

VEGETATION DYNAMICS UNDER FIRE EXCLUSION AND LOGGING IN A ROCKY MOUNTAIN WATERSHED, 1856–1996

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Abstract. How have changes in land management practices affected vegetation patterns in the greater Yellowstone ecosystem? This question led us to develop a deterministic, successional, vegetation model to “turn back the clock” on a study area and assess how patterns in vegetation cover type and structure have changed through different periods of management. Our modeling spanned the closing decades of use by Native Americans, subsequent Euro-American settlement, and associated indirect methods of fire suppression, and more recent practices of fire exclusion and timber harvest. Model results were striking, indicating that the primary forest dynamic in the study area is not fragmentation of conifer forest by logging, but the transition from a fire-driven mosaic of grassland, shrubland, broadleaf forest, and mixed forest communities to a conifer-dominated landscape. Projections for conifer-dominated stands showed an increase in areal coverage from 15% of the study area in the mid-1800s to ~50% by the mid-1990s. During the same period, projections for aspen-dominated stands showed a decline in coverage from 37% to 8%. Substantial acreage previously occupied by a variety of age classes has given way to extensive tracts of mature forest. Only 4% of the study area is currently covered by young stands, all of which are coniferous. While logging has replaced wildfire as a mechanism for cycling younger stands into the landscape, the locations, species constituents, patch sizes, and ecosystem dynamics associated with logging do not mimic those associated with fire. It is also apparent that the nature of these differences varies among biophysical settings, and that land managers might consider a biophysical class strategy for tailoring management goals and restoration efforts.

Key words: disturbance; fire exclusion; GIS modeling; land management; Rocky Mountain (USA) vegetation; spatiotemporal analysis; vegetation modeling; vegetation reconstruction; Yellowstone ecosystem.

INTRODUCTION

Many land managers are interested in maintaining ecological processes and native species in the landscape. One way to do this is through designs to minimize habitat fragmentation resulting from logging and other land uses. In the Rocky Mountains, as elsewhere, clearcut logging in recent decades has reduced the area and patch size of natural forests and raised concern for the viability and conservation of native species (Knight et al. 2000). A longer term view, however, suggests that human alteration of natural disturbance regimes may have a greater influence on forest patterns than those imposed by logging, resulting in forest patterns today that are much more homogeneous and extensive than those prior to Euro-American settlement. Knowledge of these longer-term dynamics under the influence of natural disturbance and human activities provides a

context for managing modern landscapes to achieve ecological objectives (Landres et al. 1999). In this paper, we reconstruct forest patterns in a Rocky Mountain landscape from the initiation of Euro-American settlement (mid-1800s) through the current period of fire exclusion and logging.

Fire was a dominant disturbance in the Rocky Mountains throughout the Holocene epoch. Fire return intervals in Rocky Mountain conifer forests varied from <10 yr to several hundred years, depending upon forest type and landscape setting (Romme 1982, Arno and Gruell 1986, Dieterich and Hibbert 1990, Harrington and Sackett 1992, Barrett 1994, Veblen et al. 2000, Donnegan et al. 2001). These fire regimes strongly influenced vegetation patterns. Frequent fires created and maintained grasslands, shrublands, and conifer forest savannas (Barrett 1994). Forests in landscape settings with infrequent, severe fires underwent long-term succession, often from shade-intolerant communities following fire, to late-succession old-growth conifer communities (Bradley et al. 1992). Many organisms have adapted to localized fire regimes and are dependent upon either early or late seral habitats (Hutto 1995).

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The occurrence of fire in the Rocky Mountains changed dramatically during the period of Euro-American settlement (Gruell 1983, Swetnam 1990). Increased grazing by domestic livestock reduced fuels, which limited fire spread. Since the 1950s, technology has allowed humans to effectively suppress wildfire. These modern human activities have greatly reduced fire frequency throughout much of the Rockies. Many locations that burned every few decades before the mid-1800s have not had a fire since (Littell 2002).

Photo comparisons between the late 1800s and today suggest substantial changes in vegetation structure and composition during this period of fire exclusion (Gruell 1983, Meagher and Huston 1998). Grasslands and shrublands have been invaded by conifers. Open-canopy conifer savannas have succeeded into dense, closed-canopy forests. Broadleaf species, such as aspen (*Populus tremuloides*), have been replaced by conifers, and fire-tolerant conifer species, such as ponderosa pine (*Pinus ponderosa*) and lodgepole pine (*P. contorta*), are giving way to less fire-tolerant species, such as true firs (*Abies* spp.). These changes lead to dramatically less habitat for species dependent upon grasslands, shrublands, aspen stands, and early seral conifer forests (Hansen and Rotella 2000).

Several questions remain about forest patterns during the period of transition from pre-Euro-American settlement to today. How have forest composition and stand structure changed during this time? Does the spatial patterning of community types today differ from that at the beginning of the transition? Which community types were more fragmented under the pre-Euro-American fire regime and which are more fragmented under current human activities? Have rates and directions of change varied by landscape setting, and can pre-Euro-American settlement patterns of vegetation be restored more readily in some topographic, climatic, and soil settings than others?

We attempted to answer these questions by reconstructing vegetation patterns in a study area within the Beaver Creek watershed in the Eastern Centennial Mountains of Idaho for the years 1856–1996. We integrated dendrochronological (Veblen 1992) and chronosequential (Glenn-Lewin and van der Marrel 1992) data to construct successional trajectories for the study area and then used these data to parameterize a spatial simulation model. The model projected stand age and seral stage back in time along the successional trajectories (modified from Bradley et al. 1992). We then analyzed the spatial patterns of vegetation at 10-yr intervals to reconstruct vegetation cover type and structure from 1856–1996 and quantify the associated changes in landscape pattern. We estimated the extent to which vegetation change varied among biophysical landscape groups (reflecting climatic, topographic, and edaphic settings). Finally, we considered how periods in land management history, pre-Euro-American settlement (mid-1800s–1890), early post-Euro-American

settlement (1890–1950), and recent post-Euro-American settlement (1950–1996), may have influenced vegetation patterns.

METHODS

Study area

The Beaver Creek study area lies on the south slope of the east–west trending Eastern Centennial Mountain Range in Idaho (Fig. 1) within the Targhee National Forest. This area was chosen because an intensive study of patterns of forest stands had been completed for the adjacent Camas Creek watershed, and there was interest in extending that research both geographically and ecologically. Additionally, Targhee National Forest ecologists were aware of a number of communities at risk, including seral aspen, and were motivated to conduct further successional research in the area.

Previously, forest ecologists had developed a classification scheme for habitat and community types of eastern Idaho and western Wyoming that focused on fire frequency, response of dominant tree species to fire, and postfire successional trajectories (Bradley et al. 1992). The scheme incorporated environmental characteristics such as topography, soil, climate, and vegetation to derive “fire groups.” These groups are helpful for understanding forest dynamics relative to biophysical settings. Four of the groups are well represented within the 16 500-ha study area (see Fig. 1). The driest sites at lower elevations (1800–2300 m) are dominated by mountain big sage (*Artemisia tridentata* ssp. *vaseyana* var. *pauciflora*) and Idaho fescue (*Festuca idahoensis*) communities, and sometimes include very open stands of conifer. These “sagebrush/grassland” sites are on relatively gradual terrain at the base of foothills and are thought to have burned with variable intensity every 10–40 yr during pre-Euro-American times (i.e., before the mid-1800s; Houston 1973, Bridger-Teton National Forest 1997, Caribou National Forest 1997).

Relatively moist habitats (on cooler or moister exposures) at elevations between 1900 and 2400 m in the study area are dominated by Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and aspen (*Populus tremuloides*). In the absence of fire, Douglas-fir is the successional climax; hence, we refer to this group as “moist Douglas-fir forest.” Historical fire regimes varied widely, affected by topography, weather, stand structure, and fuel loading. Fire frequency was highly variable, with return intervals ranging from 15 to >100 yr. Fire can be stand thinning or stand replacing, affecting the potential dominance by different species.

A third group, “mid- and lower-slope forest,” is dominated by lodgepole pine, but subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and Douglas-fir are also important components of these forests. This group is typified by sites that are warmer

