patches that can be caused by changes in weather during the fire, topographic heterogeneity, the relative abundance and distribution of fuels, and legacies of past fire (Noss and others, 2006).

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 that can result in accelerated water-driven erosion because of decreased infiltration and increased runoff (Johansen and others, 2001; MacDonald and Huffman, 2004).

Fire also has significant ecosystem-level consequences due to effects on nutrient cycles (Raison, 1979; Blank and others, 1994a, 1994b). 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 nitrogen) and off-site transfers of ash (Raison, 1979). Nutrient losses in gases and ash generally are proportional to heat generated and organic-matter consumed by fire (Raison, 1979; Schlesinger, 1997). Depending on fire intensity, 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). Fire extent and spatial patterning affect and are affected by topography, wind, fuel moisture, and the spatial configuration of different fuel (vegetation) types across the landscape (fig. 3.1).

There is uncertainty regarding the characteristic frequency of fire in Great Basin sagebrush steppe prior to the time of Euro-American settlement. Some researchers have estimated that pre-settlement natural fire-return intervals in sagebrush steppe were 15–25 years in mountain big sagebrush ecosystems and 50–100 years in Wyoming big sagebrush ecosystems (Miller and others, 1994; Miller and Tausch, 2001). Following a critique of methodological issues associated with previous estimates, Baker (2006) concluded that these fire rotations (the time required for fire to burn once through a sagebrush landscape) may have been 70–200 years or more in mountain big sagebrush and 100–240 years in Wyoming big sagebrush. When fire does occur, all varieties and age classes of big sagebrush typically are killed irrespective of fire intensity (Welch, 2005). As a consequence, fire in sagebrush steppe tends to create a mosaic of burned and unburned patches rather than thinning the density of shrubs within patches (Baker, 2006). Fire frequency, size, and spatial patterning affect the spatial mosaic of vegetation patches and landscape-level habitat attributes for broad-ranging wildlife such as birds (fig. 3.1).

There is a similar degree of uncertainty regarding characteristics of pre-settlement fire regimes in pinyon-juniper ecosystems of the Great Basin. West and Young (2000) suggest that many intermountain pinyon-juniper ecosystems likely were characterized by low-severity surface-fire regimes that maintained savanna-like vegetation structure prior to Euro-American settlement. In contrast, Baker and Shinneman (2004) concluded from their systematic review of fire research in pinyon-juniper ecosystems that low-severity surface fires probably were uncommon in such ecosystems prior to Euro-American settlement. They also concluded that much additional area-specific research is needed to provide a foundation for science-based management and restoration of pinyon-juniper ecosystems. 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, Romme and others, 2003; Veblen, 2003).

In an effort to clarify issues associated with pinyon-juniper fire regimes, Romme and others (2007) compared two general types of pinyon-juniper ecosystems with areas of potential tree expansion and contraction based on canopy structure, understory characteristics, and historical disturbance regimes (table 3.2). Although there is a great deal of variability within each of these types as well (for example, variability corresponding with the large number of different pinyon-juniper ecological sites in the Great Basin), this general classification scheme provides a useful framework for future research regarding management, dynamics, and restoration of systems in which pinyon and juniper species occur. Following this scheme, pinyon-juniper ecosystems discussed in this report are considered to be classified as *persistent woodlands*. Sagebrush steppe ecosystems subject to tree encroachment are classified as *areas of potential expansion and contraction* following the scheme described in table 3.2.

Insect Outbreaks.—Insect outbreaks can represent significant natural disturbances in sagebrush steppe and pinyon-juniper ecosystems of the Great Basin (Bentz and others, 2008). For example, Gates (1964) reported that 4,000–6,000 ha of sagebrush in eastern Oregon were killed through defoliation by the Aroga moth (*Aroga websteri*) in 1962, and more than 4.5 million ha of sagebrush steppe was infested by the moth to some degree by 1963. More recently, an Aroga moth outbreak was reported in northern and central Nevada during 2004–06 (Bentz and others, 2008). Recent outbreaks of grasshoppers and Mormon crickets (Orthoptera) also have occurred in portions of Utah and Nevada (Bentz and others, 2008). Factors controlling the frequency and magnitude of such outbreaks are poorly understood, but climate likely is a major driver. Hsiao (1986) reported that declines of Aroga moth populations were caused by high summer temperatures and host-plant desiccation during a 5-year study in Curlew Valley, Idaho. Climatic conditions can affect the occurrence of insect outbreaks directly through effects on insect metabolic processes and indirectly through effects on predation and food quality (Bentz and others, 2008).

The occurrence of insect outbreaks in tree-dominated ecosystems has been attributed to 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 pinyon-juniper ecosystems, outbreaks of the bark beetle *Ips confusus* (pinyon ips) can be triggered by drought conditions that weaken host-tree populations (Leatherman and Kondratieff, 2003).

Anthropogenic Drivers

In addition to natural drivers, scoping for this project identified six high-priority anthropogenic drivers that currently affect sagebrush steppe and pinyon-juniper ecosystems in the Great Basin:. (1) fire-regime alteration, (2) invasive-fire interactions, (3) livestock grazing, (4) land treatments, (5) off-highway vehicle activity, and (6) climate change. These factors interact with one another and with natural drivers to affect change and temporal variability in Great Basin ecosystems (fig. 3.4). These interactive effects and their implications for ecosystem dynamics are discussed below.

Ecosystem Dynamics

General patterns of ecosystem dynamics are illustrated here with *state-and-transition models* (Westoby and others, 1989; Bestelmeyer and others, 2003; Stringham and others, 2003; Bestelmeyer and others, 2004; Briske and others, 2005, 2008). State-and-transition models are management-oriented tools for describing and classifying ecosystem conditions (or states) and posing hypotheses about ecological factors responsible for persistent changes (or transitions) among different states (Bestelmeyer and others, 2004). Such models increasingly are being developed and used by managers and researchers to organize information about the dynamics of rangeland ecosystems, qualitatively compare and evaluate the relative benefits and risks of different management actions, and consider the effects of other drivers such as climate, natural disturbances, and invasive exotic plants (Bestelmeyer and others, 2004). For maximum utility, such models are developed for and applied to specific ecological land units (for example, specific ecological sites) because of the importance of site-specific factors such as local climatic conditions, soil-geomorphic properties, and landscape configuration for determining ecosystem responses to management actions and other drivers of change. The general models presented here do not account for these site-specific factors and require modification for application to a specific type of land unit.

To further elaborate on hypothesized mechanisms of ecosystem change, state-and-transition models are supplemented with mechanistic *stressor models*. These conceptual models illustrate how various natural and anthropogenic drivers interact to cause particular types (or pathways) of change in sagebrush steppe and pinyon-juniper ecosystems. To facilitate the consideration of indicators for long-term ecological monitoring, these models emphasize pathways and processes of ecosystem change that typically are considered undesirable with respect to agency management objectives. Relations among control models, state-and-transition models, and mechanistic stressor models are depicted in figure 1.4.
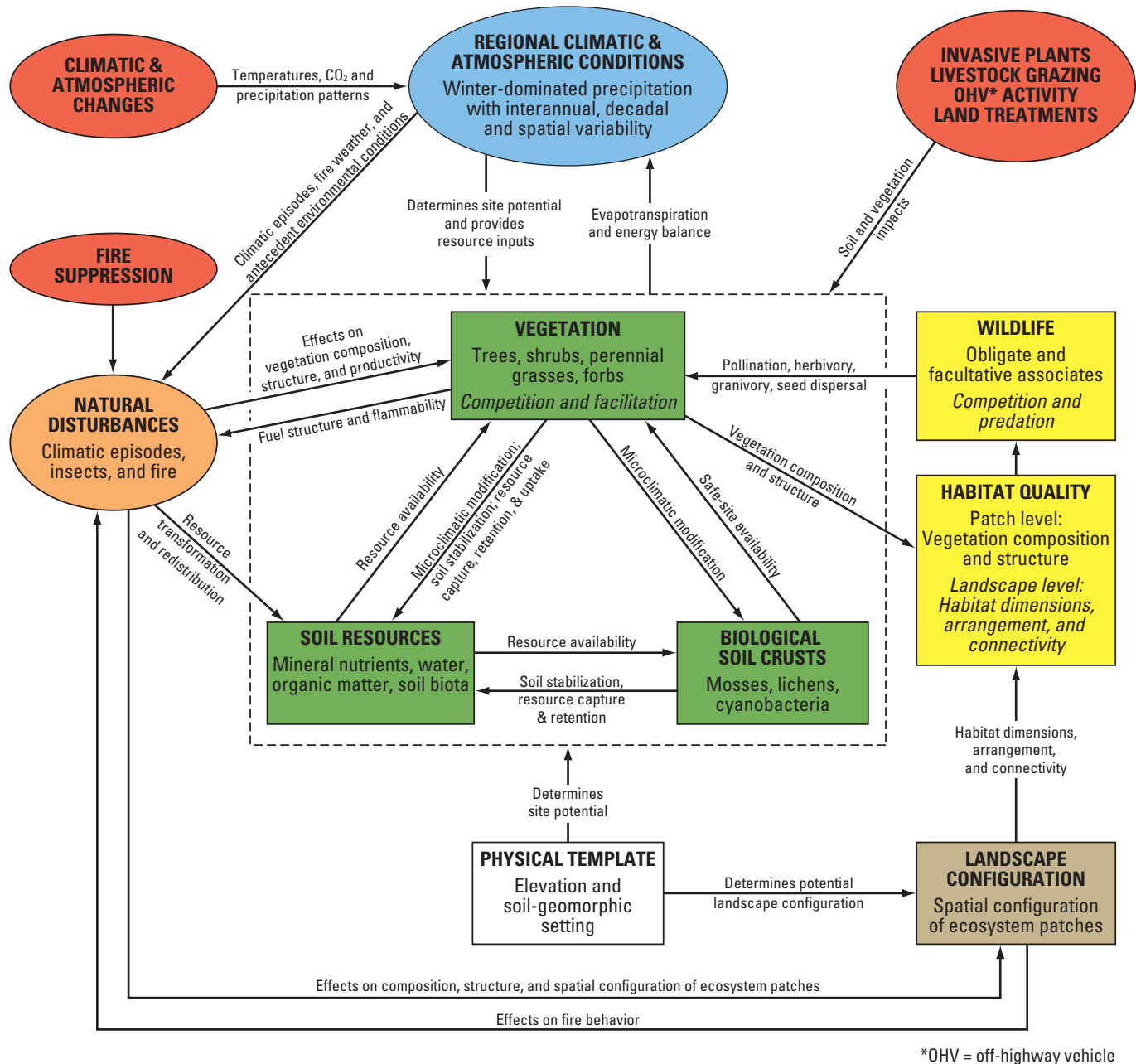
Sagebrush Steppe

Figure 3.5 illustrates a general state-and-transition model for sagebrush steppe ecosystems of the Great Basin. (For other general models depicting state-and-transition dynamics of sagebrush steppe ecosystems, see Laycock, 1991; Miller and others, 1994; West and Young, 2000; Miller and Tausch, 2001; and Connelly and others, 2004). The model depicts seven

Table 3.2.   Selected attributes of two general types of pinyon-juniper ecosystems compared with areas of potential tree expansion and contraction (derived from Romme and others, 2007).

Attributes	General type of pinyon-juniper ecosystem		Areas of potential expansion and contraction
	Persistent woodland	**Pinyon-juniper savanna**	
Site conditions	Soil and climate inherently favorable for pinyon and/or juniper—typically shallow, coarse-textured soils.	Usually on gentle upland and transitional valley locations, where soil conditions favor graminoids but can support some tree cover—typically moderately deep, coarse to fine-textured soils with a large percentage of annual precipitation in summer.	Only intermittently suitable for pinyon and/or juniper, with increased tree establishment during moist climatic periods or long disturbance-free intervals, with subsequent die-back triggered by drought, insect outbreaks, or fire—found on a wide variety of substrates and climatic conditions.
Characteristic canopy structure	Highly variable, from sparse stands of small trees on poor substrates to relatively dense stands of large trees on productive sites.	Variable from sparse tree cover limited by soil and climate conditions; to sparse tree cover limited by herbaceous competition, recurrent fire, drought, or other disturbances; to denser woodlands where tree recruitment has increased historically due to release from competition, favorable climatic conditions, and/or lack of fire.	Fluctuates between shrubland or grassland structure and tree dominance.
Characteristic understory	Sparse herbaceous cover even in absence of livestock grazing.	Variety of growth forms including grasses and shrubs	Typically shrub dominated.
Disturbance regimes and dynamics	Typical fire regimes characterized by high-severity fire with very long rotations (for example, 2 to 6 centuries); low-severity surface fires very rare; woodlands often stable for many hundreds of years with stand dynamics often driven more by drought and insect outbreaks than by fire.	Some savannas may have been maintained by relatively frequent low-severity surface fires. Livestock grazing and fire exclusion are important mechanisms responsible for driving the post-settlement conversion of savanna to woodland structure in some but not all areas. Climatic conditions also have played a role in driving vegetation changes in at least some areas. Interactions and spatial variability in these factors are poorly understood.	Livestock grazing and fire exclusion probably are important mechanisms responsible for driving the post-settlement expansion of trees into some grasslands and shrublands, but not all. Climate probably has played a role in driving these changes in some areas. Interactions and spatial variability in these factors are poorly understood. Tree expansion also occurred in some areas prior to Euro-American settlement and the phenomenon is not necessarily attributable to past land use or fire exclusion. Some drought-triggered tree mortality has recently occurred on some marginal sites.
Distribution	Throughout the West, but particularly on the Colorado Plateau.	Especially prevalent in basins and foothills of southern New Mexico, but relatively rare in the Rocky Mountains, northern Colorado Plateau, and the Great Basin.	Throughout the West, but particularly in the Great Basin.
Research needs	Develop a better understanding of the geographic distribution of this type in relation to environmental factors.	Develop a better understanding of the geographic distribution of this type in relation to environmental factors; disentangle mechanisms driving tree expansions in former grasslands and savannas (including geographic variability).	Develop a better understanding of the geographic distribution of this type in relation to environmental factors; disentangle mechanisms driving tree expansions in former grasslands and shrublands (including geographic variability).

Figure 3.4. Diagram showing control model illustrating key components (rectangles), drivers (ovals), and functional relations (arrows) of Great Basin sagebrush steppe and pinyon-juniper ecosystems, including high-priority anthropogenic drivers of ecosystem change and variability.

major states or persistent types of ecosystem condition, each of which is dynamic (rather than static) with temporal changes driven by climatic fluctuations, interactions among natural and anthropogenic drivers, and internal processes of change such as succession. In the Reference Condition (figure 3.5, Box A—ideally defined on a site-specific basis according to climate and soil-geomorphic setting), biotic and abiotic ecosystem components and processes are present and functioning within their natural range of variability. These include processes and structures that confer resistance and resilience to natural and anthropogenic drivers of change, specifically soil structure and biological crusts; vegetative structure, species composition and competitive interactions; and the natural fire regime defined by frequency, intensity and severity. These are discussed in detail in the model descriptions below.

As suggested above, the concept of "natural" commonly is defined on the basis of pre-settlement conditions. But it is important to recognize that changes in climate, atmospheric CO_2 concentrations, and landscape structure will cause future ecosystem characteristics to drift away from historic patterns of variability even in the absence of local land-use effects, leading to the emergence of *novel ecosystems* characterized by new combinations of species and associated changes in ecosystem patterns and processes (Hobbs and others, 2006; Dukes, 2007; Seastedt and others, 2008). Thus, the concept of reference conditions must be sufficiently flexible to account for uncertain future environmental trajectories.