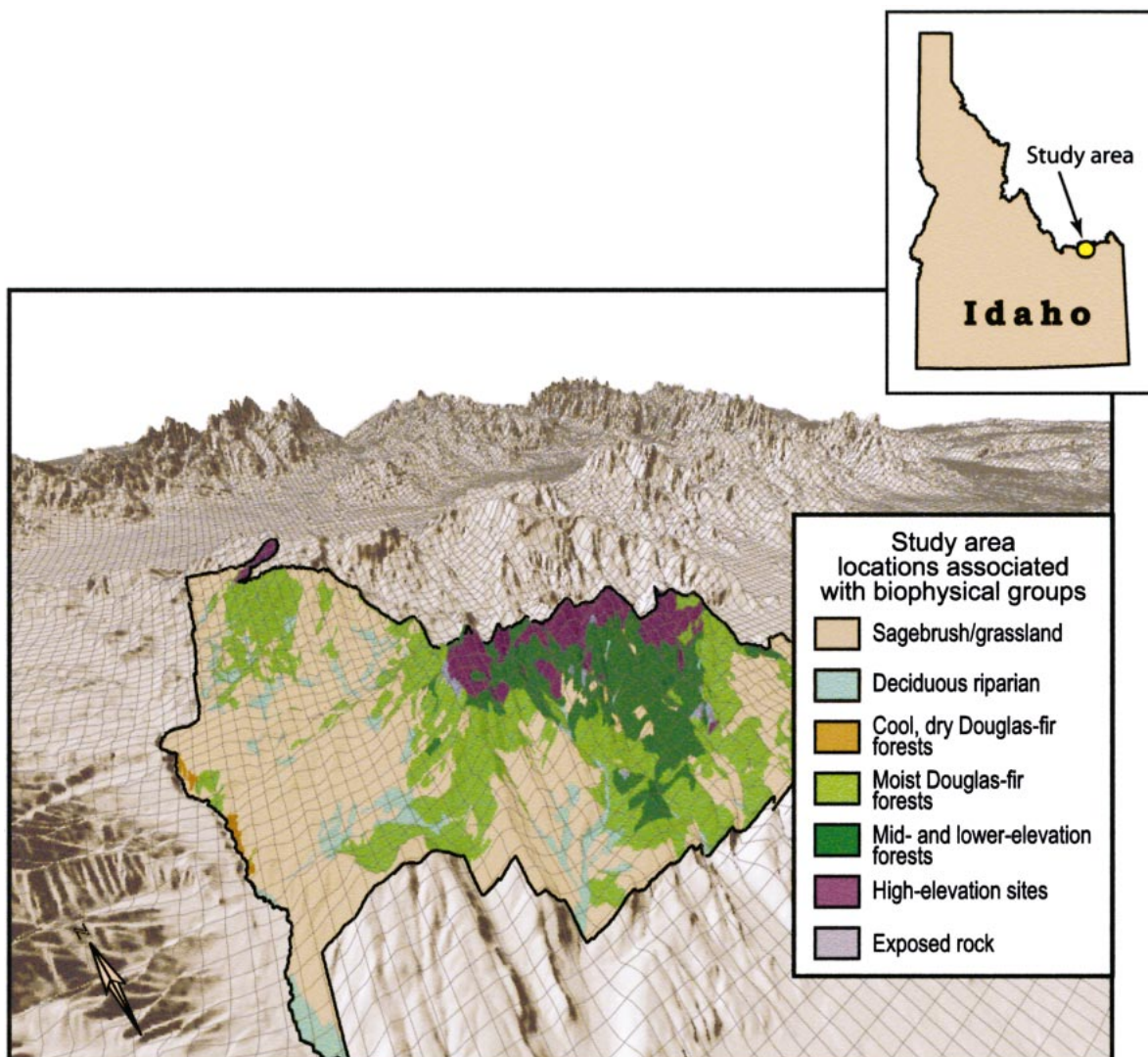


FIG. 1. Location of the East Beaver Creek study area in Idaho and the distribution of biophysical classes over a three-dimensional representation of the terrain. The lattice spacing is 400 m, and there is a fivefold vertical exaggeration of the terrain.

and/or drier than those of the previous group. Stands occur between elevations of 2050 to 2500 m in the study area and tend to have dense understory trees and a mix of dead and live overstory trees, creating a strong potential for crown fires during dry weather. Fire return interval has historically varied from tens to hundreds of years.

The "high elevation" group in the study area ranges from 2300 to >2600 m. The group is characterized by subalpine fir, Engelmann spruce, lodgepole pine, and whitebark pine (*Pinus albicaulis*). These sites have moderate to steep terrain, cold, moist, or wet site conditions, a short growing season, and, consequently, low vegetation productivity. Fire frequency is low, with return intervals of several hundred years, and fires tend

to be restricted to individual trees or small groups of trees.

No large wildfires are known to have occurred in the Beaver Creek study area for well over 100 yr. Notes from land line surveys from the 1880s mention evidence of old fires (from around the 1850s), and the few photos existing for that period show old snags. A high degree of uniformity in the current stand age indicates that fires halted abruptly somewhere during the mid-1800s, a time coincident with major changes in land use. Prior to that time, an abundance of water and a large source of obsidian in the area attracted very concentrated use by Native Americans (A. Abusaidi and R. Thompson, *personal communication*; Butler 1978; also many sites are referenced in the Targhee National

TABLE 1. Successional trajectories defined for the study area.

Order	Stage
1	<i>Abies lasiocarpa/Calamagrostis rubescens</i>
2	<i>Abies lasiocarpa/Calamagrostis rubescens</i> (shelterwood cut origin)
3	<i>Abies lasiocarpa/Spiraea betulifolia</i>
4	<i>Abies lasiocarpa/Spiraea betulifolia</i> (shelterwood cut origin)
5	<i>Artemisia tridentata/Festuca idahoensis</i>
6	<i>Populus/sagebrush/grass</i>
7	<i>Populus tremuloides/Artemisia tridentata</i>
8	<i>Pseudotsuga menziesii/Artemisia tridentata</i>
9	<i>Pseudotsuga menziesii/Artemisia tridentata</i> (shelterwood cut origin)
10, 11	<i>Pseudotsuga menziesii/Calamagrostis rubescens, Calamagrostis rubescens</i> SEDGEWAY† (two trajectories having the same successional stages, but different rates of development due to site characteristics)
12	<i>Pseudotsuga menziesii/Calamagrostis rubescens, Calamagrostis rubescens</i> SEDGEWAY (shelterwood cut origin)
13	<i>Pseudotsuga menziesii/Juniperus communis-Pseudotsuga menziesii/Festuca idahoensis</i>
14	<i>Pseudotsuga menziesii/Spiraea betulifolia/forb/shrub</i>
15	<i>Salix/graminoid</i>

Notes: Unless otherwise noted, trajectories pertain to stands arising from a "natural" origin (i.e., unlogged) or clearcut origin (i.e., where virtually no tree overstory exists). Trajectories noted as having shelterwood cut origins are assumed to have mature overstory trees present through all stages of stand development.

† SEDGEWAY refers to a soils series.

Forest Heritage Resource Survey Reports Archive). Native Americans were driven out of the area between 1850 and 1880 and grazing by livestock was introduced. The removal of fine understory fuels through grazing helped suppress wildfire. Grazing intensity was especially heavy from 1890 to 1935 (e.g., 17 000 cow and 8800 sheep animal unit months, i.e., AUMs; C. Probert, *personal communication*). By the mid-1900s, grazing was decreased to moderate intensity (9100 cow and 4700 sheep AUMs). Today, the area supports 11 400 cow and 1400 sheep AUMs. The earliest documented logging efforts in the study area date back 60 yr, but the level of activity remained minimal for the first 10–20 yr, after which active fire suppression was also introduced. More recently, clearcut and shelterwood logging has occurred, primarily in moist Douglas-fir forest settings. In total, <10% of the study area was logged by 1996.

Model development

We defined 15 successional trajectories for the study area based on climax communities described by Bowerman et al. (1996; Table 1). The trajectories were established using several sources, including successional flowcharts in Bradley et al. (1992), stand exam data from the Targhee National Forest, habitat type descriptions (Steele et al. 1983), aerial photographs, historic vegetation maps, local silvicultural expertise, and timber management history. The stand exam data represented a comprehensive inventory conducted to determine site productivity, presence of insects and disease, and stand volume, density, species composition, tree age, and growth rates. The historic vegetation maps were from the Henry's Lake Forest Reserve map collection archived at Targhee National Forest headquarters. The map archive includes a series of three mapping efforts between 1912 and 1920 for the Beaver

Creek study area. These maps were generated by field sketching vegetation boundaries on topographic maps. Vegetation categories were very general (i.e., rangeland vs. forest, to indicate potential forage areas for cattle), except for stands where aspen or Douglas-fir composed >60% of the forest cover, in which case specific forest types were described. Timber management history was used to develop alternative trajectories to account for successional effects from tree harvest. For example, stands that had been harvested and subsequently reforested by the Forest Service bypassed the initial grass/forb stage of development. Stands that had received shelterwood cuts had different structure than other stands, with both a reforested understory and mature overstory (e.g., Table 1, trajectories 2, 4, 9, and 12).

By integrating these information sources, we were able to estimate time intervals associated with each stage within a successional trajectory. Individual stages were defined in terms of tree size class, stand age, forest cover composition, and time interval required for the stage (Table 2). The trajectories assume an absence of disturbance, except for timber harvest. Since fire is believed to have been absent from the study area during the period modeled, it was not incorporated into our model. Other disturbances, such as grazing, pests, and disease, may have played some role in accelerating or retarding successional rates or in altering successional pathways, but were not addressed in this initial modeling effort. Future model development could incorporate stochastic and probabilistic disturbances to depict alternative projections of past land cover patterns.

We used stand exam records, timber inventory maps, 1:15 840-scale color air photos from 1995, and recent field visits to map the 1996 vegetation cover for the study area, assigning the appropriate successional pathway and stage to each stand. The minimum mapping

TABLE 2. Examples of three successional trajectories used in our model.

Successional trajectory†	Successional stage	Successional age	Tree age	
			AS	DF
5) <i>Artemisia tridentata/Festuca idahoensis</i> ‡	grass/forbs	0–10	NA	NA
	sage/grass/forbs	10+	NA	NA
10) <i>Pseudotsuga menziesii/Calamogrostis rubescens, Calamogrostis rubescens</i> SEDGEWAY	grass/forb, AS/seed/sap	0–5	0–5	
	AS young	6–35	6–35	
	AS mature, DF seed/sap	36–65	36–65	1–30
	AS mature, DF pole	66–95	66+	31–60
	AS mature, DF mature	96–235		61–200
	DF mature/old growth	235+		200+
14) <i>Pseudotsuga menziesii/Spiraea betulifolia</i> /forb/shrub	grass/forb/shrub	0–10	NA	
	DF and LP seed/sap	11–40		1–30
	DF and LP poles	41–70		31–60
	DF and LP mature	71–130		61–120
	DF mature, some LP, DF understory	131–210		131–200
	DF mature/old growth	210+		200+

Notes: A complete list is included in Appendix 1 of Gallant et al. (1998). Note that “successional age” distinguishes the age of the stand since the last disturbance and “tree age” distinguishes the age of the trees in the stand. There is always a lag of years for tree establishment following stand disturbance except in cases where stands have been reforested within the year following timber harvest. Abbreviations: AS, aspen; DF, Douglas-fir; and LP, lodgepole pine; NA, not applicable.

† See Bowerman et al. (1996) for type descriptions.

‡ Numbers correspond with those used in Table 1.

unit (i.e., stand size) was <2 ha, resulting in 735 stands for the study area. In cases where age data were not available, stand age was estimated from air photos or interpolated from ages of adjacent stands. Because of the high degree of stand age uniformity in the area, we felt such estimates were reasonable.

Our rule-based model was applied to the 1996 stand map to “turn back the clock” on vegetation cover. The model looped backwards through time steps, passing along information on successional trajectory and stage, stand age, and timber management history (unlogged vs. clearcut or shelterwood cut, and age and type of stand at time of cut) for each stand (Fig. 2). For every loop of the model, a specified number of years (we used 10) was subtracted from the age of a stand and the successional stage was updated if the existing one was no longer appropriate (for the new stand age). Since nearly all of the successional stages of our trajectories have a duration >10 yr (except for the grass/forb stage of some trajectories), a 10-yr time-step interval is sufficient for representing each possible stage.

As stands are cycled backwards through their respective trajectories, their ages eventually become zero. In the case of logged stands in the study area, information on stand type, age, and trajectory at the time of harvesting was incorporated into our model, allowing the stands to continue being mapped back in time. For example, a logged stand that is 50 yr of age in 1996 can be modeled back for five time intervals on the current trajectory, then reset to the appropriate trajectory for the stand characteristics that existed at the time of logging. When stand age became zero in mixed stands (aspen and conifer), we assumed that similar mixed components occupied the sites prior to that time, so we maintained these map units in mixed forest types for the duration of the model, though we were no longer

able to attribute a stand age to them. Our rationale here was threefold: (1) few sites in this area can be considered “stable” (i.e., nonseral) aspen, (2) all other sites contain species that are seral to conifers, and (3) current seral aspen stands include Douglas-fir trees of several hundred years of age, indicating that both aspen and conifers have long been mixed components of these sites. There was no method for determining the age of sagebrush/grassland, willow, or pure aspen stands for development of the 1996 stand map. Barring the occurrence of major environmental change or disturbance, these stand types have probably occupied the study area for the duration of our modeling period, due to their reproductive strategies. We held these stands constant over time in the model. Were we to modify the model to predict future vegetation cover, then these stands could be altered through processes such as fire, fire exclusion, grazing, and climate change.

We evaluated model output by comparing the predicted vegetation patterns for 1920 with those shown on the historic maps. This was a simple visual assessment. A quantitative assessment was not appropriate, as the spatial and thematic resolutions differed significantly between products. For instance, the historical maps included 195 stands, with a mean mapping unit area of 85 ha, while our model included 735 stands, with a mean mapping unit area of 23 ha. Additionally, no accuracy assessment was available for the historic maps, so the value of a quantitative comparison was unclear. We found that model output for 1920 vegetation cover generally equated well with the vegetation patterns shown on the historical maps. In a couple of cases, the historic maps indicated that our successional trajectories appeared to underestimate how rapidly certain stand types progressed from aspen or grassland/sagebrush to conifer forest. Accordingly, we made ad-

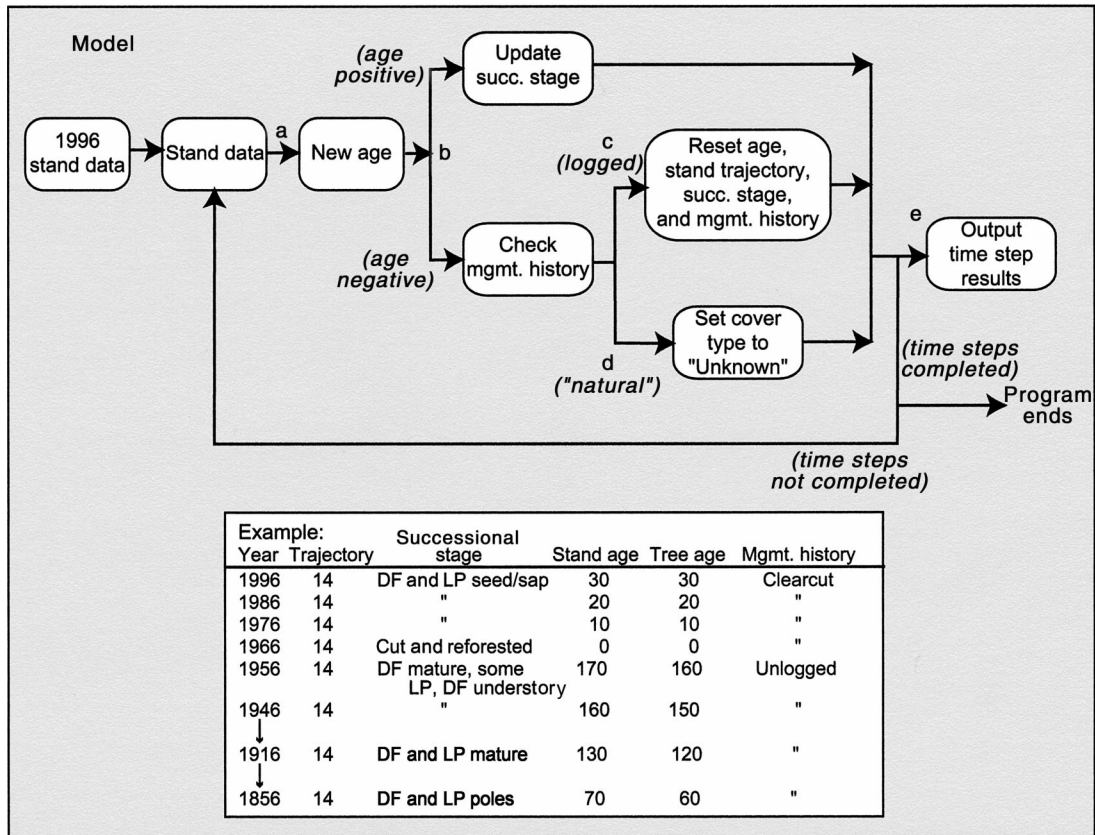


FIG. 2. Flow of information through the model showing where (a) specified number of years are subtracted from each stand's age; (b) stands having new ages >0 will have their successional stages updated (if necessary), and stands having new ages ≤ 0 will be checked for their management histories to determine whether information is available about previous stands; (c) stands that were logged are reset for the age, successional trajectory, and successional stage at the time of cutting; (d) stands for which no additional historic information is available are designated as "unknown cover type" for the remainder of the model time steps; (e) stand information resulting from each time step is output to a file that can be imported by a geographic information system; (f) the program continues looping through the specified number of time steps. The box at the bottom of the figure shows how information for an example stand of trajectory 14 (see Table 2) is updated at each 10-yr time step. Note that in 1956 the stand age and tree age are no longer equivalent. This is because the ("natural") stand was assumed to be unoccupied by trees (grass/forb stage) for the first 10 yr following its time of origin. Abbreviations: DF, Douglas-fir; LP, lodgepole pine.

justments to the length of time associated with these particular successional stages within their associated trajectories.

Output from the model was imported into a geographic information system (ARC/INFO, Environmental Systems Research Institute, Redlands, California, USA) for mapping and interpreting results, and into additional analytic software for quantifying spatial patterns of stands.

Analyses

Quantifying changes in vegetation composition and structure.—The successional trajectories and their stages presented >100 potential stand designations at each time step. For a meaningful (and interpretable) spatial analysis, it was necessary to aggregate the results into themes. We chose two themes with relevance for management in the Targhee National Forest: cover

types and structural characteristics. For "cover types," model output was aggregated into nine classes (Table 3). When a stand's age cycled back to "0," the stand was considered "undefined." In cases of mixed forests, the stand was maintained as a mixed type even after its age cycled back to zero. These "pre-origin" stands were designated as conifer-dominated mixed stands if they were associated with the moist Douglas-fir forest group, and aspen-dominated mixed stands if they were associated with the mid- and lower-slope forest group (however, as aspen is the seral dominant on many of these sites, this assumption may lead to underestimation of aspen; Steele et al. 1983). For "structural types," model output was aggregated into 10 classes: five conifer-dominated classes, three aspen-dominated classes, one class for nonforested stands, and an "undefined" class for when stand age became 0 (Table 3). The conifer-dominated structural classes recognized

TABLE 3. Successional stages output from each model time step were aggregated into the cover classes and structural classes shown below.

Cover type classes	Structural classes [¶]
Conifer forests	Conifer-dominated seedlings/saplings
Very-open conifer forests	Conifer-dominated poles
Scattered clumps of conifers	Conifer-dominated mature trees
Conifer-dominated mixed forests	Conifer-dominated old growth
Aspen-dominated mixed forests	Conifer-dominated retention cut
Aspen forests	Aspen-dominated seedlings/saplings
Willow [†]	Aspen-dominated young trees
Nonforest [‡]	Aspen-dominated mature trees
Undefined [§]	Nonforest [‡]
	Undefined [§]

[†] Willow stands were held constant in our landscape. These stands occur only in riparian wetland sites and likely have persisted for the duration of the modeling period, as abundant moisture is known to have been available when the area was occupied by Native Americans.

[‡] Includes sagebrush/grasslands and nonvegetated cover types (exposed rock).

[§] Assigned when stand age reached 0 and no further information about the stand was known or assumed.

[¶] Definitions: Seedlings, trees < 5 cm in diameter at breast height (dbh); saplings, 5–10 cm dbh; poles, 10–30 cm dbh; mature trees, > 30 cm dbh.

typical stand stages, including seedling/sapling, pole, mature, and old growth. Also included was a structural class for the multicanopied conditions resulting from a shelterwood cut. These stands are characterized by an open canopy overstory of mature trees and a lower, denser, canopy layer of younger trees. Three aspen-dominated structural classes were recognized, including seedling/sapling, young, and mature.

We used the FRAGSTATS (McGarigal and Marks 1995) program to quantify spatial patterns for each time step. Note that while our model tracked “stands” as the minimum mapping unit, FRAGSTATS calculations were based on the patches that resulted from aggregating the stands into cover type or structural classes. We looked at the number, size, and density of patches, and availability of edges for each cover type and structural class. We also looked at the variety of patch types and the degree to which they were intermixed across the study area.