Despite uncertainties associated with current and future trajectories of change, six additional persistent conditions of sagebrush steppe ecosystems are pertinent for purposes of management and monitoring (fig. 3.5; table 3.3). Relative to reference conditions, five of these (conditions B-F) represent differing degrees of alteration attributable to effects of land-type conversions, invasive exotic plants, altered fire regimes, and land uses such as livestock grazing and off-road vehicle travel. Due to the extent to which sagebrush steppe ecosystems have been altered, the integrity of these systems and the long-term viability of several associated wildlife species are imperiled on a regional basis (Leopold, 1941; Billings, 1990; Miller and others, 1994; Noss and others, 1995; Miller and Rose, 1999; Beck and Mitchell, 2000; Knick and others, 2003; Connelly and others, 2004; Thines and others, 2004; Welch, 2005; Chambers, 2008). Depending on site-specific ecosystem properties and histories (for example, specific ecological sites), there may be numerous expressions and intergradations of these five basic types of altered sagebrush steppe ecosystems. Moreover, it may prove impossible for managers to perfectly restore ecosystems once they have been changed from the reference conditions, particularly in the context of climate change. Condition G (fig. 3.5) represents a restored condition that has resistance and resilience but differs from the reference condition.

Transition to Dominance by Exotic Annual Grasses.—Figure 3.6 illustrates multiple drivers and processes that may lead to increasing dominance of exotic annual grasses such as cheatgrass (*Bromus tectorum*), red brome (*B. rubens*) and medusahead (*Taenatherum caput-medusa*) in sagebrush steppe and other types of dryland ecosystems. In addition to propagule availability (not depicted in the model), safe sites (Harper, 1977) and soil resources (water and mineral nutrients) are critical factors enabling the establishment and proliferation of invasive exotic grasses. Soil disturbance is a primary mechanism that increases the availability of safe sites for the establishment of exotic annual grasses in sagebrush steppe by damaging the functional integrity of biological soil crusts (Mack and Thompson, 1982).

Davis and others (2000) 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 and dominance by exotic species (Johnstone, 1986; With, 2002), including patterns of cheatgrass invasion in sagebrush steppe ecosystems of the Great Basin (Chambers and others, 2007; Norton and others, 2007).

Transition to Dominance by Trees.—"Encroachment" and increasing dominance of trees and/or shrubs in grasslands, savannas, and shrubsteppe vegetation is one of the most widely documented patterns of vegetation change in dryland ecosystems around the world (Archer, 1994; Miller and Rose, 1999; Archer and Stokes, 2000). Factors proposed most commonly as explanatory mechanisms include excessive grazing by domestic livestock, fire-suppression efforts, and climate (fig. 3.7). 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 excessive grazing 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). 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 fire-suppression efforts as a driver of ecosystem change (Archer, 1994; Archer and others, 1995).

These same factors have been proposed as mechanisms enabling increases in tree establishment in sagebrush steppe ecosystems of the Great Basin (Miller and Tausch, 2001; Miller and others, 2005). In shrubsteppe ecosystems, tree establishment also can be facilitated by shrubs that ameliorate environmental conditions experienced by tree seedlings (Chambers, 2001). Fire-regime alteration has been suggested as a major driver of tree encroachment in the Great Basin (Miller and Tausch, 2001; Miller and others, 2005), but spatial variability in the relative importance of this factor is poorly understood (Baker, 2006; Romme and others, 2007).
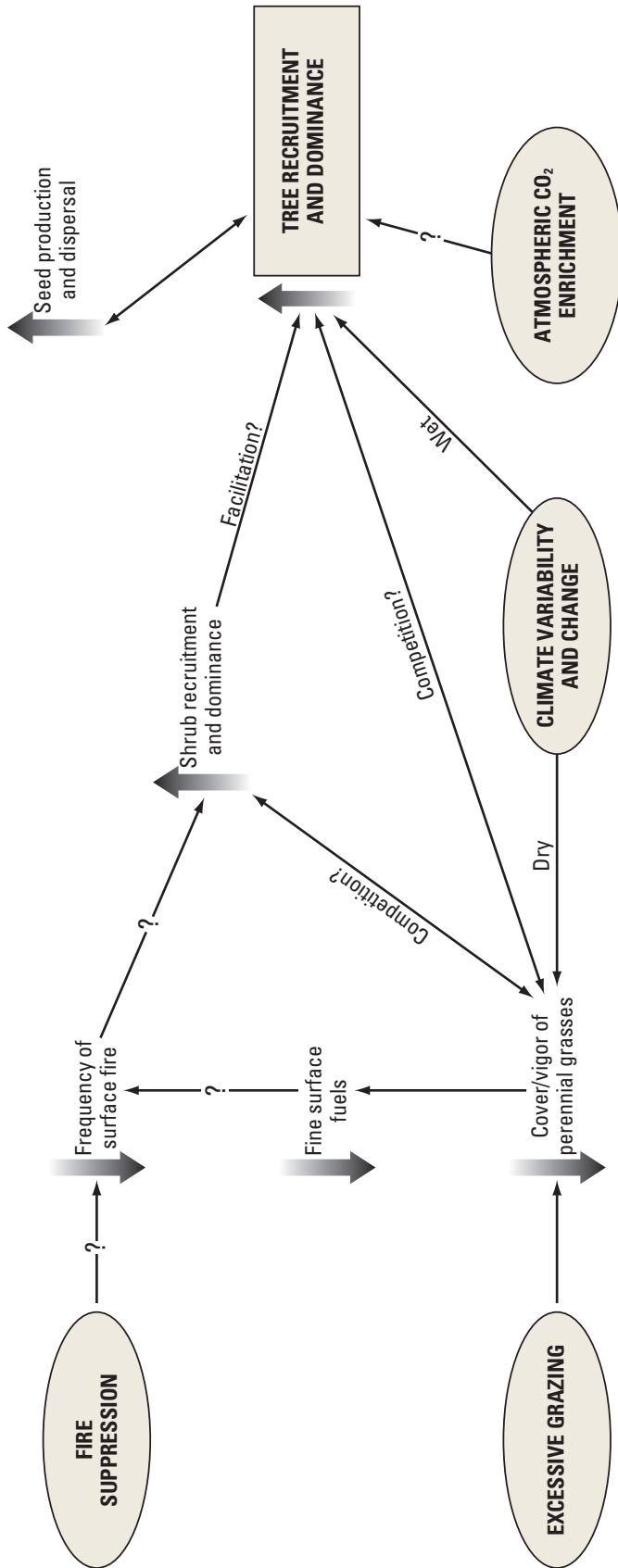
Figure 3.5. General state-and-transition model for sagebrush steppe ecosystems of the Great Basin.

Table 3.3.   Characteristics of six general persistent conditions of sagebrush steppe ecosystems in the Great Basin.

[Letters B-G refer to boxes depicted in figure 3.5]

State	General characteristics
B. Degraded sage-brush steppe	Dominated vegetatively by sagebrush with an understory of exotic annual grasses. Native understory plants and the associated soil seed bank have been depleted by excessive herbivory. Biological soil crusts and associated ecosystem functions (soil stabilization, nutrient cycling, hydrologic processes, resistance to exotic annual grass establishment) have been degraded due to soil-surface disturbances. As a consequence, resilience to natural disturbances and anthropogenic drivers is degraded—thereby increasing risks of further degradation.
C. Introduced seeding	Dominated by nonnative forage grasses such as crested wheatgrass (*Agropyron cristatum*), resulting from previous efforts to increase livestock forage or otherwise improve degraded rangeland conditions (Pellant and Lysne, 2005). Native plant diversity and habitat quality for native wildlife species typically are low relative to reference conditions for sagebrush steppe.
D. Exotic dominated	Dominated by exotic annual grasses such as cheatgrass and typically perpetuated by a positive feedback between annual grass dominance and the occurrence of high-frequency surface fires (for example, D'Antonio and Vitousek, 1992; Brooks and others, 2004). Habitat quality and native biodiversity are low relative to reference conditions, and the potential for accelerated erosion may be high if ground cover provided by annual grass populations fluctuates strongly in relation to climate.
E. Tree dominated	Represents a transition from shrubsteppe vegetation structure to woodland vegetation structure. Associated with this major structural change, habitat conditions and the functioning of key ecosystem processes (for example, disturbance regimes, rates of geomorphic and biogeochemical processes) also are significantly altered relative to reference conditions. Resistance to drought and high-severity wildfire may be reduced, potentially resulting in increased risk of severe erosion or conversion to dominance by exotic annual grasses (West, 1999).
F. Severely eroded	Characterized by an extreme loss or alteration of soil resources and biogeochemical / hydrologic processes. Site conditions have been altered to the degree that characteristic species can no longer be supported on the site.
G. Restored	Results from successful ecological restoration of key ecosystem components and processes that are required for long-term sustainability of an ecosystem that is structurally and functionally similar to the reference condition. Depending on site history (for example, legacies of past land-use activities), as well as on ecological and socioeconomic constraints to restoration, it may not be possible to fully restore the damaged ecosystem to reference conditions. But a successfully restored ecosystem should be able to sustain a wide range of valued ecosystem services without further management intervention. As with the reference condition, the prospects of changing climatic and atmospheric conditions indicate the need for a flexible notion of restoration targets. Legacies of past land-use activities, multiple management objectives, and shifting concepts of reference conditions and restoration targets suggest that managers and restoration practitioners will increasingly be developing "designer ecosystems" as they seek to restore native diversity and resilience to damaged ecosystems (Pimm, 1996; Palmer and others, 2006; Seastedt and others, 2008).

Figure 3.6.   Stressor model illustrating multiple drivers and processes that may lead to increasing dominance of dryland ecosystems by exotic annual grasses. Question marks indicate uncertainty regarding the relative importance of particular factors.

Figure 3.7.   Stressor model illustrating multiple drivers and processes that may lead to increasing tree recruitment and dominance in sagebrush steppe ecosystems. Question marks indicate uncertainty regarding the relative importance of particular factors.
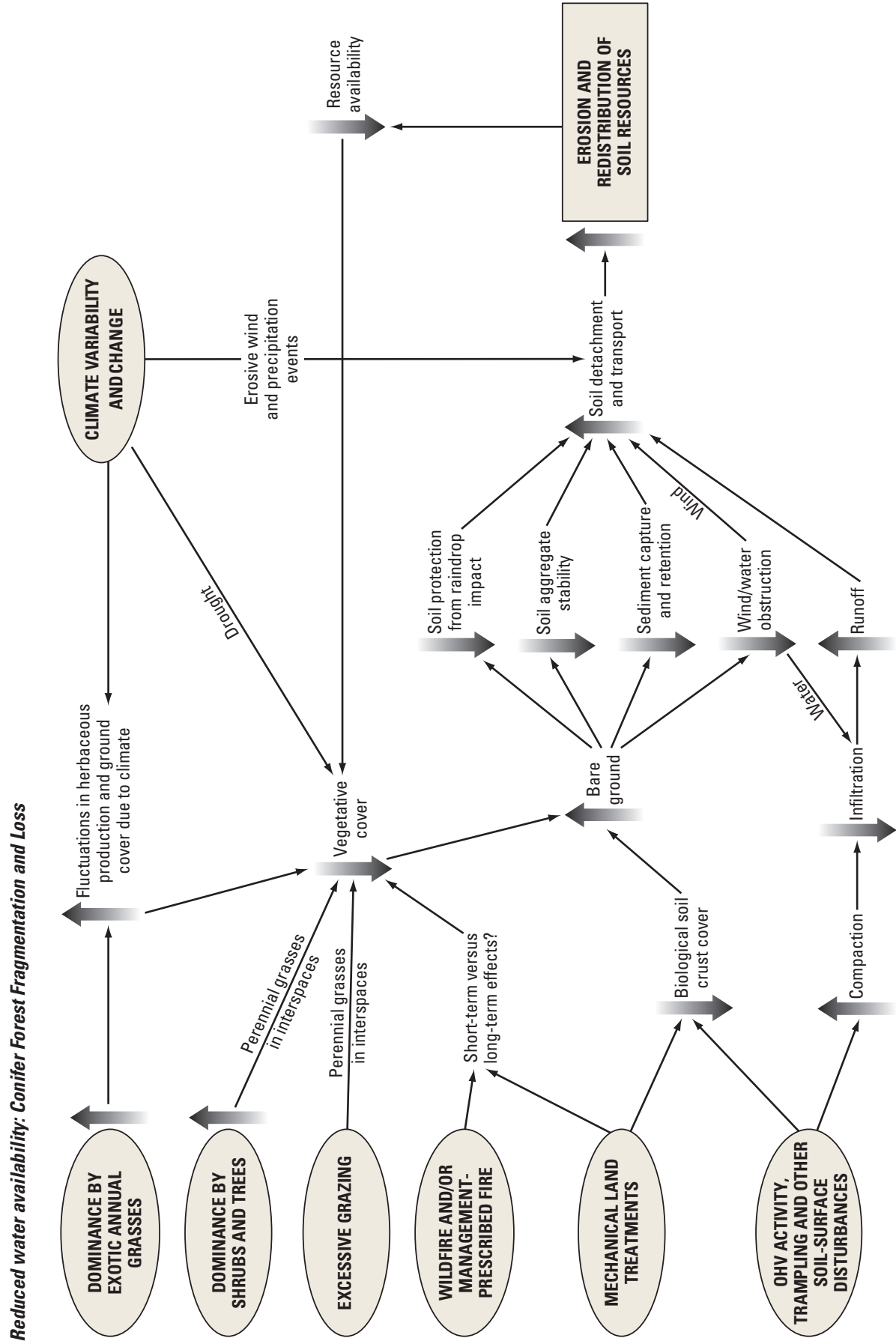
Soil Erosion and Loss of Site Potential.—Figure 3.8 illustrates multiple drivers and processes that may lead to increasing rates of soil loss and redistribution in sagebrush steppe and other types of dryland ecosystems. Soil resources can be eroded and redistributed by wind and water. The relative importance of wind- versus water-driven erosion depends on soil properties, topography, vegetation structure, and the relative frequency and magnitude of erosive wind versus precipitation events (Breshears and others, 2003). Wind erosion has been determined to greatly exceed water erosion in some shrubland ecosystems (Breshears and others, 2003), although such comparisons have not been conducted for sagebrush steppe.