Stratifying by biophysical settings to interpret vegetation change.—The extent of our study area was fairly arbitrary, related to Targhee National Forest boundaries, drainage basin topography, adjacency to previously studied area, and conservation concerns. Thus, we expected the study area to encompass sufficient environmental variability to make it difficult to detect and interpret trends in vegetation patterns. To help account for environmental variability, we stratified the study area by the biophysical settings describe earlier, and interpreted the cover type and structural class patterns within each biophysical group (see Fig. 1).

Determining the potential effects of management on landscape pattern.—We considered the influence of management by analyzing cover type and structural class patterns that existed or were projected to exist at the close of three periods: (1) P_p , pre-Euro-American settlement (before 1890), representing the period prior to fire suppression, livestock grazing, and timber har-

vest; (2) P_e , early post-Euro-American settlement (1890–1950), where intensive grazing of livestock provided an indirect method of fire suppression; and (3) P_r , recent post-Euro-American settlement (1950–1996), where moderate grazing of livestock and active suppression efforts excluded wildfires, and timber harvest introduced a new means of disturbance. We also focused on the abundance, size, shape, and location of young structural patches at the end of P_p and P_r to assess how these aspects of young seral stands may have changed over time. Patches having young stand structure at the end of P_p were assumed to represent wildfire origin unless they occurred in high elevation settings, where they were assumed to result from encroachment. Young patches at the end of P_r were categorized as originating from logging or encroachment (those not resulting from logging were assumed to be the result of encroachment by conifers from adjacent areas). Boxplots (McGill et al. 1978) were constructed to compare abundance and size of patches and FRAGSTATS was used to analyze the shape complexity of the patches.

RESULTS

Changes in vegetation cover type and structure

Eighty-five percent of the study area had stands whose age exceeded 100 yr (10 time steps); 73% of the area had stands whose age exceeded 140 yr (the entire period modeled). Thus, the 1996 stands held much information about past vegetation composition. The most striking landscape changes projected by the model were a major shift from the prevalence of aspen-dominated patches in the past to conifer-dominated patches in the present (Figs. 3 and 4), and a corresponding shift from younger to mature structural classes (Fig. 5). In the mid-1800s, more than one-third of the landscape was projected to have been dominated

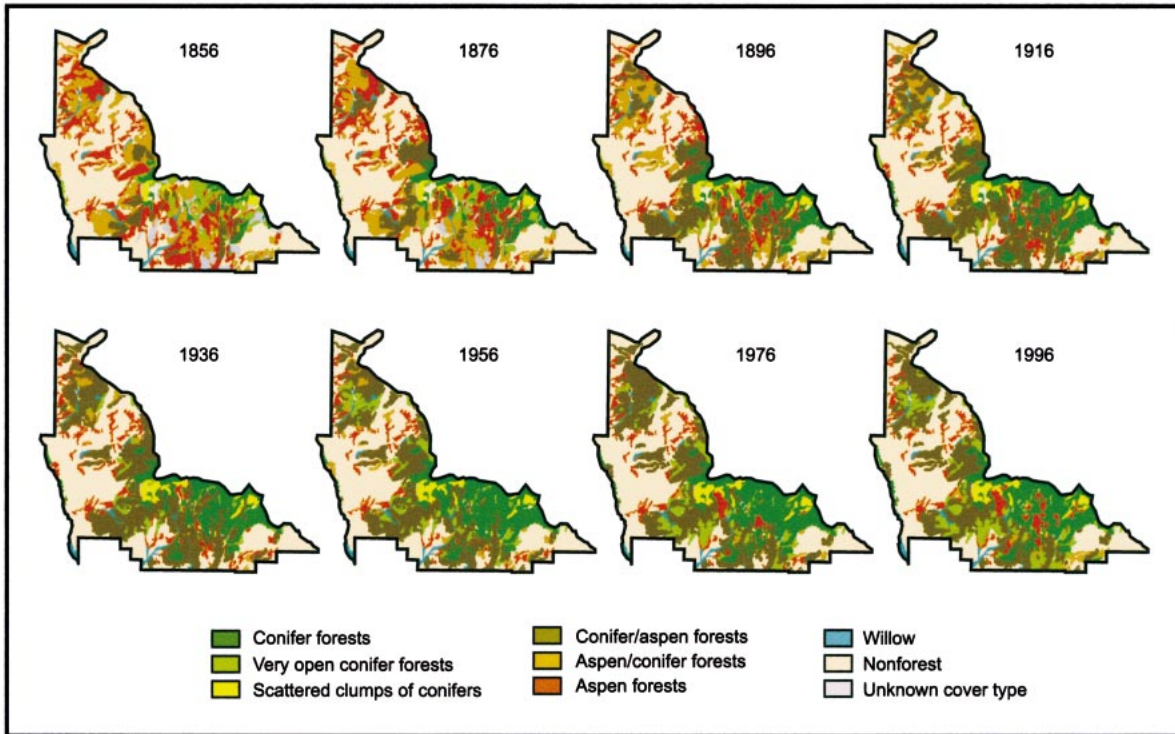


FIG. 3. Cover type maps for a subset of the time steps modeled. A shift over time is evident, from the steady change in the aspen-dominated stands (red and medium brown hues) to the more recent conifer-dominated stands (green and dark brown hues). “Unknown cover type” pertains to stands for which information about cover classes becomes unavailable once stand age cycles back to “0.”

by aspen, occurring both in pure stands (3305 ha) and in mixed stands (2548 ha). By 1996, aspen was limited to riparian areas or mixed stands dominated by conifer. Distribution of conifer-dominated forests appears to have increased steadily through time, from ~15% landscape coverage in the mid-1800s to half of the landscape now. Today, most of the forest stands are of mixed composition dominated by conifers (3782 ha), though much acreage is also occupied by relatively pure, closed-canopy conifer stands (2416 ha; Fig. 6).

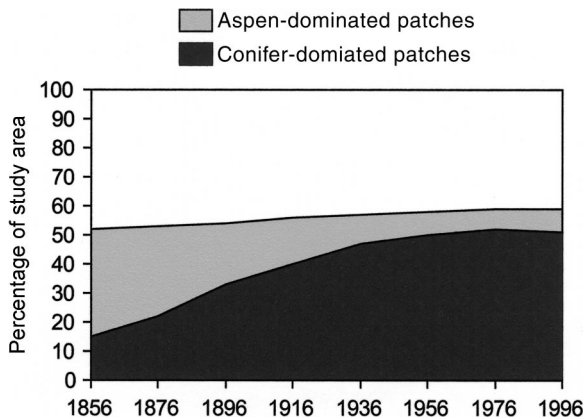


FIG. 4. Changes in area of conifer-dominated patches vs. aspen-dominated patches, as modeled through time.

Very few young structural patches of conifer (609 ha; Fig. 7), and none of aspen, can be found in the landscape by 1996, as young stand structure by then has been limited to areas that were logged and reforested (a small portion of the study area) or that were previously unforested and are undergoing encroachment by trees (high elevation sites or dry, sagebrush/grassland sites). In the mid-1800s, our model indicates that 65% of the landscape was dominated by young conifers (seedlings and saplings), while young stands now only represent ~8% of coniferous forest landscape.

Stratifying by biophysical class to interpret vegetation change

A temporal comparison of conifer patches at the landscape level indicates that there have likely been numerous small patches (≤ 10 ha) throughout the period modeled. Little change is projected to have occurred in the size distribution of conifer patches, except for an increase in the number of small patches from the mid-1800s to the early 1900s, and the coalescence of some patches into a few large patches (Fig. 8, see column for “Entire study area”). We stratified the conifer patches by biophysical group to see if this helped in interpreting where such changes had occurred in the landscape. This indicated that few presettlement co-

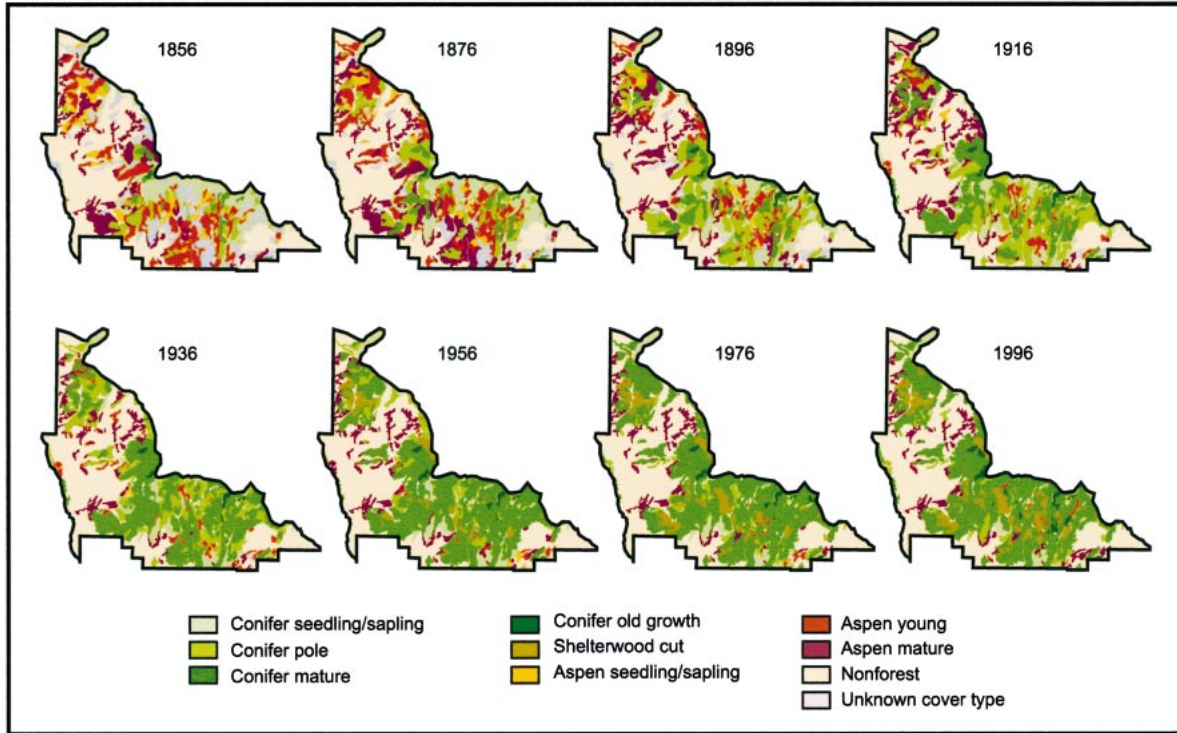


FIG. 5. Structural class maps for a subset of time steps modeled. Conifer-dominated stands have matured without wildfire disturbance since the mid-1800s; thus, few young conifer stands exist today. Most of the aspen stands remaining are mature, though there has been a decline (from past to present) in abundance in all structural classes of aspen. “Unknown cover type” pertains to stands for which information about structure becomes unavailable once stand age cycles back to “0.”

nifer stands existed in the sagebrush/grassland sites, and those that did were small (with one exception). Model results showed that infiltration of very open stands of conifers into sagebrush/grassland sites re-

sulted in an eightfold increase in the total number of conifer patches over time (Fig. 8, see column for “Sagebrush/grassland”). By 1996, conifer patches ranged in size from a few hectares to a few hundred hectares and covered ~15% of the area comprising these sites.

Conifer patches in moist Douglas-fir forest sites have generally maintained a similar distribution profile

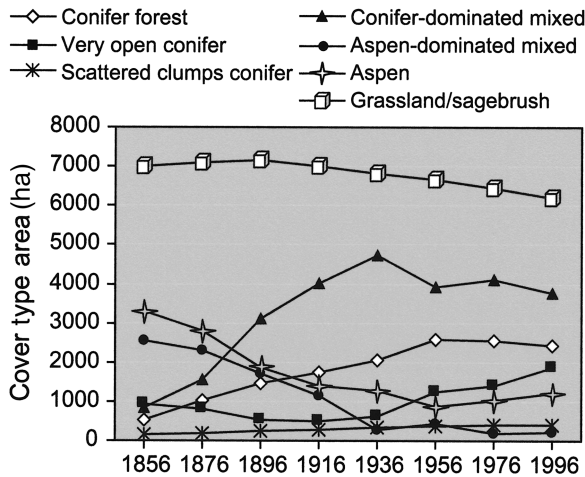


FIG. 6. Area in cover type classes, as modeled through time. All conifer-dominated types cover more area now than prior to Euro-American settlement. All aspen-dominated types have diminished greatly in area. Grassland/sagebrush areas have also decreased in area, due to encroachment by conifers.

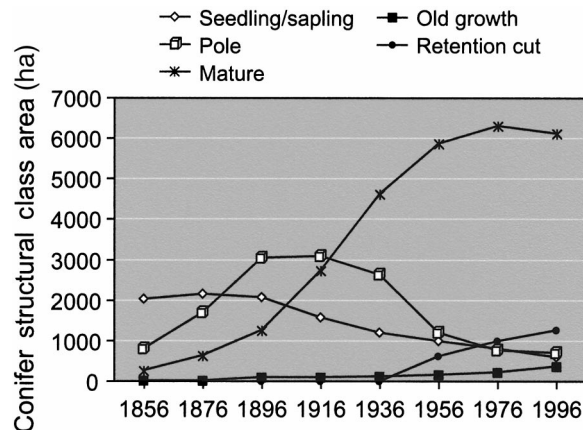


FIG. 7. Area in conifer-dominated structural classes, as modeled through time.

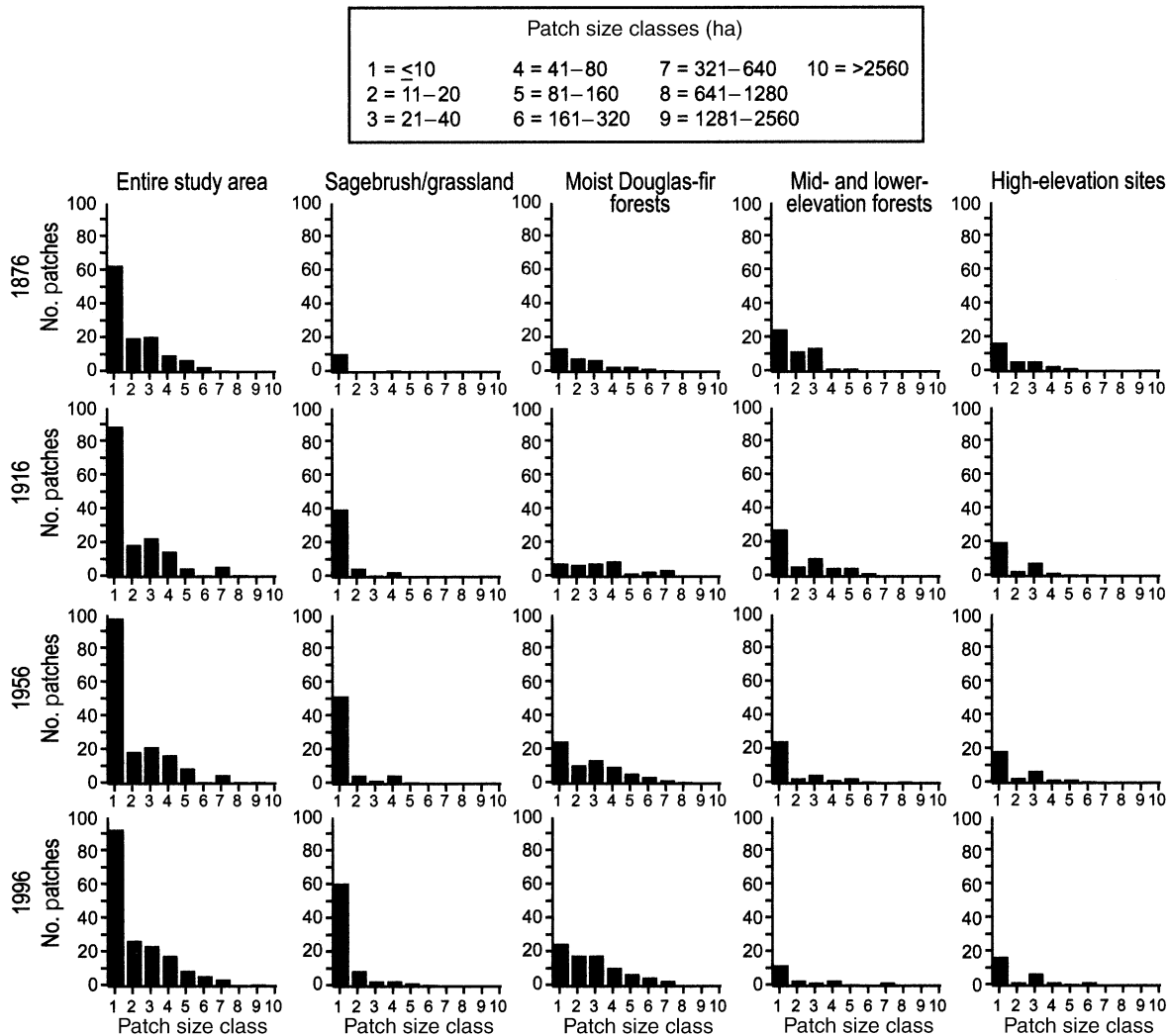


FIG. 8. Profiles of conifer-dominated patches. Rows of histograms show how the distribution of patches for the entire study compares with distributions in different biophysical groups. Columns of histograms show how distributions change over time within the same group.

through time, though there has been an increase in the latter half of the 1900s in the number of patches across all size classes (see Fig. 8 column for “moist Douglas-fir forests”). Conversely, the number of conifer patches in the mid- and lower-elevation forest sites has decreased from past to present; however, this is because the sizes of patches have increased due to coalescence. Coniferous patches at high elevation sites have remained about the same in size and number over the 140 yr modeled, due to very slow growth rates at these sites.

The size and number of aspen-dominated patches have decreased considerably through time (Fig. 9, see column for “Entire study area”). Additionally, aspen-dominated patches have only occurred in two of the biophysical groups, with reduction in numbers and sizes of patches occurring in both groups. In the mid-

and lower-elevation forest sites, model output indicated a dramatic decrease in relative abundance, from 83% estimated coverage in 1856 to <5% by 1996.

Young conifer patches have decreased in number (from past to present) across the landscape (Fig. 10, column for “Entire study area”), occupying an estimated 12% in 1856, to <4% by 1996. Such stands have completely disappeared from mid- and lower-elevation forest sites (see Fig. 10). Young stands nearly disappeared from the moist Douglas-fir forest sites until reforestation, following timber harvesting in the latter half of the 1900s, reintroduced a few young patches. Young stands in the sagebrush/grassland and high elevation settings all appear to be sites that have undergone encroachment by trees (as no stand-replacing disturbances are known to have occurred during the period modeled).