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 reduce soil stability by disrupting biological soil crusts that protect and retain soils against erosive forces of wind, rain, and runoff (Williams and others, 1995a; Belnap and Gillette, 1998; Okin and others, 2001). Soil-surface disturbances also 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). Decreases in vegetative ground cover and biological soil crusts also can result in accelerated erosion due to diminished capacity to obstruct erosive wind and overland flow of water (Davenport and others, 1998; Reid and others, 1999; Ludwig and Tongway, 2000). Yeo (2005) examined vegetation and soil-surface properties inside and outside 19 long-term grazing exclosures in sagebrush steppe and salt desert scrub in east central Idaho and determined that erosional features (for example, pedestals and evidence of soil movement and overland water flow) were more pronounced outside the exclosures—indicating greater soil stability and hydrologic functioning inside exclosures where interspaces were no longer subject to trampling by livestock. Increasing dominance of shrubs and trees may result in accelerated rates of runoff and erosion due to competitive reductions in herbaceous ground cover and its capacity to stabilize soils, obstruct overland flow, and capture sediment in interspaces among woody plants (Wilcox and others, 1996). This process may be accelerated further where intercanopy soil-surface disturbances increase the connectivity of flow paths on hillslopes and reduce the capacity of shrub or tree mounds to capture overland flow (Spaeth and others, 1996; Eldridge and Rosentreter, 2004). In some settings, relatively small reductions in herbaceous ground cover may trigger large increases in runoff and erosion (Davenport and others, 1998). Factors contributing to the occurrence of such erosion thresholds include soil structure, texture and rock content; slope length and gradient; and the spatial distribution of vegetation patches, biological soil crusts, and other features that control the connectivity of flow paths (Davenport and others, 1998).
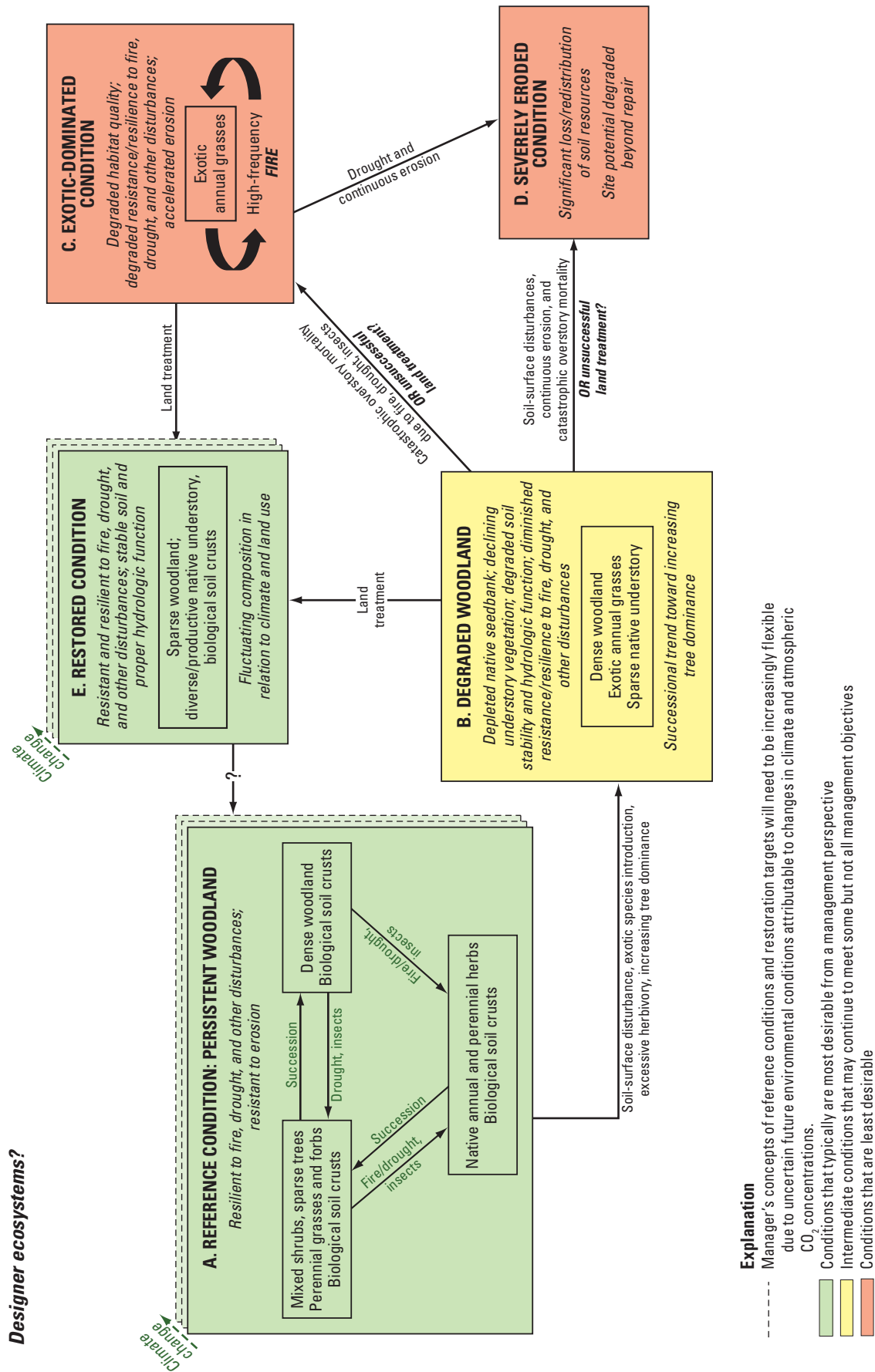
Increasing dominance of exotic annual grasses, mechanical land treatments, and fire also may result in accelerated soil loss. Relative to perennial plants and biological soil crusts, annual plants are likely to experience greater climate-driven fluctuations in cover. Thus, dominance by annuals may result in greater exposure of bare ground to erosive forces of wind and water during drought periods if annuals fail to germinate. Mechanical land treatments, such as use of an anchor chain or pipe harrow (Stevens and Monsen, 2004), can have multiple effects on erosional processes. Where such treatments are conducted to remove intact vegetation, reductions in vegetation structure and associated soil disturbance may result in significant short-term increases in soil erosion by wind. Treatments may reduce erosion by water where they disrupt existing flow paths, enhance soil-surface roughness, and thus facilitate retention of overland water flow. However, net effects of treatments on soil loss will depend on factors that determine the relative magnitude of water- versus wind-driven erosion as well as long-term treatment effects on vegetation cover and soil stability. Although most treatments are undertaken with the intent of reducing soil loss through long-term increases in cover of perennial grasses, monitoring efforts rarely are adequate for evaluating short- versus long-term treatment effects. Similarly, removal of vegetation by fire can generate large increases in soil erosion by wind (Whicker and others, 2002) and water (Johansen and others, 2001), but net effects on soil loss will depend on rates of post-fire vegetation recovery, soil properties, and topographic setting. Finally, climate plays a key role in erosion due to effects on vegetation cover (for example, rates of post-treatment and post-fire vegetation responses) and the frequency of erosive wind and precipitation events. As soil resources are lost due to erosional processes, declining resource availability may generate a positive feedback that facilitates further decreases in vegetative ground cover and further increases in erosion (for example, Friedel and others, 2003; Sparrow and others, 2003; Tongway and others, 2003).

Pinyon-Juniper Woodlands

Figure 3.9 illustrates a general state-and-transition model for pinyon-juniper ecosystems (persistent-woodland types) of the Great Basin. The structure of the model is similar to that depicted for sagebrush steppe ecosystems, with the Reference Condition (fig. 3.9, Box A) characterized by biotic and abiotic ecosystem components and processes present and functioning within their natural range of variability, but potentially drifting away from historic conditions due to effects of changing climate and atmospheric CO_2 concentrations. The model depicts four additional persistent conditions of pinyon-juniper ecosystems. Key characteristics of a degraded woodland (fig. 3.9, Box B) are altered understory plant community composition (shift in relative dominance from native perennial grasses and shrubs to dominance by exotic annual grasses), a depleted native seedbank, and loss of soil

Reduced water availability: Conifer Forest Fragmentation and Loss

Figure 3.8.   Stressor model illustrating multiple drivers and processes that may lead to increasing erosion and redistribution of soil resources in dryland ecosystems.

Designer ecosystems?

C. EXOTIC-DOMINATED CONDITION

Degraded habitat quality; degraded resistance/resilience to fire, drought, and other disturbances; accelerated erosion

Exotic annual grasses

High-frequency **FIRE**

Land treatment

Drought and continuous erosion

D. SEVERELY ERODED CONDITION

Significant loss/redistribution of soil resources

Site potential degraded beyond repair

Soil-surface disturbances, continuous erosion, and catastrophic overstory mortality

OR unsuccessful land treatment?

Catastrophic overstory mortality due to fire, drought, insects

OR unsuccessful land treatment?

E. RESTORED CONDITION

Resistant and resilient to fire, drought, and other disturbances; stable soil and proper hydrologic function

Sparse woodland; diverse/productive native understory, biological soil crusts

Fluctuating composition in relation to climate and land use

Land treatment

B. DEGRADED WOODLAND

Depleted native seedbank; declining understory vegetation; degraded soil stability and hydrologic function; diminished resistance/resilience to fire, drought, and other disturbances

Dense woodland
Exotic annual grasses
Sparse native understory

Successional trend toward increasing tree dominance

Climate change

?

A. REFERENCE CONDITION: PERSISTENT WOODLAND

Resilient to fire, drought, and other disturbances; resistant to erosion

Dense woodland
Biological soil crusts

Succession

Drought, insects

Fire/drought, insects

Mixed shrubs, sparse trees
Perennial grasses and forbs
Biological soil crusts

Succession
Fire/drought, insects

Native annual and perennial herbs
Biological soil crusts

Soil-surface disturbance, exotic species introduction, excessive herbivory, increasing tree dominance

Climate change

Explanation

- - - - -   Manager's concepts of reference conditions and restoration targets will need to be increasingly flexible due to uncertain future environmental conditions attributable to changes in climate and atmospheric CO_2 concentrations.

Conditions that typically are most desirable from a management perspective

Intermediate conditions that may continue to meet some but not all management objectives

Conditions that are least desirable

Figure 3.9. General state-and-transition model for pinyon-juniper (persistent woodland) ecosystems of the Great Basin. Dashed boxes associated with the reference (A) and restored (D) condition indicate that managers' concepts of reference conditions and restoration targets will need to be increasingly flexible due to uncertain future environmental conditions attributable to changes in climate and atmospheric CO_2 concentrations.

stability due to soil-surface disturbances. As a consequence of altered understory composition, resilience to drivers such as high-severity fire is reduced and the risk of conversion to dominance by exotic annual grasses is increased relative to the reference condition (West, 1999; Romme and others, 2003)—even if high-severity fire is considered to be "natural" for pinyon-juniper ecosystems. Processes leading to increasing dominance by exotic annual grasses (fig. 3.6) and to soil erosion and redistribution (fig. 3.8) are similar to those described for sagebrush steppe ecosystems. Depending on site-specific ecosystem properties (for example, specific pinyon-juniper ecological sites), there may be numerous expressions and intergradations of these basic types of altered or degraded pinyon-juniper ecosystems.

Summary Points

Sagebrush steppe and pinyon-juniper woodlands together account for about 60 percent of the land area in the Great Basin. These ecosystems are dominated by varying proportions of shrubs, perennial grasses, and other herbaceous plants, trees, and biological soil crusts, and they provide numerous benefits to society including habitat for valued wildlife species, livestock forage, fuel wood, watershed services, and recreational opportunities. The capacity of these systems to provide this suite of benefits is threatened by numerous processes that can lead to persistent alterations in vegetation composition and structure, soil resources, and patterns of ecosystem dynamics. In sagebrush steppe, dominance by invasive exotic grasses and dominance by encroaching tree populations are the two most persistent and pervasive vegetation changes that have had widespread implications for ecosystem dynamics and management. In pinyon-juniper woodlands, increasing dominance by invasive exotic plants likewise has significant management implications through potential effects on risks attributable to wildland fire. Some of the most important anthropogenic stressors that contribute to the occurrence of these persistent changes include excessive herbivory by livestock, altered fire regimes, and soil-surface disturbances by livestock trampling and off-highway vehicle use. Ecosystem responses to these and other anthropogenic factors commonly depend on climatic conditions and natural disturbance regimes. Projecting the future dynamics and condition of these ecosystems over the next 50 years is hampered by the need to better understand effects of changing climatic conditions and atmospheric CO_2 concentrations on soil resources, competitive relations among plants, and fire regimes. Future dynamics and condition of these ecosystems also are hampered by a need to understand how ecosystems responses to the interactive effects of climate and land use vary spatially in relation to soil-geomorphic properties, landscape configuration, and patterns of human growth and infrastructural development.

Aspen Forests

In the Great Basin, aspen forests grow in relatively pure stands associated with upland riparian corridors and in 'snow pockets' where delayed snowmelt results in mesic soil conditions later into the growing season. In both situations aspen forest stands tend to be small ($\leq$ 8 ha) and individual trees often do not meet their growth potential due to environmental limitations. Nevertheless, aspen groves provide valuable habitat for a range of species, most notably cavity nesting birds and bats (DeByle and Winokur, 1985; Dobkin and others, 1995; Parsons and others, 2003) and also provide valuable forage. Aspen most commonly regenerates by means of vegetative sprouting from the root system following disturbances, such as a fire that kills the mature trees. However, rare episodes of seedling recruitment occur (Jelinski and Cheliak, 1992). Aspen stands appear to be decreasing across the west (for example, Beever and others, 2005). Fire suppression has been identified as the most widespread proximal factor, but elk browsing and domestic cattle grazing also have been recognized (Rogers, 2002; Larsen and Ripple, 2003). Developing a specific set of conceptual models for this system is beyond the scope of this study.

Mixed Conifer Forest Model

By S.P. Finn

Distribution and Management Significance

Coniferous forests (excluding pinyon-juniper woodlands) cover 4.4 percent of the Great Basin landscape (derived from Kuchler, 1970), typically at high elevations on many of the 300+ interior mountain ranges and in the Sierra, Cascade, Wasatch, and other ranges that form the west, north, and east margins. Interior forest stands are patchily distributed at the coarse-scale whereas peripheral stands are more continuous and grade into other forest-types in adjacent ecoregions (Cronquist and others, 1972). In spite of their limited distribution, Great Basin forests contribute significantly to the biodiversity of the ecoregion; a host of plants, animals, and fungi closely linked with coniferous forest structure and microclimate are not found in other Great Basin systems. In the arid Great Basin, the distribution of vegetative communities primarily is determined by soil moisture, which is a function of the amount and timing of precipitation, insolation, geomorphic setting, elevation, and local soil properties. Coniferous forest replaces lower-elevation woodland and shrubland cover-types only where water is abundant enough in the soil-root zone during the growing season such that the balance between soil moisture, groundwater, and transpiration favors evergreen trees (Charlet, 1996). Forests are limited at their upper elevational bound by the extreme weather (strong winds, blowing ice, winter drought) and late season snow cover of the alpine tundra (Stevens and Fox, 1991; Sveinbjornsson, 2000).

Across the region, conifer forest stands are isolated by arid, shrub-dominated basins. Their present location is the result of either long-term climate trends that favored shrubland and grassland cover types at low elevations (Martin and Mehringer, 1965), or bird-aided conifer seed dispersal to suitable high-elevation growing locations that were (and are) separated by inhospitable interstices (Wells and Berger, 1967). Currently, the position of interior conifer forest patches on the Great Basin landscape is not unlike an archipelago of oceanic islands. The arrangement presents an ideal backdrop for natural experiments in continental island biogeography (Wells, 1983; Brown, 1978), as well as potential dispersal barriers for the many low-vagility plant and animal species that inhabit forest patches. The literature suggests that some boreal-associated trees are capable of direct or bird-aided dispersal among mountain ranges (Wells, 1983). More vagile species of birds (Behle, 1978), mammals (Skaggs and Boecklen, 1996; Lawlor, 1998), and butterflies (Wilcox and others, 1986) also are capable of dispersal among isolated forest patches (Brown, 1971). However, individuals of many less-mobile taxa, including some birds and butterflies, are not likely to cross the vast shrubland matrix surrounding montane forest patches. Some of these disjunct or isolated populations may be particularly vulnerable to extirpation because they are unlikely to receive immigrants from nearby patches (Brown, 1971; Johnson, 1975; Wilcox and others, 1986; Beever and others, 2003; Grayson, 2005). Thus, changes in the rates or intensities of ecosystem drivers, like climate change or fire regime, that influence the location or continuity of Great Basin coniferous forests may have significant effects on the composition and diversity of associated biota.

Nearly all Great Basin forests are managed by the U.S. Forest Service (USFS) or BLM for multiple uses. Great Basin National Park is managed to conserve its natural and historic value and provide for visitor enjoyment. Historically, most forests in the region were heavily logged between 1860 –1890 when nearly all merchantable timber was harvested for mining and homesteading (M. Hampton, U.S. Forest Service, oral commun., 2008). Commercial timber harvest continues only in forests along the boundary and a few interior forests in southeast Oregon. Great Basin forests also produce wood for fuel and other local uses, livestock forage, watershed and ecosystem services, and a variety of recreational opportunities. Forests positioned on or near other desirable resources (for example, mineral deposits or wind energy potential) may be altered as a consequence of commodity production and transport.

Components and Processes

### Climate and the Physical Template – Determinants of Site Potential

Interactions among a suite of abiotic factors (climate, elevation, landform, geology, and soils) determine the potential vegetative structure of a given site (Jenny, 1980; Long, 2003) and form integral portions of our conifer forest subsystem model (fig. 3.10).