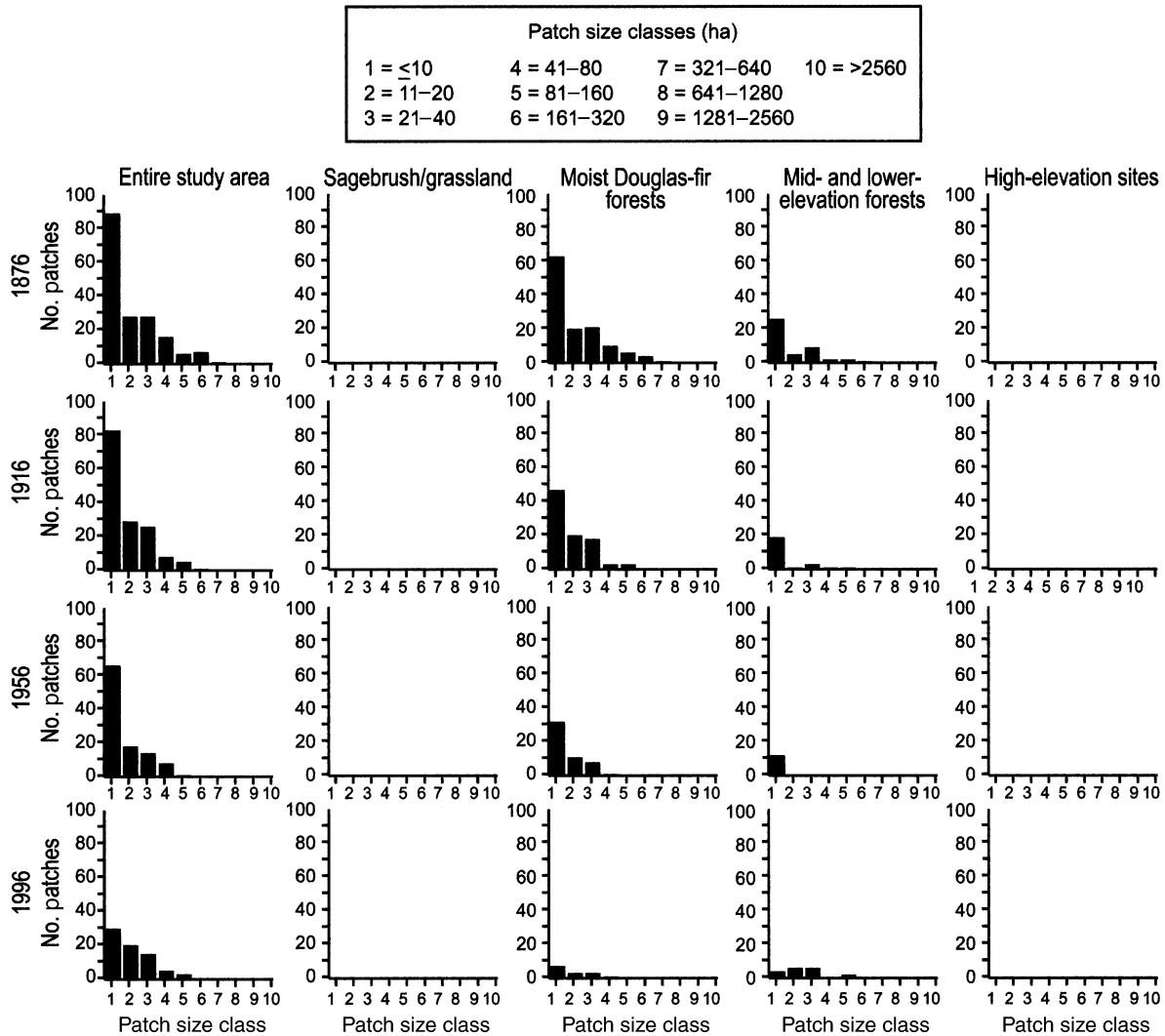


FIG. 9. Profiles of aspen-dominated patches. Rows of histograms show how the distribution of patches for the entire study compares with distributions in different biophysical groups. Columns of histograms show how distributions change over time within the same group.

The spatiotemporal distribution of mature conifer stands shows an increase in the number and size of patches over time (past to present) across the entire landscape and within all biophysical classes (Fig. 11); however, the distributions differ among classes. Relative abundance of mature conifer patches modeled for moist Douglas-fir forest and mid- and lower-elevation forest sites for 1856 was 3% and 6%, respectively, while relative abundance measured for 1996 was 70% and 57%, respectively. Sagebrush/grassland sites, which appear historically to have supported only young stands (presumably controlled by frequent wildfires), now include numerous patches of mature conifer (see Fig. 11, column for “Sagebrush/grassland”), though these cover only 7% of the area. Mature conifer stands now cover 70% of the area in high elevation sites.

Determining the potential effects of management on landscape pattern

Pattern metrics for vegetation cover classes across the entire study area are similar for the three management periods (Table 4, see column for “Entire study area”). Within biophysical classes, however, the spatiotemporal effects of management practices are more evident. For example, patch density in moist Douglas-fir forest stands was higher than landscape-wide density during P_p , but was comparable at the close of the other two periods. With the intensive grazing and associated fire suppression of P_E , some merging of patches occurred, as evidenced by the impressive increase in the largest patch index (from 7% in P_p to 20% by the end of P_E), and decreases in patch density and edge density. Changes in landscape pat-

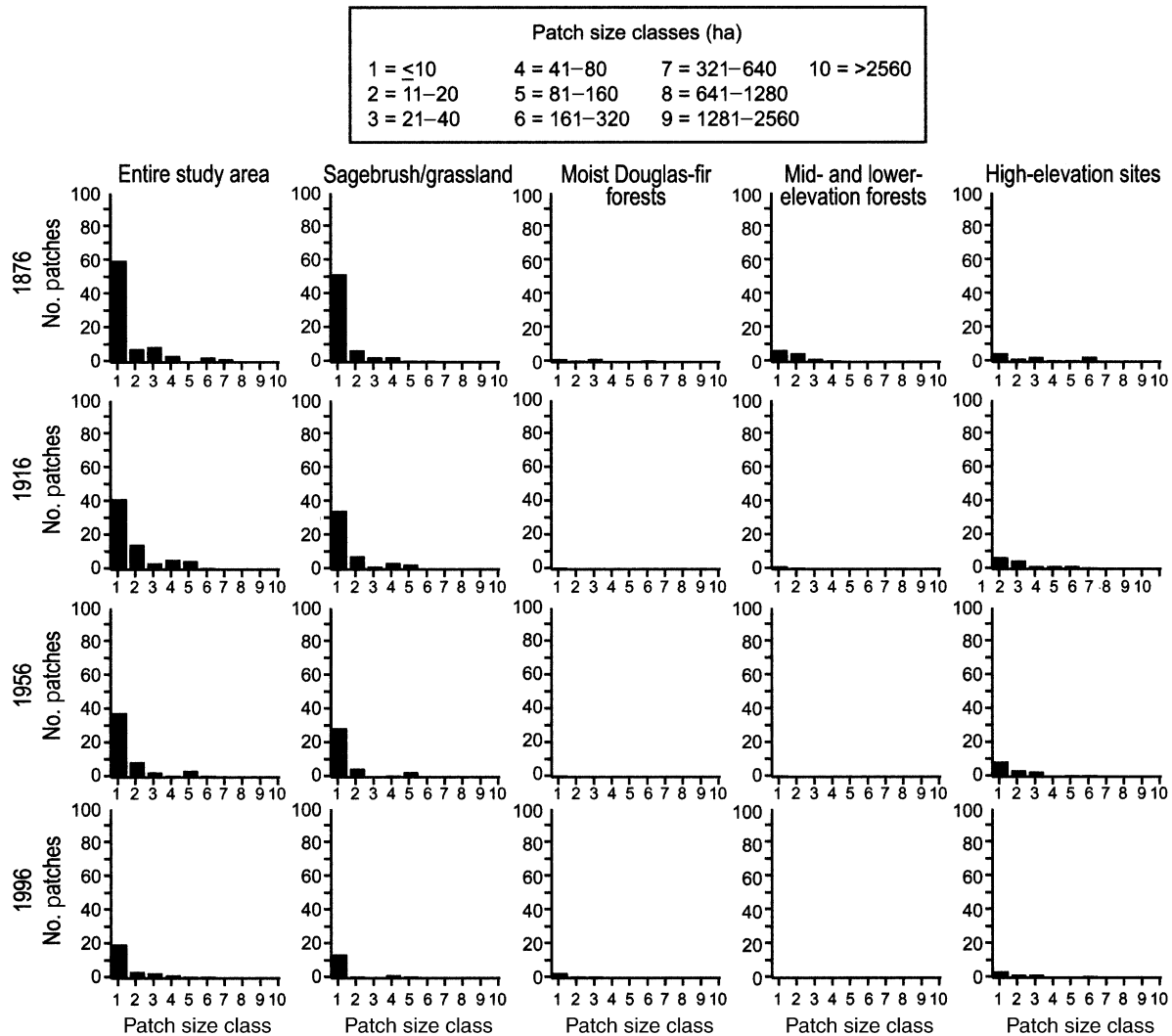


FIG. 10. Profiles of seedling/sapling-aged, conifer-dominated patches. Rows of histograms show how the distribution of patches for the entire study compares with distributions in different biophysical groups. Columns of histograms show how distributions change over time within the same group.

tern between P_E and P_R are also indicated by the decrease in the largest patch index, from 20% to 12%, as a result of timber harvest.

In the mid- and lower-elevation forest stands, patch density was more than twice that measured for the entire study area during P_P , but was reduced to nearly comparable levels by P_R (see Table 4). Edge density for these sites notably decreased after fire suppression was introduced, but has remained substantially higher than that measured for the study area as a whole. The effects of fire suppression are also obvious in changes to the largest patch index, which jumped from <10% during P_P , to 40–50% during P_E and P_R , due to patch coalescence.