Conifer forests in the Great Basin typically are found on sedimentary (limestone, dolomite, sandstone, siltstone) and igneous (rhyolite, andesite, basalt, granite) parent materials that mostly arose from continental rock uplifted in fault-block mountain ranges (Hunt, 1974). Those formations tend to be highly stable through human time scales, but forests also can develop locally on alluvium and colluvium, which are more prone to short-term geomorphic change and disturbances. In the Basin and Range Province, these landforms have been repeatedly modified during recurrent periods of active erosion and deposition as well as by soil formation during periods of greater landscape stability (Peterson, 1981). Spatial patterning of soil properties such as depth, particle size, and degree of profile development are highly complex across the landscape (Peterson, 1981). Coniferous forests are supported by a diversity of parent materials, landforms, and soils that complicate generalizations made about their physical and biotic characteristics. Different types of soils and plant communities tend to be associated with different landforms as well as with finer-scale elements of landforms (Peterson, 1981; Monger and Bestelmeyer, 2006).

Climatic factors are dynamic over much shorter temporal scales than topography and geology and therefore exert more proximate influences on the location and composition of Great Basin coniferous forest. Timing of precipitation is important to vegetative cover because it influences the annual hydrologic budget that determines factors such as soil moisture and evapotranspiration rates. Precipitation arrives primarily as winter snow throughout much of the region (Bailey, 1995) but the eastern part of the Great Basin often receives monsoon rainfall concentrated in late summer (Tyler and others, 1996). In the Great Basin, coniferous forests generally are found only on sites where average annual precipitation exceeds about 25 cm on south-facing slopes and about 17 cm on north-facing slopes (fig. 3.11). Climate effects, however, are mediated by elevation and landform. Increasing elevation generally leads to an increase in precipitation, solar radiation, and wind and a decrease in temperature (Peet, 2000). Temperature and solar radiation, among other climate variables, also are influenced by slope-aspect. For example, south-facing slopes tend to be drier and conifer forests there lie at higher elevations (fig. 2.13). Climate trends and climatic contributions to trends in other drivers (for example, fire regime) over the next 50+ years are likely to exert the most significant influence on Great Basin coniferous forest ecology.
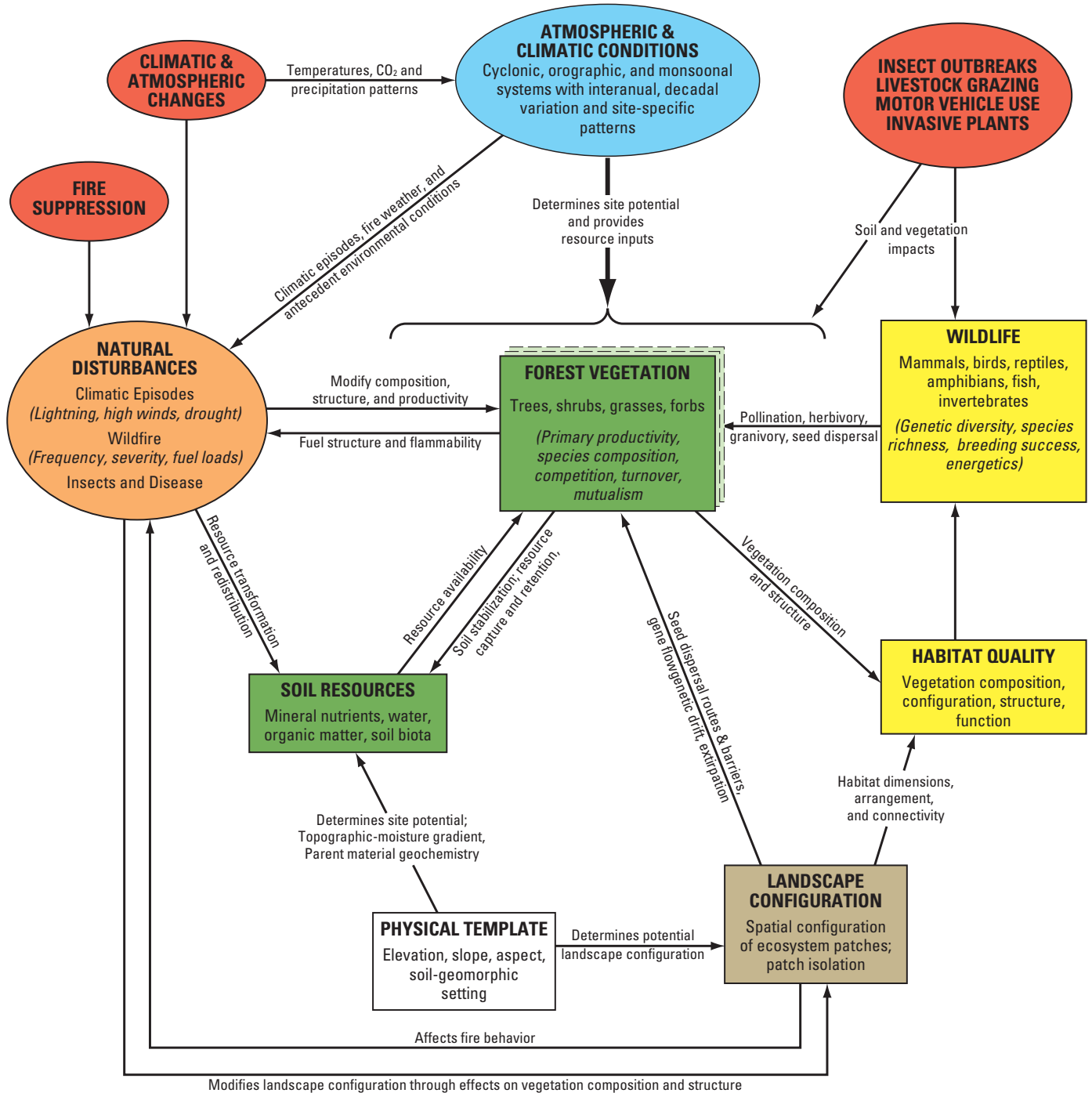
Figure 3.10. Conifer Forest Control Model illustrating key structural components (green rectangles), primary natural (blue oval) and anthropogenic (orange ovals) drivers, and functional relations (arrows) of Great Basin forest ecosystems. Heavy arrows indicate more important functional relations. Hypothetical alternate states that emphasize mountain sagebrush, mountain mahogany, aspen, or several conifer mixes, are indicated by the multiple dashed boxes for Forest Vegetation. States may change due to disturbances, climate variation, pest outbreaks, etc.
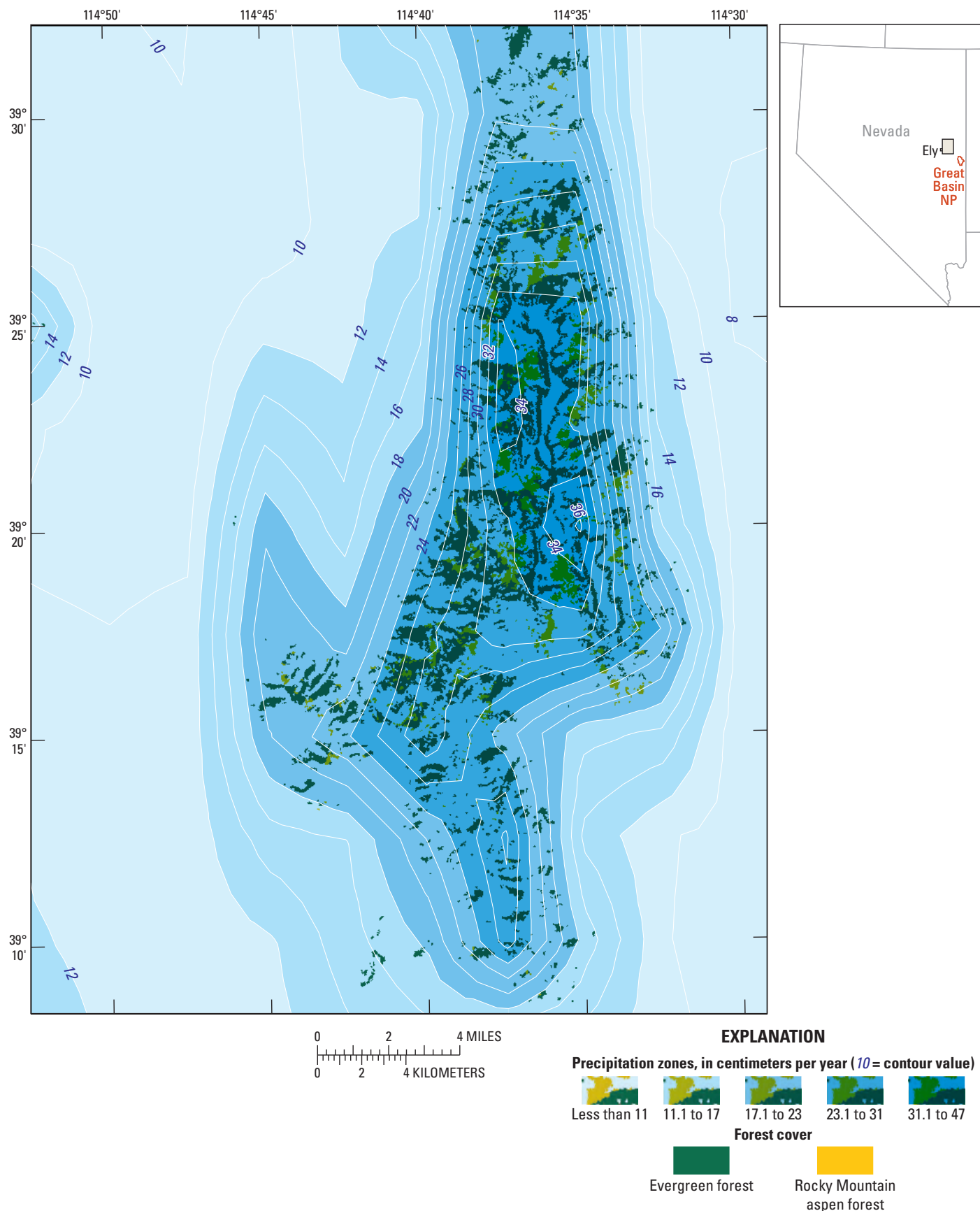
Figure 3.11.   Coniferous and aspen forest distribution in the Great Basin is highly correlated with precipitation as shown here in the Schell Creek Range of eastern Nevada. Precipitation data from PRISM Group (2004).

Vegetation, Soil, and Wildlife Resources

Vegetation.—Great Basin coniferous forest overstories are composed of a mix of tree species originating from Rocky Mountain or Sierra Nevada floras. In some places, relatively monotypic stands occur (Burns and Honkala, 1990; Charlet, 1996). Tree species richness generally decreases as distance from the western Rocky Mountains increases (Hamrick and others, 1994). Of the 15 species of Pinaceae in the Great Basin, ponderosa pine (*Pinus ponderosa*), limber pine (*Pinus flexilis*), and white fir (*Abies concolor*) are the most widely distributed (Pase and Brown, 1994; Charlet, 1996). In some places, fire adapted stands (that is, mature ponderosa pine) are being replaced by shade-tolerant species (that is, white fir) in part as a result of aggressive fire suppression. Douglas fir (*Pseudotsuga menziesii*) and Engelmann spruce (*Picea engelmannii*) are important components in some areas, for example Great Basin National Park. Bristlecone pine (*Pinus longaeva*), a species noted for its longevity, is an important constituent of the conifer community in many southern Great Basin mountain ranges. Bristlecone pine trees usually exist in open stands between 2,700 and 3,500 m elevation on exposed rocky sites above more densely stocked forest. At lower elevations and in mesic snow pockets, mixed conifer forests commonly include patches of deciduous trees dominated by quaking aspen (*Populus tremuloides*). Understory vegetation is an important part of the forest ecosystem although the composition and density varies with overstory species composition and closure and site disturbance regimes. Understories generally are composed of conifer seedlings, grasses (*Poa spp.*, *Pseudoroegneria spicata*), forbs (*Lupinus spp.*, *Voila spp.*), and shrubs (*Ribes spp.*, *Symphoricarpos spp.*) growing most densely in canopy gaps. Shade intolerant shrubs such as mountain big sagebrush (*Artemisia tridentata vaseyana*) and mountain mahogany (*Cercocarpus ledifolius*) may play successional roles in forest development or arise as alternate stable states in place of conifer forest (fig. 3.10). Other shrubby trees include dwarf maple (*Acer glabrum*), which grows in moist shady areas with broken canopy between 1,500 and 2,400 m, and serviceberry (*Amelanchier spp.*) most commonly found on shaded north-facing slopes.

Vascular plants perform many important functions in Great Basin forests. Their presence forestalls erosive effects of wind and precipitation; enhances the capture of nutrients, seeds and surface water; provides copious amounts of organic matter to the soil; and generates oxygen during photosynthesis. Additional functions performed by forest vegetation include sequestration of carbon, mediation of microclimates, and functions within the hydrological cycle. Large woody plants also provide coarse fuel which, in the arid Great Basin, retain relatively little moisture and are characterized by slow decomposition rates. Conifer trees and other forest vegetation provide food and shelter to a broad range of consumers and detritivores.

Soils.—Soils and soil development are intricately tied to the vegetation community they support. Extant vegetation often is a critical contributor to the upper soil horizon where most biological activity in soils occurs. Ultimately, however, soils are a product of the underlying parent material that largely determines the chemical and physical properties of the soil. Soils supporting Great Basin coniferous forests tend to be gravelly to very gravelly loams and silt loams that have moderate to high permeability, and range from very shallow to deep. Mollisols, in the form of Xerolls and Ustolls, are dominant on Great Basin mountain slopes (U.S. Department of Agriculture, 1998). Xerolls are freely drained Mollisols found in parts of California, Idaho, Nevada, and western Utah. Xerolls tend to be dry for extended periods in summer, but moisture moves through most of the soils in winter and is stored above the deep layers or above bedrock in normal years. Ustolls (also known as Borolls) are Mollisols of the cold-winter semi-arid plains and steppes; they are associated with monsoonal precipitation patterns in the eastern part of the region. Xerolls and Ustolls tend to have a xeric, aridic, or ustic moisture regime, meaning limited amounts of soil water may be present but they generally experience moisture stress during much of the growing season. Xerolls and Ustolls typically have a frigid or cryic temperature regime.

Soils provide nearly all mineral nutrients used by the plant communities they support. In a healthy state, they are the site of most decomposition of organic material, retain water and facilitate infiltration, provide a stable substrate for plant roots, and harbor a diverse community of micro- and macro-organisms that contribute to stability and diversity to the biotic community.

Wildlife and Habitat Quality.—Great Basin coniferous forests host a diverse complement of vertebrate and invertebrate animals. Across the region, species such as silver-haired bat (*Lasionycteris noctivagans*), ermine (*Mustela erminea*), Nuttall's cottontail (*Sylvilagus nuttallii*), and an abundance of birds including band-tailed pigeon (*Patagioenas fasciata*), dusky grouse (*Dendragapus obscurus*), Williamson's sapsucker (*Sphyrapicus thyroideus*), and flammulated owl (*Otus flammeolus*) are associated with Great Basin coniferous forests. Because dispersal rates vary among species, some forest-associated wildlife populations exhibit a metapopulation structure whereas less-vagile species persist largely as isolated populations with little if any exchange of individuals or genes (Brown, 1978; Cutler, 1991).

Animals perform significant functional roles in Great Basin forest ecosystems. Acts of herbivory, granivory, and digging contribute to enhanced seed dispersal, altered plant distributions, and soil-nutrient turnover. An example is the Clark's nutcrackers (*Nucifraga columbiana*) role as dispersers of whitebark (*Pinus albicaulis*; Tomback, 1982) and limber pine (Tomback and Kramer, 1980) seeds.

Ungulate herbivores, native and introduced, generally are not abundant in the upper elevation Great Basin conifer forests; therefore, their current influence on these systems probably is less than on low elevation shrub and grasslands (see Sagebrush Steppe Model). However, the legacy effects of historical livestock grazing in western coniferous forests is still not fully understood (Fleischner, 1994). Domestic herbivores tend to concentrate under the canopy of forest edges for shade. Effects on vegetation structure and composition and on soil and hydrologic processes from large ungulates in upland forest-types usually are greatest near lower treeline edges, access roads, and water sources (Fleischner, 1994; also see Chapter 4, Stream and Riparian Models).

We know very little about functional contributions of most vertebrates; however, we know even less about many aspects of invertebrate life-histories and their influence on Great Basin forests. Bark beetles (*Coleoptera: Scolytidae*) are one invertebrate group that is relatively well-studied and their influence on conifer forest health and function can be quite significant (Powers and others, 1999). The potential effect of insect outbreaks is addressed in the section, "Drivers of Ecosystem Change."

Drivers of Ecosystem Change

Climate Variability and Change

Climate, including variations across all spatial and temporal scales, is the overriding driver of landscape condition. Increasing temperature and CO_2 concentrations in recent decades appear to be of an unprecedented magnitude and rate (Intergovernmental Panel on Climate Change Working Group I, 2001; Connely, 2003) prompting our scoping efforts to identify climate change as a key ecosystem driver in the Great Basin. From the perspective of ecosystem responses, the causes of climate changes are somewhat irrelevant; it is more important to understand the rate and directionality of climate-induced landscape change so we rely on appropriate models to evaluate future climate scenarios. As described in the atmospheric model, existing climate models generally lack details necessary to understand climatic influences on the topographically diverse Great Basin. Nearly all climate models predict that warmer conditions will prevail in the Great Basin during the next few decades, but the same models disagree over the amount and timing of precipitation over the next 50–90 years. A decrease in precipitation would indicate that forest systems in the region may shrink, move upslope, or disappear from the landscape (for example, Diffenbaugh and others, 2003; Parmisan and Yohe, 2003). Indeed, resampled plots at Great Basin National Park demonstrate that Engelmann spruce is declining in permanent plots within riparian forest habitat at all but the highest elevations, and that the minimum elevation of the species' distribution rose 175–200 m from 1992 to 2001 in three of

four drainages studied (Beever and others, 2005). Recent mortalities in some pinyon-juniper stands (Shaw and others, 2005) also might indicate changes in Great Basin vegetation due to climate change (Rehfeldt and others, 2006). Loss of forest would impact plant and wildlife communities associated with forest cover types.

Increased precipitation, especially that falling in winter and remaining as snowpack, may favor conifer forest cover at the expense of xeric shrubland (Thompson and others, 1998; National Assessment Synthesis Team, 2000). Still other models predict that Great Basin conifer forest distributions will remain relatively unaffected by climate shifts over the next century (Rehfeldt and others, 2006).

Because plants will respond to climate changes individualistically (Smith and others, 2000) community-level responses remain open to interpretation. Furthermore, forest cover changes resulting from increasing greenhouse gasses and consequent climate change likely will be mediated by many additional factors including nutrient cycling feedbacks, age-dependent responses, and species interactions (Diffenbaugh and others, 2003). Moreover, invasive species that disperse rapidly are likely to find opportunities in newly forming communities (Dukes and Mooney, 1999; National Assessment Synthesis Team, 2000). Thus, the species composition of future communities may differ substantially from those occupying similar habitats today.

Wildfire

As is the case throughout most of the intermountain west, upland forests of the Great Basin are disturbance-driven ecosystems. Wildfire is the most widespread and significant disturbance agent in the region (Peet, 2000). A direct effect 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). High-severity fires in woodlands and forests result in near-complete mortality of overstory trees, whereas low-severity fires consume primarily herbaceous surface fuels, litter, and fire-sensitive understory vegetation including seedling and sapling trees. Mixed-severity fires result in a mosaic of patches that can be caused by variations in topography, weather, fuel loading, and previous fire or other disturbance history (Noss and others, 2006). Effects of fire on vegetation structure have many ecosystem-level consequences. Reduction in vegetation cover reduces or eliminates food and cover for most forest-dependent wildlife although post-fire vegetation recovery typically increases forage for some herbivores. Erosion of soils, nutrients, and organic matter by water and wind may be exacerbated by fire-caused reduction of vegetative cover and forest floor litter. Soils may become hydrophobic as a result of severe burns leading to accelerated water runoff and decreased infiltration. Fires also may positively or negatively affect nutrient cycles and other soil functions and properties on short- or long- time scales (Raison, 1979; Whicker and others, 2002).

Natural fire return intervals are estimated to be between 7–30 years in Great Basin conifer forests (Miller and others, 2005; Stevens and others, 2007). Pre-settlement wildfires within conifers probably were low-severity and reduced fine fuels while having minimal effect on mature trees. However, fires impacting conifer patches are affected by adjacent cover types. Thus, severity of a specific fire is influenced by adjacent cover-types and the fire history of those patches as well as their topographic relationships. Because many lower elevation patches are now degraded sagebrush, pinyon-juniper, or annual grass-dominated sites, fire frequencies and intensities generally have increased in upslope conifer stands. Wildfires spreading from adjacent habitats are correspondingly expected to occur more frequently or more intensely, thereby affecting coniferous forest structure, composition, and location.

Livestock Grazing

Livestock management is arguably the most profound post-settlement human legacy on the Great Basin landscape. Introduction of cattle, sheep, and horses to a landscape nearly devoid of large herbivores in the late 1800s quickly resulted in the decline and eradication of many native grass species and other environmental consequences (Young, 1994). The vast majority of grazing effects were focused in low elevation shrublands, but forests were not spared from damage. Theodore Rixon was quoted by P.H. Roberts (1963) as stating:

> "At the beginning [of livestock grazing in the southwestern US] the mountains and heavily timbered areas were used but little, but as the situation grew more acute in the more accessible regions the use of these areas became more general and in course of time conditions within them were more grave than elsewhere... The mountains were denuded of their vegetative cover, forest reproduction was damaged or destroyed, the slopes were seamed with deep erosion gullies, and the water-conserving power of the drainage basins became seriously impaired."

The high elevation, slightly wetter pastures available in the Great Basin were useful to herders because they generally provided better summer forage than the more xeric basins. As rangeland resources declined due to overstocking, sometimes coupled with drought, forage in the conifer forest understory began to be heavily impacted. Although stocking rates have declined from the early years of livestock management and the sheep industry all but collapsed in the middle of the 20th century, livestock grazing management continues to be an important driver in Great Basin conifer forests and the effects of historic and current disturbance are priority considerations when evaluating landscape change.

Invasive Plants

Like many Great Basin ecosystem drivers, the effects of exotic, invasive plant infestations are better understood for lower-elevation shrublands and woodlands even though they are a significant forest management concern. Within the last decade, cheatgrass has expanded its range in the pine forests of the southern Sierra Nevada and central Great Basin. The ecological consequences of cheatgrass invasion into forested habitats are not as well documented as in shrub-dominated landscapes (for example: D'Antonio and Vitousek, 1992) although USGS scientists are beginning to assess its effects (M. Brooks, U.S. Geological Survey, oral commun., 2008). Other invasive species recorded in Great Basin forests include Dalmatian toadflax (*Linaria dalmatica*), diffuse knapweed (*Centaurea diffusa*), hoary cress (*Cardaria draba*), and Canada thistle (*Cirsium arvense*). However, very little specific information exists on the landscape-scale effects associated with these invasions.

Motor Vehicle Use

Motorized vehicle use is a relatively recent phenomenon in the Great Basin and, consequently, little information exists on its effects on ecosystem components and processes. Motor vehicle use is known to accelerate erosion, potentially increasing silt loads in spring pools and streams (Trombulak and Frissell, 2000). It also contributes to fragmentation of formerly contiguous land cover patches. Resource agencies expend significant time and money managing roads and vehicle access; however, enforcement of transportation policies in such a huge area can be cost-prohibitive. Thus, much of the landscape alteration that is occurring is not well regulated or documented. The quantitative effects of this disturbance across the ecoregion are virtually unknown and, although the effects on the spatially-restricted conifer forest may be less significant that the broader shrubland systems, forest cover is typically identified as a destination by recreationists, hunters, and firewood collectors. Therefore, conifer stands may be disproportionally impacted by motor vehicle use.

Insect Outbreaks

Native bark beetles (*Coleoptera: Scolytidae* and *Curculionidae*) were not initially identified as a priority ecosystem driver of coniferous forests but we include them here because future insect outbreaks may be closely linked with future climates and disturbance regime trends. At least five species of beetles cause natural, cyclical disturbances to conifer species found in the Great Basin. Beetle population abundances and distributions are likely to covary with climate change and historical land-use management practices (Bentz

and others, 2008). For example, mountain pine beetle and spruce beetle activity is believed to have increased in direct response to warming temperatures (Hansen and others, 2001; Logan and Powell, 2001). Drought-driven moisture stress can increase tree susceptibility to insect colonization. Drought periods also increase the activity of the fir engraver (*Scolytus ventralis*) in fir stands throughout the Great Basin (Bentz and others, 2008). Bark beetles affect trees directly through their subcutaneous boring action and by facilitating fungal infestations that interrupt the tree's water transport system. Mortality or dieback resulting from insects is likely to interact with changing fire regimes and influence forest health and persistence. Recent concerns also have focused on the introduction of exotic tree pests (Lee and others, 2007).

Ecosystem Dynamics

The following section describes conceptual models of Great Basin coniferous forests. As hypotheses, these models will be iteratively refined on the basis of new knowledge. These simple models are unlikely to capture all possible ecological processes and outcomes. By themselves, the models do not provide any quantification or predictive framework that will enable managers to anticipate and mitigate change on a site-specific basis. However, they do provide a starting point for a framework. Our general models do not account for site-specific factors and may require modification for application to a specific type of land unit. Some of the conceptualizations we present (figs. 3.11–3.14) are modified from work done for the National Park Service's Upper Columbia Basin and Northern Colorado Plateau Inventory and Monitoring Networks (Garrett and others, 2004; O'Dell and others, 2005). The models are best viewed as working hypotheses that can be improved with carefully designed monitoring and subsequent analyses.

The Reference Condition

Because a valid accurate conceptual model accounts for all important ecological states and processes it should accurately describe ecosystem-wide reference conditions. The significant system drivers and interactions are partially a function of a given site's history. Conversely, identifying an ecological reference point has temporal and spatial complications that are especially difficult for Great Basin forests. Indications are that conifers stands were nearly continuous in the early-Holocene Great Basin (Grayson, 1993). Grayson (1993) suggests that the Great Basin 'came to look as it looks today' during the middle Holocene, around 4,500 years before present, although he cautions that reference conditions will differ in different areas. A more practical reference point for conifer forests may be defined as the condition that existed when Europeans arrived in the region in the early 1800s because timber removal to support mining and livestock introductions began in earnest by about 1860.

Before that time Native Americans set landscape-altering fires in the Great Basin (Vale, 2002) and although the frequency and extent of ecosystem management and alteration caused by Native Americans is hotly debated (for example, Swetnam and Baisan, 1994; Anderson and Moratto, 1996), it is relatively certain that aboriginal influences on Great Basin forests had less impact than those of Euro-Americans (Fule and others, 1997).

The concept of the reference state, however, must be sufficiently flexible to account for uncertain future trajectories in environmental conditions because, given enough time, even the most identifiable reference conditions are subject to 'drift' based on millennial-scale trends in climate and landscape structure.

State-and-Transition Model

General patterns of ecosystem dynamics can be effectively illustrated using state-and-transition models (Westoby and others, 1989; Bestelmeyer and others, 2003). State-and-transition models are management-oriented tools for describing and classifying ecosystem conditions (or states) and posing hypotheses about ecological factors responsible for changes (or transitions) among different states (Bestelmeyer and others, 2004). Such models have been very effectively used by managers and researchers in shrubland and other systems but the modeling exercise rarely has been applied to forested systems of the Great Basin. We developed a generalized state-and-transition model for Great Basin coniferous forests (fig. 3.12), borrowing from work presented by Miller (Sagebrush Steppe models NRCS Ecological Site Descriptions, accessed June 23, 2009, at http://esis.sc.egov. usda.gov/Welcome/pgESDWelcome.aspx this volume; fig. 3.5, p. 82) and models being developed by NRCS (accessed June 23, 2009, at http://esis.sc.egov.usda.gov/esis_report/fsReport. aspx?id=F030XC279NV&rptLevel=communities&approve d=yes) for their Ecological Site Description process. In this model, we depict three general states: the Reference Condition describing a healthy conifer forest experiencing cyclical, successional processes; a degraded forest impacted by some combination of system stressors; and a severely degraded condition, possibly leading to a permanent change in plant community (fig. 3.12; table 3.4). Factors driving transition from one state to another are analogous to the key drivers identified during our scoping effort and include: climate change, wildfire, livestock grazing, exotic plant invasions, motor vehicle use, and insect outbreak. We use our definitions of 'driver' and 'stressor' (see Glossary) to identify drivers within the reference condition when they are operating under natural ranges of variation and stressors in the transition portion of the model when individual or combined effects move the system outside natural successional processes.
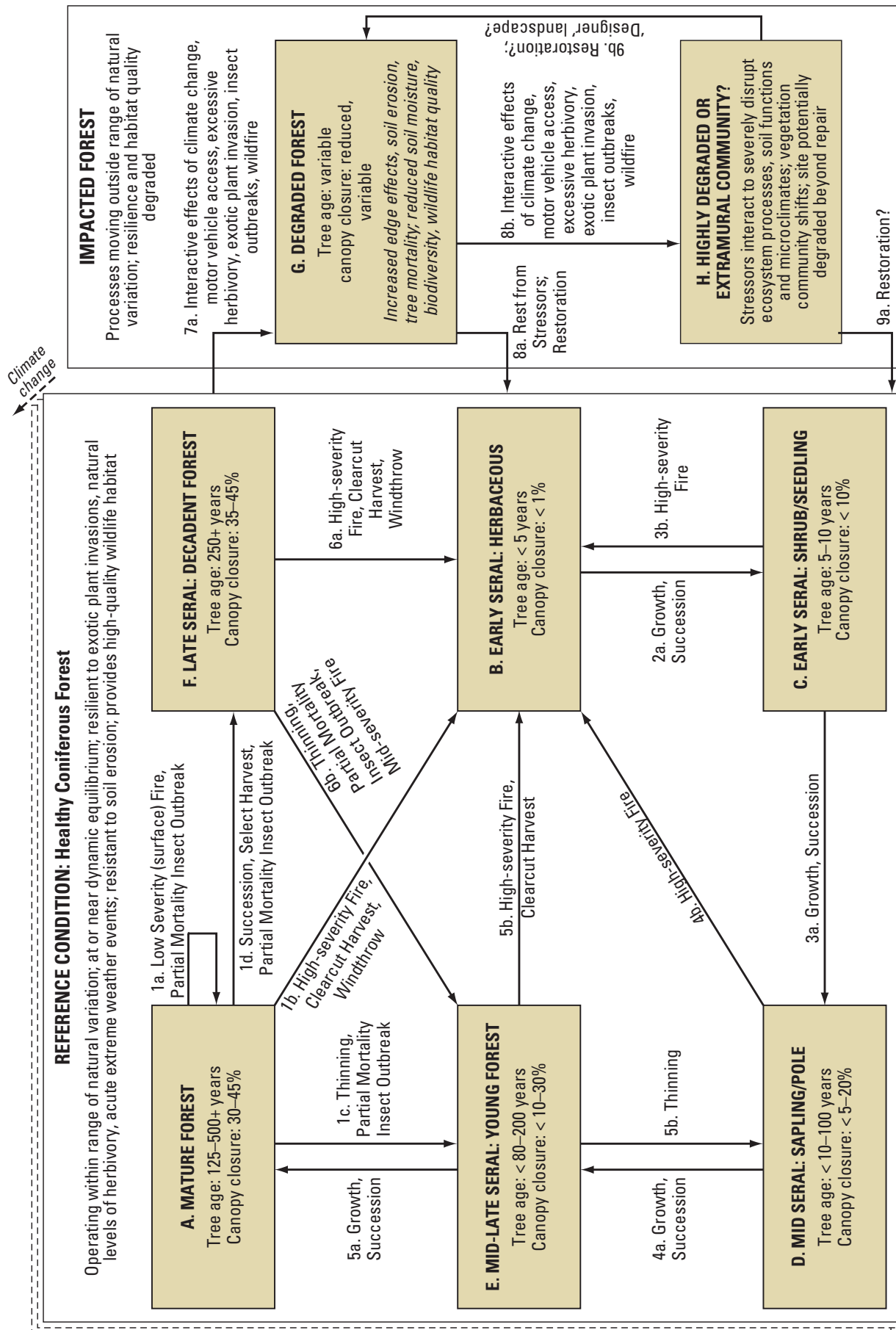
Figure 3.12. Generalized state-and-transition model for interior Great Basin Coniferous forests. This model will be refined and further developed as GBILM and partners generate further discussion and information.