At the landscape level, analyses of structural class patches are a little more revealing of change over time than are vegetation cover type classes. Changes in

structural class patches from pre- to postfire suppression periods are relatively larger than changes from pre- to postlogging periods (Table 5). The study area experienced a decrease in patch density and in patch edge over time, but no change in the size of the largest patch or the complexity of patch shapes. Interspersion among patch types increased slightly. Metrics calculated for the landscape as a whole, however, are not mirrored by those within biophysical classes. For examples, while moist Douglas-fir forests have also experienced a decrease in patch density and edge density over time, the overall densities were notably higher than those summarized for the entire landscape, and there has been an increase in patch shape complexity. As coniferous patches matured and coalesced during the fire suppression years of P_E , the largest patch size increased to cover 18% of the area. The introduction

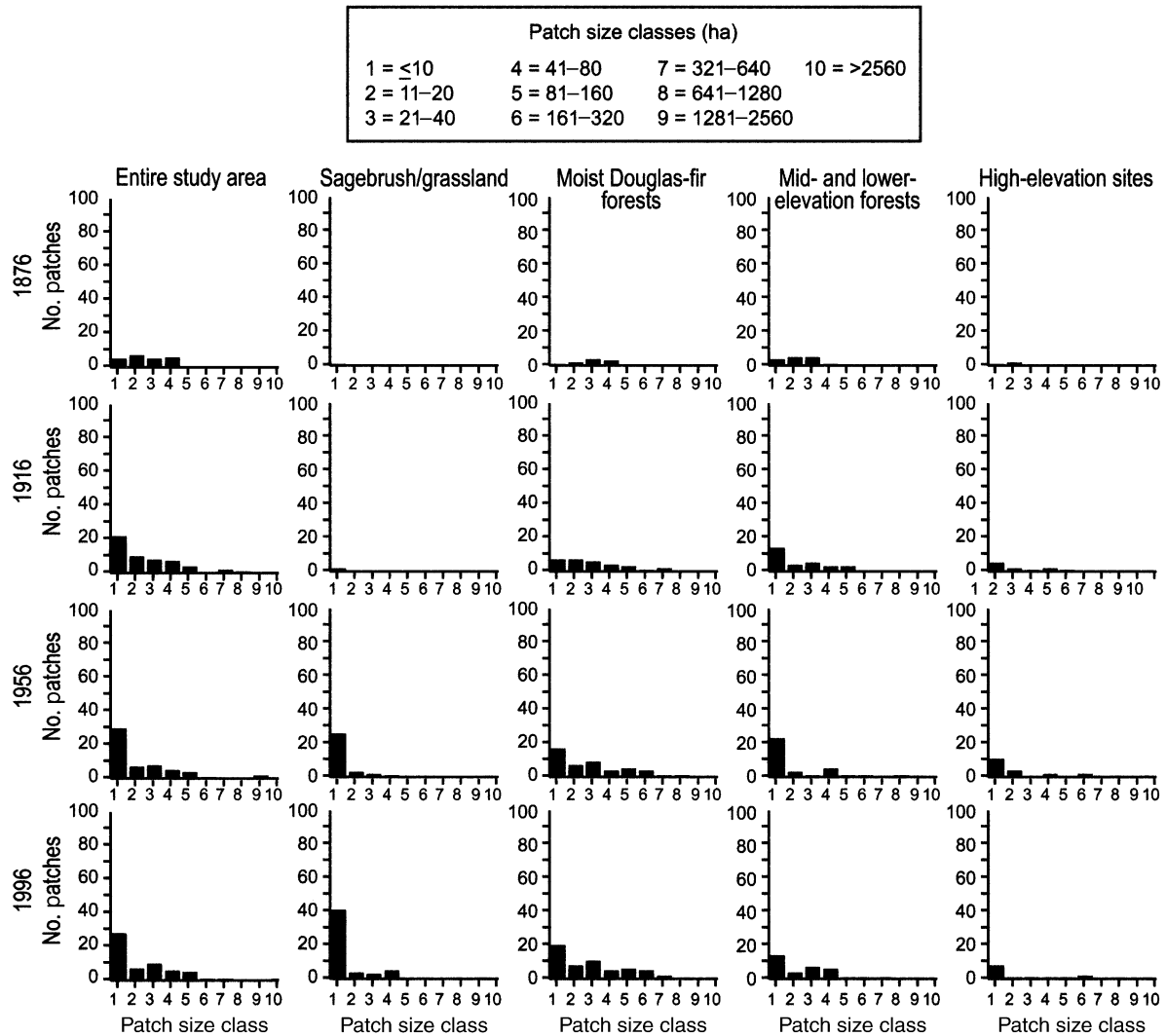


FIG. 11. Profiles of mature, conifer-dominated patches. Rows of histograms show how the distribution of patches for the entire study compares with distributions in different biophysical groups. Columns of histograms show how distributions change over time within the same group.

of timber harvesting in P_R , resulting in reintroduction of young structural stands within the matrix of mature stands, decreased the size of the largest patch to 12% of the area.

Subalpine forest stands have exhibited a small decrease in patch density through time, though density was always greater than that measured landscape-wide. Edge density fluctuated, and was more similar to that measured for the moist Douglas-fir forests than summarized landscape-wide. The coalescence of patches into large, continuous areas of mature conifer during the fire suppression years of P_E resulted in a major decrease in edge availability in the subalpine forest class. Timber harvesting within the larger patches during P_R caused an increase in edges, which was offset by the coalescence of adjacent maturing stands; therefore, largest patch index values for P_E and P_R are sim-

ilar. Interspersion of patch types for structural classes increased from pre- to postfire suppression management periods. This may be a function of the number of structural classes occurring in the landscape; if there are fewer classes, it is easier to intersperse them equally than if there are a greater number of classes. In this biophysical group, there are fewer structural classes in P_E and P_R than in P_P (due to loss of seedling/sapling structural stands).

We compared the total area, size, number, and location of young structural class patches at the end of P_P with those at the end of P_R (i.e., from the 1996 stand map). Young patches in the earlier period accounted for ~25% of the study area, with 10% of the patches attributable to aspen stands and 90% attributable to conifers. Young patches at the close of P_R covered 8% of the study area and all were coniferous.

TABLE 4. Comparison of selected landscape metrics for cover type patches over three management periods for the entire study area, moist Douglas-fir forest settings, and mid- and lower-elevation forest settings.

Metric	Entire study area			Moist Douglas-fir forests			Mid- and lower-elevation forests		
	P _P	P _E	P _R	P _P	P _E	P _R	P _P	P _E	P _R
Patch density (no./100ha)	1.9	1.8	1.6	2.4	1.9	1.7	4.4	2.7	1.8
Edge density (m/ha)	44	42	42	83	76	77	89	70	71
Largest patch index [†] (%)	27	27	29	7	20	12	8	40	50
Mean shape index [‡]	1.9	1.9	2.0	1.9	1.9	1.9	1.7	1.8	2.0
Interspersion [§]	52	54	53	66	75	76	62	81	82

Note: Abbreviations are as follows: P_P, pre-1890; P_E, 1890–1950; and P_R, 1950–1996.

[†] The percentage of the largest patch relative to the landscape area.

[‡] A measure of mean patch shape complexity, where shape complexity for an individual patch is calculated by dividing its perimeter by the square root of its area and then adjusting by a constant for a square standard. This unitless index equals 1 when patches in the landscape are square and increases in value (without limit) as patch shapes become more irregular (McGarigal and Marks 1995).

[§] A measure of the degree of interspersion/dispersion among different patch types. Values approach 0 as the distribution of adjacencies among patch types becomes increasingly uneven, and 100 when all patch types are equally adjacent to all other patch types. The metric expresses the observed interspersion over the maximum possible interspersion for the given number of patch types (McGarigal and Marks 1995).

Because of the lack of fires, young patches in the sagebrush/grassland and high elevation biophysical sites at the close of P_R must have formed from encroachment of trees, while those in the moist Douglas-fir forest and mid- and lower-elevation forest sites arose from logging. We made similar assumptions about the origins of young stands in P_P, except we substituted fire for logging. We generated boxplots to compare sizes of the young patches in P_P and P_R (Fig. 12). These indicate much similarity in size distribution for young patches resulting from encroachment, but much difference in sizes for those resulting from disturbance (i.e., fire in P_P and logging in P_R). Approximately 40% of the young patches representing encroachment in P_P occurred at the timberline sites. Over time, there was less area available for tree colonization at these sites, and this is reflected in P_R, where only one fourth of the encroachment occurred at the higher elevations.

Patches that we assumed were formed from fire were generally larger and covered a wider range in sizes than patches formed from timber harvest. Although the number of patches created from disturbance (45 from P_P and 37 from P_R) is not greatly disparate between the two management periods, the area covered is a fivefold difference. Young patches derived from disturbance

represented about half of the total area of young stands in P_P, but only one-third of the total area of young stands today.

DISCUSSION

Review of results

We used 1996 data on vegetation characteristics within a study area and extensive information on stand succession to construct a deterministic model that would map the vegetation cover back through time at 10-yr intervals. Because the age of forest stands in 1996 was known (and exceeded the period modeled for 73% of the study area), as was fire history (i.e., no fires) and logging history, we felt confident that projecting the stands back through their respective successional trajectories would provide a plausible picture of change in the area.

Model output revealed that the primary forest dynamic in the study area is not fragmentation of conifer forest by logging, but the transition from a fire-driven mosaic of grassland and shrubland, broadleaf forests, and coniferous forests to a conifer-dominated landscape. Model output showed 15% of the area dominated by conifer forest in 1856, increasing to 51% by 1996.

TABLE 5. Comparison of selected landscape metrics for structural class patches over three management periods for the study area, moist Douglas-fir forests, and mid- and lower-elevation forests.

Metric	Entire study area			Moist Douglas-fir forests			Mid- and lower-elevation forests		
	P _P	P _E	P _R	P _P	P _E	P _R	P _P	P _E	P _R
Patch density (no./100ha)	2.0	1.7	1.5	2.9	2.5	2.2	4.2	3.4	3.2
Edge density (m/ha)	45	40	39	87	72	69	88	64	68
Largest patch index [†] (%)	27	27	27	6	18	12	19	31	32
Mean shape index [†]	1.9	1.9	1.9	1.8	1.9	1.9	1.8	1.8	1.8
Interspersion [†]	53	58	58	60	71	73	60	74	67

Note: Abbreviations are as follows: P_P, pre-1890; P_E, 1890–1950; and P_R, 1950–1996.

[†] See definition in Table 4 footnotes.