Table 3.4.   Characteristics of three general states of coniferous forest systems in the Great Basin.

[Letters A-H refer to boxes depicted in figure 3.12]

| State	General characteristics
A-F. Reference Condition	Climate and physical template within natural ranges of variation. Most of region dominated by mature or maturing conifer trees but portions in earlier successional stages and dominated by forbs, shrubs and/or sapling conifers. Soils, litter, and seed banks mostly intact though some erosion evident, especially on steep slopes in disturbance zones. Resilience to anthropogenic disturbances generally high. Native flora and fauna predominate. Predicted climate change likely to favor upslope movement of the entire community (for example, Parmesan and Yohe, 2003; Beever and others, 2005).
G. Degraded Forest	Dominant vegetation shifts in terms of species composition, overstory structure, and vigor. Edge effect increase due to driver impact on periphery of stand. Soil moisture and plant biomass reduced. Increased susceptibility to wildfire, plant invasions, herbivore effects, and extreme weather events. Resilience degraded; soil stability and hydrologic functions altered. Wildlife habitat quality reduced. System is likely restorable with rest from certain stressors and/or active restoration.
H. Highly Degraded	Characterized by depauperate vegetation community with increasing invasive species. Soil moisture severely reduced such that coniferous trees no longer favored. Overstory structure disrupted by interactive effects of insect damage, wildfire, motor vehicle use, invasives, and climate change. Wildlife habitat altered to the degree that assemblages change, with potential cascading effects. Some species extirpated. Highly degraded systems may not be restorable to reference condition due to ecological or financial limitations and novel, extramural communities may develop. Managers may need to consider targeting 'designer ecosystems' (for example, Pimm, 1996).

State-and-transition models are best applied to specific land units (for example, specific ecological sites) because of the importance of site-specific factors such as local climatic conditions, soil-geomorphic properties, and landscape configuration for determining ecosystem responses to management actions and other drivers of change. Our general model does not account for these site-specific factors or the broad diversity found in Great Basin coniferous forests. They will require modification for application to specific forest types and adjustments as our understanding of forest processes improve.
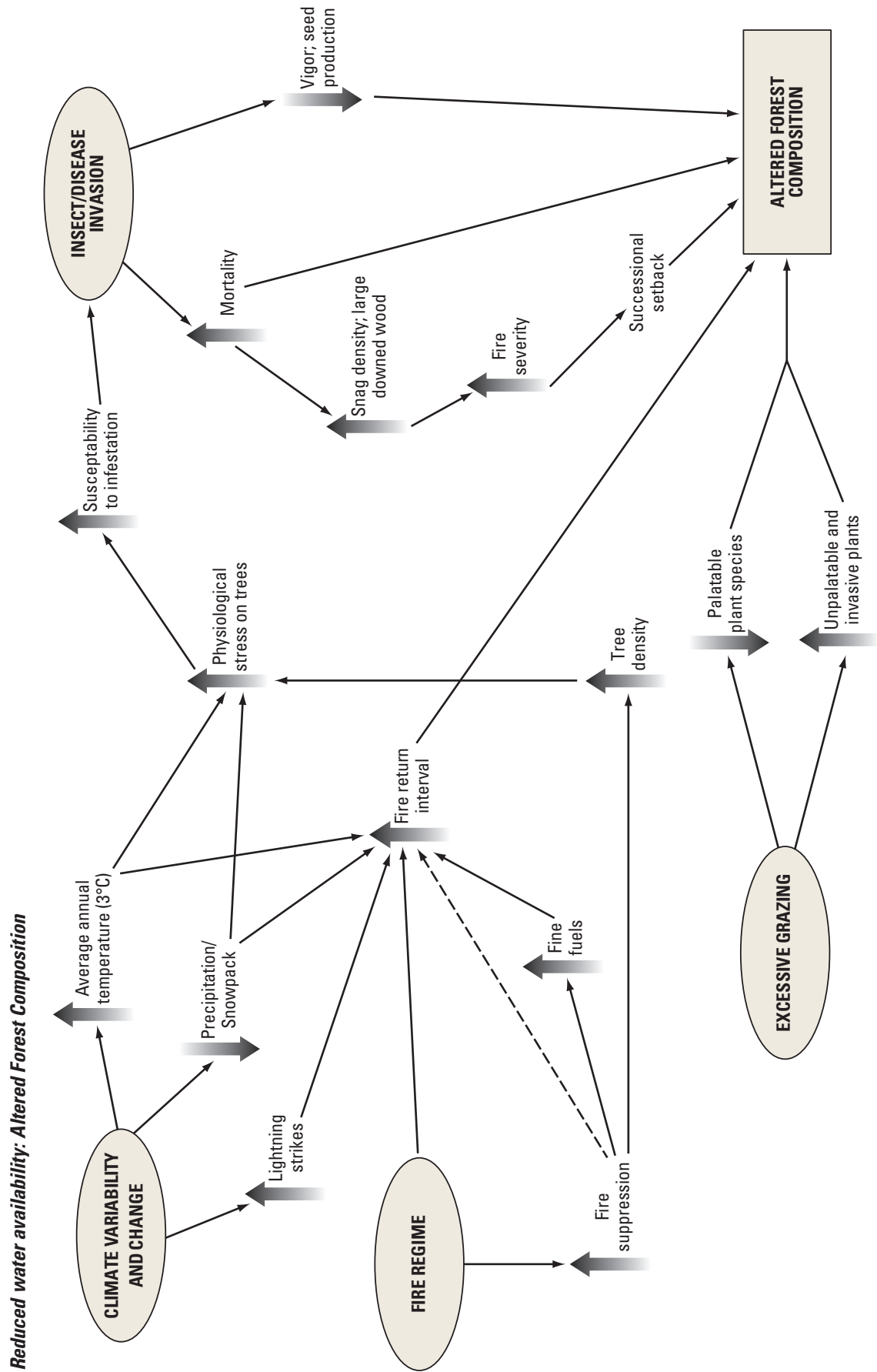
Stressor Models

Ecosystem drivers become system stressors when their effects move the system outside the range of natural variability that we characterize as the reference state. Hypothetical processes by which drivers/stressors singly or interactively cause persistent changes in the structure and functioning of coniferous ecosystems are depicted in figures 3.13–3.15. These mechanistic models illustrate potential landscape changes that alter conifer forest systems and are of concern with respect to management objectives. These Stressor Models were developed based on information found in Shafer and

others (2001), Diffenbaugh and others (2003), Kupfer and others (2005), Vankat (2005), Rehfeldt and others (2006) and Millar and others (2007). Arrows and boxes in these models are potential monitoring targets. We hypothesize two possible outcomes of driver-stressor interactions that primarily are driven by water availability, the most limiting abiotic factor in these systems except near upper timberline. In one scenario, reduced water availability leads to decreasing forest patch size and potential extirpation of the entire stand (fig. 3.13). A second possible outcome is significant alteration of tree species composition, which may threaten individual species of plants and animals. This outcome could hypothetically result from a decrease (fig. 3.14) or increase (fig. 3.15) in water availability. Climate models generally agree that temperatures will increase, which will effectively reduce soil moisture. As a result, reduced water availability may represent the model needing the most study. Additional trajectories are likely and will be the subject of subsequent quantitative models.

Anthropogenic drivers include directional global climate change, the feedback loop generated by the combination of exotic plant invasions and fires, selective grazing and trampling by livestock, and motor vehicle use (primarily off highway vehicles). Natural drivers, which also may become stressors when compounded by other natural or anthropogenic drivers, include climate variability, lightning-caused wildfire, and insect outbreaks.

*Reduced water availability: Conifer Forest Fragmentation and Loss*
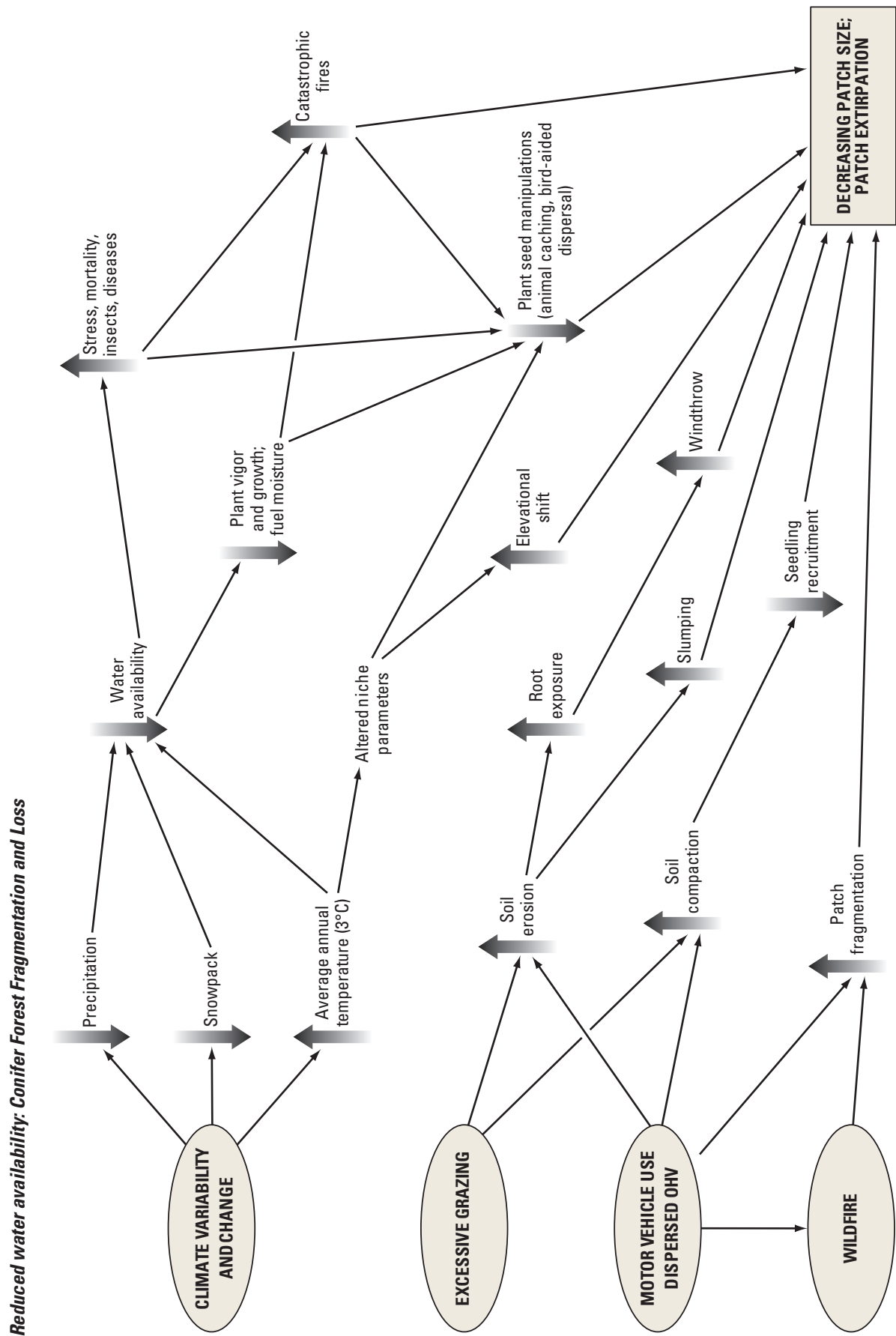
Figure 3.13. Stressor Model illustrating processes by which multiple drivers (ovals) can lead to decreased coniferous forest patch size or complete replacement of a forest patch in the Great Basin. Decreasing patch size or patch extirpation primarily would be driven by reduced precipitation and soil moisture.

Reduced water availability: Altered Forest Composition

Figure 3.14.   Stressor Model illustrating processes by which multiple drivers (ovals) can lead to altered coniferous forest stand composition in the Great Basin. In this case, 'forest composition' includes all taxa (plants, animals, fungi, and microbes). Altered stand composition may result in significant changes in functional groups and consequent changes in nutrient storage and cycling, soil moisture characteristics, biodiversity, and ecosystem services.

Increased water availability: Conifer Forests Increase
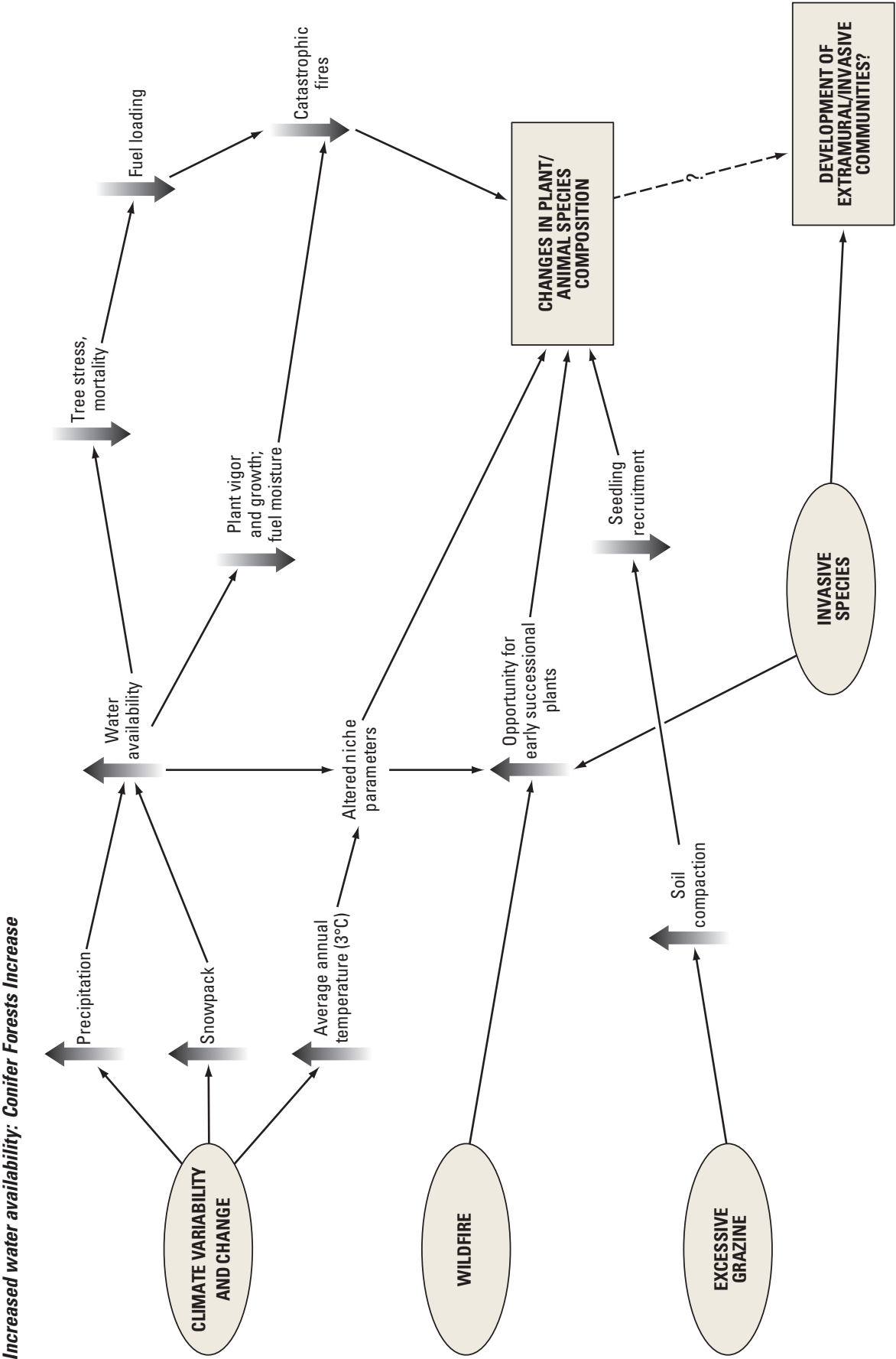
Figure 3.15. Stressor Model illustrating processes by which multiple drivers (ovals) can lead to altered species composition in Great Basin coniferous forests in the face of a climate-change induced increase in precipitation. Altered species composition may result in significant changes in functional groups and consequent changes in nutrient storage and cycling, soil moisture characteristics, biodiversity, and ecosystem services.

The landscape altering fire-invasive annual grass cycle has been thoroughly documented for low-elevation shrubland systems in the western U.S. (Mack, 1981) and current research is exploring the effects of exotic annual grass invasions in conifer forests (M. Brooks, U.S. Geological Survey, oral commun., 2009). Because impacted and at-risk shrublands abut conifer forest throughout the Great Basin, forest types may be threatened even if annual grass invasions are not altering fire return intervals within the forest cover types (for example, Swetnam and Betancourt, 1998). Fires ignited in shrubland may spread upslope and into conifer forest. However, fires driven by fine-fuel annual grasses tend to be lower in severity and, ignoring potential interactions, are likely to proliferate as ground fires in the forest. Although this may present significant alterations to understory plant communities and animals associated with them, forest cover is more devastatingly impacted by high-severity fires, especially if the fire extends to tree crowns. Fuel moisture in Great Basin conifer forests tends to be very low throughout most of the fire season, rendering a higher susceptibility to stand-altering fires. Records of forest patches being totally removed by catastrophic fire can be found, although total stand removal appears to be historically quite rare. Future scenarios that couple climate change and insect outbreaks with exotic plant invasions and fire indicate that conifer forest—especially smaller isolated stands—may be increasing in susceptibility.

Grazing effects, although not well documented in many coniferous forest types of the Great Basin, generally include alteration of ecosystem processes by decreasing the cover of herbaceous plants and litter, disturbing and compacting soils, decreasing water infiltration rates, and increasing soil erosion (Belsky and Blumenthal, 1997; Beever and Pyke, 2004). Long-term browsing of aspen saplings by wild and domestic ungulates probably accelerates the process of conifer expansion and leads to their eventual dominance over aspen communities (Miller and others, 2001). We hypothesize that grazing will continue to alter forage plant species composition and dominance and affect natural soil functions and movements. We hypothesize that grazing alone would have negligible effects on conifer forest integrity but when interacting with other drivers, these effects contribute to system alteration.

The effects of increased motor vehicle use in Great Basin forests have not been addressed in the ecological literature. However, accounts from other areas indicate that motor vehicle use can lead to increases in soil compaction and erosion (Helvey and Kochenderfer, 1990), opportunities for invasive species (Tyser and Worley, 1992; Gelbard and Belknap, 2003), high incidence of human-caused fire, and a reduction in habitat quality due to increasing fragmentation (Trombulak and Frissell, 2000).

The influence of human-induced climate change on Great Basin forests is more difficult to forecast. Numerous efforts have attempted to forecast potential climate-change induced shifts of western plant communities (Thompson and others, 1998; National Assessment Synthesis Team, 2000; Shafer and others, 2001; Diffenbaugh and others, 2003; Rehfeldt and others, 2006). Global and regional climate models generally agree that air temperatures will increase 3–5 °C over the next century primarily due to a two-fold increase in atmospheric CO_2 (Intergovernmental Panel on Climate Change Working Group I, 2001). Some models predict an increase in moisture (National Assessment Synthesis Team, 2000) whereas others forecast decreased precipitation (Giorgi and others, 1998a; Thompson and others, 1998) or relatively constant precipitation (Diffenbaugh and others, 2003) in some or all seasons over the next century. Increased precipitation, especially that falling in winter and remaining as snowpack, likely would promote an increase in forest cover at the expense of shrub and woodland habitats (National Assessment Synthesis Team, 2000). If alternate models are correct and precipitation decreases couples with increased temperatures, forests are likely to migrate uphill, replace alpine habitat, and become reduced in size. We elected to conceptualize both possibilities (figs. 3.13–3.15). Long-term climate change also may increase storm intensity (Groisman and others, 2004) and increase climate variability overall (for example, Meehl and Tebaldi, 2004), which likely would increase lightning strikes and tree windthrow, potentially increasing fragmentation within forest patches.

Summary Points

Coniferous forest landcover is found on many of the high-elevation mountain ranges of the interior Great Basin and on the mountains forming the west, north, and east boundaries. Forests are usually positioned high on the slope between lower-elevation shrubland or pinyon-juniper woodland and upper elevational alpine tundra. Coniferous forests contribute a distinct flora and fauna to the region's biodiversity, perform important hydrological functions, sequester and store carbon, and provide a variety of other ecosystem services (air quality, recreation) and goods (fuel wood, forage), many of which are largely unquantified.

Our understanding of the function of Great Basin mixed conifer forests remains incomplete. Some common assumptions about forest ecosystem processes, including those presented here, need to be tested rigorously. The models of Vankat (2005) for Colorado Plateau montane forests contain additional submodels that may be applied to the Great Basin when sufficient data becomes available. If current climate predictions hold true, shifts in the location,

extent, and composition of forests likely will occur. However, the magnitude and direction of change remains uncertain because climate models depicting local-scale effects, particularly models forecasting the amount and timing of precipitation, forecast a broad spectrum of potentials. Therefore, one primary need is improved weather monitoring to provide baseline data, understand the interactive effects of microclimate, topography, and soil moisture on species persistence, and validate downscaled global climate models. We also need data for predicting how fire severity and frequency, insect outbreaks, and plant and animal distributions will interact with future climates to influence forest-patch distribution and associated fauna. For example, although recent biogeographical analyses indicate that small mammals may use lowland riparian corridors as dispersal routes (for example, Lawlor, 1998), it is unclear whether these avenues will remain available under some climate change scenarios. Understanding the dispersal ability of a whole suite of plants and animal species will aid in predicting future persistence and composition of forest patches in the region.

Forest patches in the Great Basin are highly variable both within a mountain range and among similar forest-types on adjacent ranges. We need to improve our understanding of spatial variability to better elucidate the potential for dispersal and recolonization of depauperate patches and recovery of disturbed sites. What spatial factors facilitate or inhibit movement of individuals, seeds, and genes? Which plant and animal populations are truly isolated and which function as part of metapopulations? Rigorous, quantitative, spatially explicit models are needed to begin making testable predictions based on our qualitative conceptual models.

We also need better understanding of specific plant and animal habitat relationships in order to understand potential threats to species persistence and to prioritize management activities. Very few forest-associated species currently are understood well enough to integrate into our stressor models and generate species-response hypotheses. Information that is available needs to be cataloged and evaluated before initiation of specific modeling exercises that begin identifying vital monitoring indicators.

Limited empirical data (Shaw and others, 2005; Rehfeldt and others, 2006) support our hypothesized threats to coniferous forest persistence, vigor, and integrity. Researchers, modelers, and land managers should coordinate their efforts to monitor, understand, and respond to these trends.

Alpine Tundra Models

By D.M. Miller

Distribution and Management Significance

Alpine tundra occurs in only 0.3 percent of the Great Basin landscape. Specifically, it occupies patches on mountain tops at elevations ranging from 10,000 to 13,000 ft and above sagebrush or tree communities. Alpine tundra is present in the Great Basin's highest peaks including the Snake (home of Great Basin National Park), White, Ruby, East Humboldt, Jarbidge, Sweetwater, Toiyabe, and Toquima Ranges and Steens Mountain. The alpine zone is subject to harsh climatic extremes that limit plants and animals to those specially adapted to narrow tolerances. As a result, the alpine is a fragile zone that is easily disrupted and also difficult to manage because of its remoteness. It includes transitional upper treeline species of concern such as the bristlecone pine (the State tree of Nevada) and the American pika (*Ochotona princeps*), a mammal threatened with extirpation.

Ecosystem Components

The alpine tundra environment generally is characterized by thin, weakly developed rocky soils and prostrate vegetative growth forms (Patten, 2005). The short, cold-restricted growing season, intense radiation, wide daily and annual temperature variations, extreme winds, thin air, and long-lasting snow create a short and harsh growing season that greatly limits the flora and fauna (Scott and Billings, 1964). Short-stemmed perennial herbs, lichens, and mosses are common, as are prostrate forms of woody shrubs (Pase, 1994). At the transitional zone between timberline and alpine tundra, krummholz tree growth forms are common. Bristlecone pine and limber pine are typical species in this transitional zone in the southern Great Basin. Although this transitional zone supports larger woody vegetation, we treat it in our alpine models because of the predominant influence of harsh climatic and geomorphic processes.

The floras of the Great Basin alpine tundra total about 600 species, reflecting species in common with alpine zones of the Sierra to the west and the Rocky Mountains to the east. In fact, this diversity rivals that of the alpine zones found in these larger and more continuous mountain masses. Ground-dwelling animals that commonly inhabit the alpine tundra include yellow-bellied marmot (*Marmota flaviventris*), mountain pocket gopher (*Thomomys monticola*), alpine chipmunk (*Tamias alpinus*), Palmer's chipmunk (*Tamias*

palmeri), western heather vole (*Phenacomys intermedius*), Inyo shrew (*Sorex tenellus*), long-legged myotis (*Myotis volans*), and the pika. Common nesting birds are the white-crowned sparrow (*Zonotrichia leucophrys*), black rosy-finch (*Leucosticte atrata*), American pipit (*Anthus rubescens*), and horned lark (*Eremophila alpestris*).

Abiotic factors, especially climate, tend to overwhelm biotic factors in structuring the alpine tundra (Cannone and others, 2007). The plant and animal communities of the alpine tundra are subject to natural disturbances from geologic processes, making these environments potentially very sensitive to climate changes. Current response to the last 50 years of increasing temperatures includes uphill shifts of many species distributions (Kullman, 2002; Beever and others, 2005) and associated changes in plant community composition. The delicate balance between persistence and extirpation in these extreme conditions could be altered with additional disruptions from climate change.

Drivers of Ecosystem Change

Natural Drivers

Natural drivers in the alpine tundra primarily are climatic and geologic processes (fig. 3.16), which combine with limitations of plant and animal physiological processes to limit growth and diversity of the biota. Climatic influences chiefly are extreme cold, short growing season, fierce, abrasive winds carrying ice and snow particles, and large temperature variations on all times scales from daily to annual. High-intensity solar radiation, particularly ultraviolet (UV) radiation, forces plant adaptations such as epidermal reflection. Lower partial pressure of CO_2 reduces photosynthetic rates and requires adaptations by alpine tundra plants (Richalet, 2007). Geologic processes include a wide range of effects of freeze-thaw cycles, such as soil disturbance on a daily to annual basis and movement of rocks. Steep slopes may have little plant stabilization, resulting in repeated movement of talus and scree. Geologic effects in a few places may include glacial activity (for example, possible rock glaciers in Great Basin National Park).

Anthropogenic Drivers

Anthropogenic drivers include climate change, direct trampling and contamination by humans and livestock, wet and dry deposition of air pollution, introduced fire, road effects, and plant harvesting (fig. 3.17). Climate change, the single most pervasive driver, is causing increased temperatures that may limit environments suitable for many alpine species due to limitations to upward migration. Climate change is likely to increase storm intensity by increasing the variability of climate overall, leading to increased intensity and frequency of wind related impacts. Increased solar radiation from reduced atmospheric ozone will slowly increase incident UV radiation. High CO_2 concentrations may reduce the competitive advantage of photosynthetically efficient plants thereby changing the ratio of C3 to C4 plants, decreasing resistance to exotic plant invaders, and altering species composition. High temperatures probably will reduce the total area of tundra by upward migration of timberline (Kullman, 2002) through differential upward migration of specific tree species (Beever and others, 2005), and through alteration of freeze-thaw activity and intensity. A change from snow to rain precipitation may increase erosion, particularly in plant-diminished patches previously disturbed by trampling, or by late-summer drought caused by reduced snowmelt. Cannone and others (2007) inferred that soil instability and disturbance creates migration barriers inhibiting upward movement of plants, altering the plant community toward disturbance-adapted species. As a result, it may be particularly productive to monitor the plant and bare-ground mosaic in those alpine zones most sensitive to climate change effects.

Reduced snow cover from shorter winters also may affect plant species composition, in particular the plant species that occupy snowbank margins such as Eschscholtz's buttercup (*Ranunculus eschscholtzii*; Charlet, 1991). Human trampling and harvesting of plants disturbs soil crusts and surface horizons as well as plant mats, increasing wind and water erosion. Deposition of anthropogenic nitrogen may result in fast transmission downslope to streams without any bio-filtering due to the high cover of rock and snow (Seastedt and others, 2004; Ashton and others, 2008). Impacts from nitrogen may aggregate at timberline, aggravating climate change effects where the bristlecone pine focal species is common.

American pikas have high energetic requirements and a disinclination for long-distance (>300 m) movements or dispersal making them especially sensitive to high temperatures (MacArthur and Wang, 1974; Smith, 1974; Peacock, 1997; Morrison and others, 2008). They are still widely distributed, and are locally common where they occur. Collectively, these traits make them valuable early-warning indicators of change in Great Basin alpine ecosystems. Numerous extirpations of historically recorded pika populations have occurred recently in the Great Basin (Beever and others 2003), and the rates of population loss and upslope migration of pika distributions have increased markedly in the last decade (Beever and others, unpub. data, 2008). Because pikas harvest, store, and process herbaceous vegetation and are important to seed dispersal and banking, their extirpation may significantly impact tundra plant communities. Pikas also redistribute nitrogen and other minerals and act as prey for alpine carnivores, and thus may be considered keystone species.
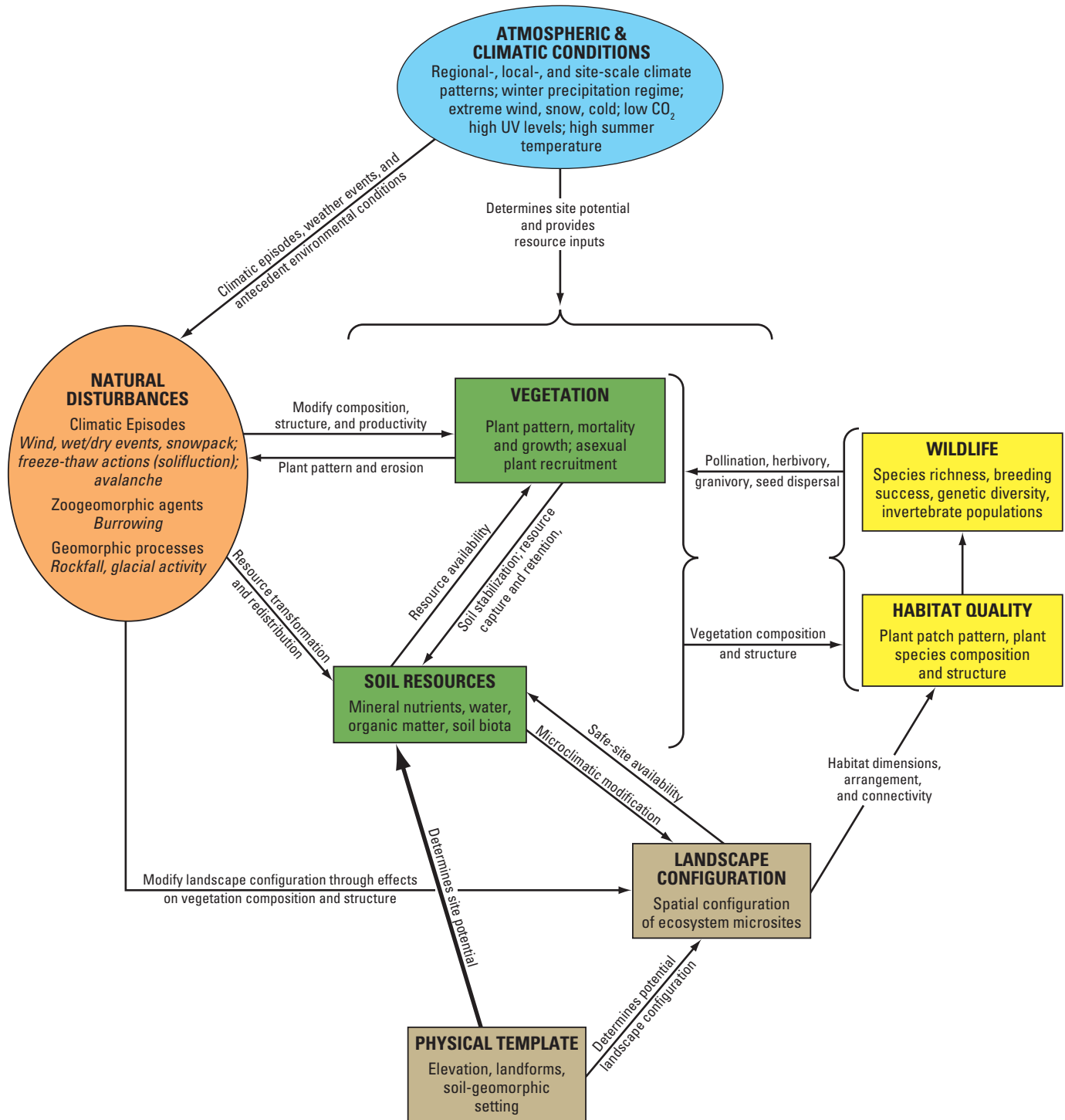
Figure 3.16. Control model showing major components, drivers, and processes in the alpine tundra system. Ovals represent drivers and rectangles represent major functional components of the ecosystem. Note that, unlike other dry systems, the physical template is shown as a participating component for the timescales of interest because geomorphic processes can rapidly change the template in the alpine tundra. Plant pattern, species composition, and mortality rates might all be useful attributes to monitor, as well as mammal populations and ecotone movement such as upward movement of timberline.
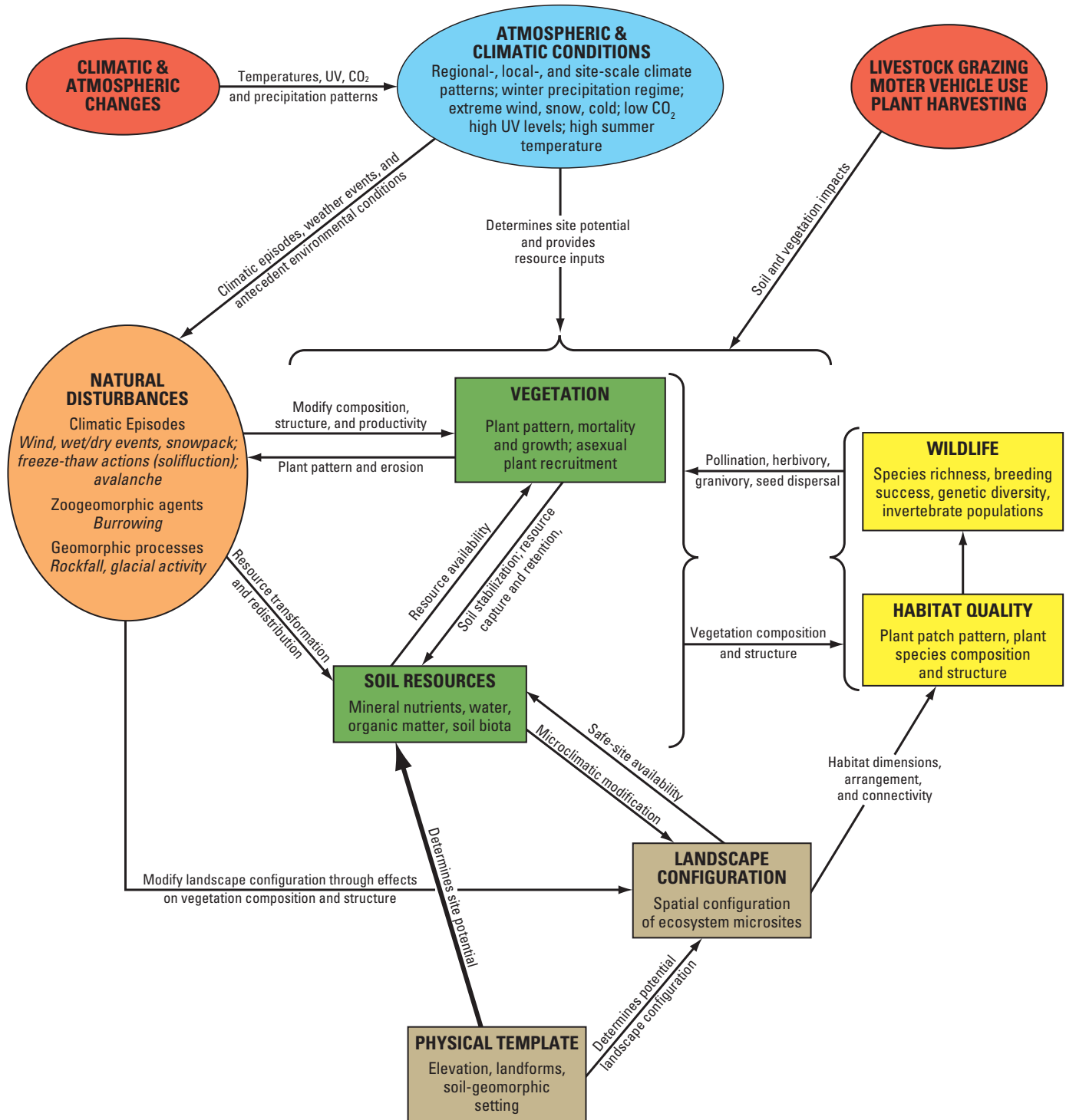
Figure 3.17.   Major anthropogenic stressors for the alpine tundra system (ovals).

Ecosystem Dynamics

The control model (fig. 3.16) illustrates several components and processes important to the alpine tundra environment, many of which are common to the previously described dry systems models. Extreme climatic conditions and steep topographic gradients produce large variations from site to site in terms of microclimate, soils, and hydrology. Physical characteristics such as rocky talus slopes are crucial shelter sites for animals. As a result, the alpine tundra consists of small patches of different soil types, plant communities, and habitat. This fine scale patch interaction links several components within the control model: landscape configuration, soil configuration, and microsite potential are components that vary on the scale of meters in many cases and differs from the presumably coarser scale variation in low-elevation dryland systems.

Geomorphic processes change the landscape of alpine tundra more rapidly than communities in low elevations. Geomorphic processes include freeze-thaw of rock and soil, as well as rockfall to create talus, creep of colluvium, landsliding, creeping of solifluction lobes, and even glacial activity. Snowpack is a critical feature of the alpine zone and illustrates the connection between biotic and abiotic features. The combination of snowfall and wind creates patterns of snow accumulation on lee sides of ridge crests (fig. 3.18). Snowbanks that persist into summer gradually melt back and successively foster plant communities that vary in accordance with—and are dependent on—the timing of snow retreat. Changes in timing and amount of snowfall, temperature and associated timing of snowmelt, and winds associated with snow deposition can all alter the snowbank processes.

Over long periods of time, nivation hollows develop linear depressions formed below and parallel to ridgelines. Nivation hollows form by sub-snowpack processes of sediment transport by meltwater as snowbanks recede. The hollows enhance future snow capture and thus feed back into the snowpack-driven processes. Long-term effects include more mesic or hydric soils in downslope positions in meltwater meadows. Relatively dry rocky crests, snowdrifts, and areas below the drifts have characteristic plant communities and soils governed by water availability and timing of snowmelt and subsequent drying. The snowfield and associated plant community patterns may shift rapidly with climate change as historical geomorphic-climate combinations spatially decouple.

Zoogeomorphic agents including grazing, trampling, and burrowing are prominent as well (Hall and Lamont, 2003); these are dependent on soil depth and soil moisture, which vary by climate factors, topography, and plant cover, and therefore are linked to patch-scale processes described above (fig. 3.19).

One monitoring objective in Great Basin alpine environs is to identify reliable monitoring cues. Vegetation composition and cover, including spatial patterns, are fundamental indicators of environmental stress (Kammer and Mohl, 2002). Along with climate factors (including snowcover and atmospheric pollutant deposition) and visitor use, monitoring plant communities should signal alterations to the tundra environment. Identifying reliably responding plants for monitoring should be a primary goal of future research. Animals well adapted to alpine conditions may be strongly affected by altered conditions mediated by climate change. Mammalian and invertebrate responses to changing
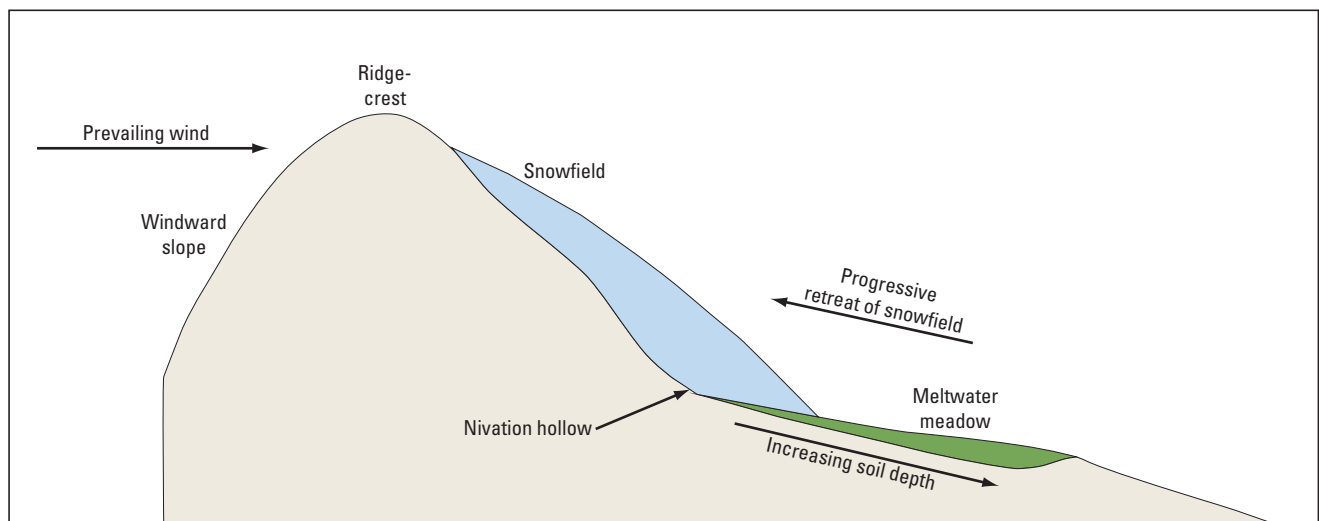
Figure 3.18. Simplified illustration of topographic and climatic effects in the alpine tundra zone. Plant communities vary with position from the meltwater meadow upward, because they are tuned to the timing of snowfield retreat and the long-term accumulation of soil, which is unevenly distributed.
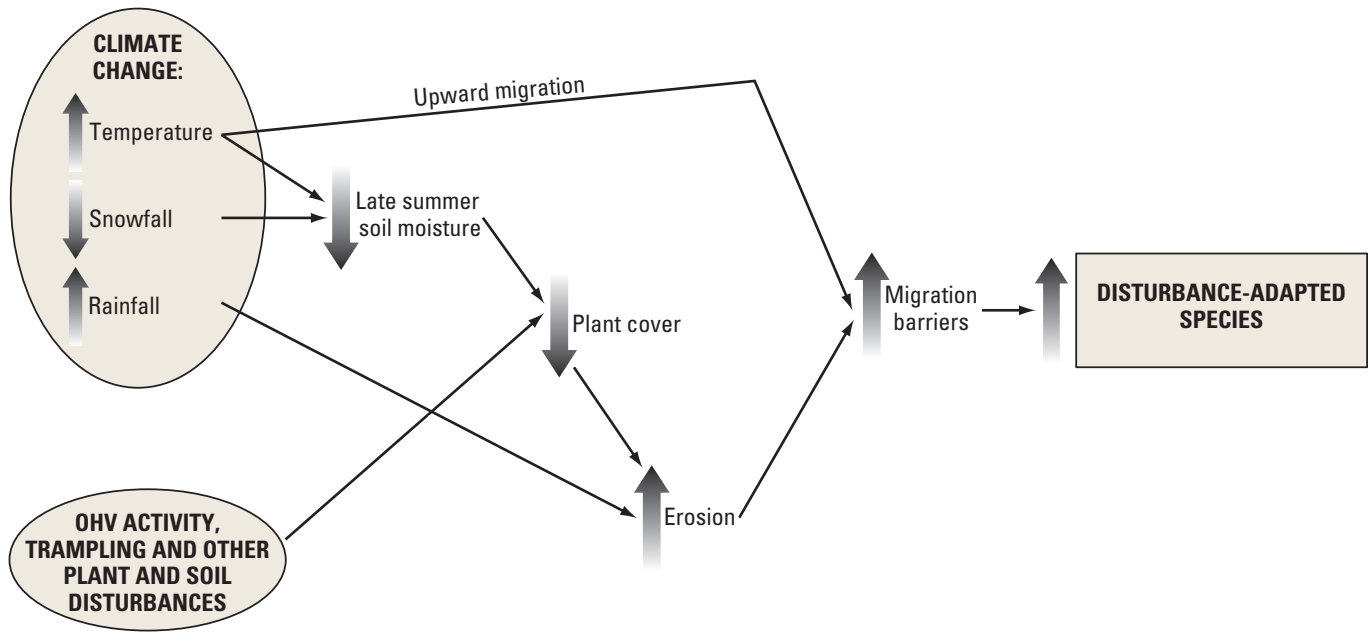
Figure 3.19.   Stressor model showing climatic and other effects in the alpine-tundra zone. Plant communities are impacted by changing climate conditions directly and by inhibited upward migration caused by increased eroded and disturbed ground. Both contribute to an increase in disturbance-adapted species.

temperature regimes such as acute or chronic metabolic stress from excessive heat or cold, or increased mortality due to alterations of food supply, could be tracked as changes in population dynamics making them excellent monitoring targets. Some animals also play important functional roles as described previously for the pika.

Loss of the tundra ecosystem due to climate change most likely will result in a large loss of gamma diversity with loss of populations and genotypes (McDonald and Brown, 1992; Hunter, 2002). The high mountains of the Great Basin will not recover quickly from loss of tundra because they lack connectivity with other tundra environments. Evidence from mammals in paleoecologic and recent time indicates that species differ in their vagility and their degree of obligate relationship to alpine habitats (Grayson and Livingston, 1993; Lawlor, 1998; Grayson and Madsen, 2000). As a result, changes in alpine habitat may have ripple effects in broader mammal communities.

Summary Points

It is probable that warming temperatures and other climatic factors associated with climate change will impact tundra environments by shifting plant and animal community distributions, as well as by altering geomorphic processes, but little research is available to allow projections to be made. It is an important topic for study, because transitions to new plant community states may make recovery of existing habitat difficult (Laycock, 1991; Stringham and others, 2001). Knowledge of the processes that link components of the alpine ecosystem generally are poorly understood in comparison with some low-elevation Great Basin biomes. As a result, nearly all aspects of the alpine ecosystems in the Great Basin are in need of further study. Paleoecological studies may shed light on which plant and animal populations survived past climate changes, and inform hypotheses for survival and extirpation in the future when characteristics of past climate is well known.