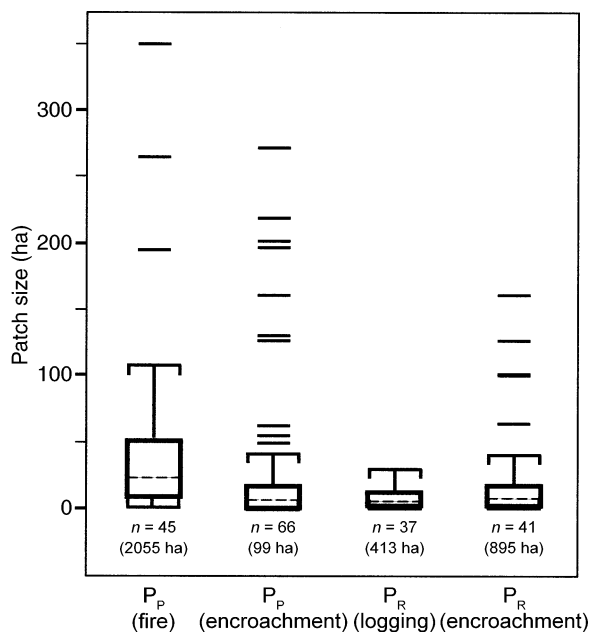


FIG. 12. Boxplots of the distribution of patch sizes of young stands resulting from P_p and P_r management practices. Within each period, patches are further defined by their origin (fire vs. encroachment [assumed] for P_p and logging vs. encroachment [known] for P_r). Total area is given in parentheses beneath the sample sizes. The dashed line within each box represents the median patch size. The upper and lower bounds of the rectangles represent the quartiles of the patch size distribution. The brackets outside the shaded boxes indicate a span of 1.5× interquartile range. Outliers are shown individually.

There was a corresponding 75% reduction in the amount of area dominated by aspen during this interval. Comparison of historic vegetation maps (~1912–1920) with 1996 cover indicated more than a 40% loss in area dominated by grasslands and shrublands. The area covered by seedling/sapling conifers modeled for the mid-1800s decreased from about 12% to 4% by 1996, while the area in mature and old growth conifers increased from 2% to nearly 40%. The spatial patterning of vegetation of the landscape has shifted, with reduction in patch sizes of aspen-dominated stands and major increases in patch sizes of conifer-dominated stands.

These trends are consistent with other studies in the Rocky Mountains. Many ponderosa pine ecosystems have shifted from open savannas to dense pine forests, with increases in tree densities of more than an order of magnitude (e.g., Covington and Moore 1992, Fulé et al. 1997, Mast et al. 1999), and a corresponding decrease in average stem diameter. In eastern Oregon, fire-tolerant species have been replaced by fire-intolerant and pest-susceptible species. Consequently, a large die-off from insect infestation is in progress there.

In western grasslands, fire-sensitive species were historically confined to rockier or less productive surfaces (Miller and Rose 1995), where understory fuels

were sparser (Arno and Gruell 1986). Natural expansion of evergreens into sagebrush steppe occurred during cooler, moister periods, but currently such expansion coincides with warmer, drier climate (Miller and Rose 1999). Extensive encroachment by coniferous species into grasslands has been documented throughout the Rocky Mountains (e.g., Gruell 1983), as has deterioration of aspen (Schier 1975). In the west, aspen rarely regenerates through seedling establishment, relying almost exclusively on clonal growth (Schier 1981). Where aspen succeeds to conifers, removal of conifers is necessary to stimulate aspen suckering (Bartos et al. 1991), without which aging aspen will decay and die out. Such changes as these in the Rocky Mountain forests and steppes are likely to continue into the future. Simulation studies in Bryce Canyon National Park, Utah, suggest that conifer forests will increase in area and density for another 100 yr under the current regime of suppressing fires (Betz 1994).

Fire exclusion is widely believed to be an important driver of these vegetation dynamics (e.g., Houston 1973, Jones and DeByle 1985a, Covington and Moore 1992, Harrington and Sackett 1992, Wadleigh and Jenkins 1996), and studies of fire history provide strong evidence that fire frequency has dropped dramatically since pre-Euro-American settlement (e.g., Swetnam 1990, Barrett 1994, Fulé et al. 1997). New evidence, however, suggests that climate variation may also play a role in these forest dynamics. The long-term record indicates a relationship between periods of warmer, drier climate and increased fire frequency (Millspaugh et al. 2000). The climate of the Greater Yellowstone Ecosystem has warmed and dried since the end of the Little Ice Age in the late 1700s (Whitlock 1993). Coupling the reduced winter severity and longer growing seasons with fire suppression may amplify the process of tree growth.

Stratification of the landscape by biophysical groups revealed that vegetation dynamics varied among groups and that within-group dynamics often differed from the landscape as a whole. At high elevation sites, there was relatively little change in vegetation composition and age structure. And, although we were unable to model the riparian settings, an informal comparison of the 1920 and 1996 vegetation maps indicated little change in the distribution of aspen and willow communities there, as well.

In the sagebrush/grassland sites, the primary trajectory of change was toward encroachment by conifers. Change in the moist Douglas-fir forest and mid- and lower-elevation forest sites was from aspen- to conifer-dominated stands. Aspen is dependent upon fire in these biophysical settings. It proliferates through suckering following fire and dominates until outcompeted by Douglas-fir and other conifers later in succession (Bradley et al. 1992).

This variation across biophysical settings is consistent with our understanding of the environmental tol-

erances of the dominant plant species. The cold temperatures and heavy precipitation of the high elevation sites favor coniferous over broadleaf trees or other life forms. Fire is highly infrequent and usually limited to single trees. Fire suppression likely did not play a significant role in succession on these sites. Similarly, aspen and willow communities in riparian zones changed little because these are truly wetland or very moist sites, and their wet soils exceed the tolerances of conifers and the moisture limits fire. The climate and soils of the moist Douglas-fir forest and mid- and lower-elevation forest sites, in contrast, are within the tolerances of both deciduous and evergreen species. Both can occur here, and species presence is a result of the interplay between disturbance and competition. Fire favors aspen, but in time conifers take over. Sagebrush/grassland settings are also maintained by fire, as well as by high interannual variability in precipitation. Historically, trees that occurred in these settings were widely spaced, due to low seedling survival because of intense understory competition and frequent ground fires (Belsky and Blumenthal 1995). In the absence of fire, shrubs eventually dominate these systems because of a greater efficiency at water extraction and usage. Over time, shrub density increases, aided by livestock preference for herbaceous species, and offers a protective environment for the establishment of tree seedlings by sheltering them from livestock damage, providing shade, trapping snow, and collecting summer rainfall (USDA Forest Service 1995).

Following Euro-American settlement, the natural disturbance mechanism of fire was replaced by logging. Since then, the total area logged has been much less extensive than the burned areas of the past, and has been confined to the moist Douglas-fir forest and mid- and lower-elevation forest biophysical classes. Even within these classes, the area in seedling- and sapling-aged stands may now be only about one-third of what it was before Euro-American settlement. While logging can mimic fire in terms of creating canopy openings, selectively cut stands favor dominance by fire- and pest-sensitive species (Belsky and Blumenthal 1995), and clearcut sites are often planted with conifers within a year of harvest, eliminating the natural establishment of early seral species. Where forest openings are created, aspen may be unable to recover because of the difficulty in sending out suckers in areas where soil has been compacted by logging (Schier et al. 1985). In the past, even-aged silvicultural systems that yielded even-aged stands were often employed. Wildfire, however, often yielded a mosaic of age classes. Logged sites in the Rocky Mountains, in addition to fostering even-aged stands, have tended to be more uniform in size and more geometric in shape relative to burned sites. This has created a more consistent texture in patch sizes and ages throughout the mountains than would have resulted from wildfire, and might have implications for the spread of disturbance (such as from

insects or future wildfires). Finally, duff accumulations in old growth forests today can be an order of magnitude greater than under the fire regimes preceding Euro-American settlement (Harrington and Sackett 1992). Once on fire, deep duff layers are prone to significantly greater temperatures than shallow layers, putting tree roots and cambiums at greater risk to damage. Thus, trees that survived past wildfires are at greater risk of mortality from today's fires.

Ecological consequences and management implications

Fires increase the diversity of plant species composition and age structure across the landscape. This is manifested in the spatial (geographic) patterning and grain size of different community types. Within stands, fire can create more variation in the canopy structure, which provides more variety in microhabitats available for plants and animals. The biological heterogeneity that is created and maintained by wildfire affects the severity and magnitude of future wildfires. Periodic fires maintain younger seral species, which are more resistant to fire. Periodic fires also keep duff and litter accumulation in check, such that future fires are likely to be lesser in extent and severity. With prolonged absence of fire, vegetation cover becomes more uniformly composed of fire-sensitive, pest-susceptible species, and the added duff and litter accumulation almost ensure that any future fire will be stand-replacing and extensive, such as with the 1988 Yellowstone fires and a number of large Rocky Mountains wildfires of 2000. These larger disturbed areas then effect a new grain size on the landscape, making it potentially easier for disturbances to spread in the future. This is particularly important when we consider that climate is becoming warmer and forest growth rates appear to be increasing in the Rocky Mountains. So, the rate at which the landscape can become covered by mature coniferous forests may be more rapid in the future, if the practice of fire suppression continues.

Fire plays different roles in different biophysical settings. In the moist Douglas-fir forests, it reduces competition from shade-tolerant species, favoring aspen and lodgepole pine. Subalpine fir and Engelmann spruce are favored under fire exclusion (USDA Forest Service 1995) in this biophysical class. In the mid- and low-elevation forest settings, the relatively more moist conditions and slower rates of fuel accumulation generally result in smaller fires, promoting dominance by one or more seral species, stand openings, and mosaics of different ages and species composition. Without fire, earlier seral dominants such as aspen and lodgepole pine are eventually overcome by spruce and fir. If the spruce/fir forest persists long enough, a severe fire can bring about a successional process where spruce and fir alone dominate the seral stands, as the seed and rootstock of earlier seral dominants will no longer be available on the site (Bradley et al. 1992). At high

elevation sites, fires are infrequent and effects are localized. Stand replacing fires are rare, usually originating in lower elevations. Fires in sagebrush/grassland sites can cause earlier green-up of warm-season grasses, improved seed germination, and greater production of herbaceous species (Lyon et al. 2000). Additionally, fires initiated in different years and at different seasons promote a greater variety in species composition across the landscape, which supports a greater variety of animals. Lack of fires, especially if coupled with grazing, favors shrubs and subsequent encroachment by trees.

With the trend towards more ubiquitous cover by mature conifer stands, the natural distinctions in vegetation patterns associated with different biophysical settings are harder to discern. If there is interest in regaining a degree of landscape heterogeneity more comparable with the past, then management goals could be determined based on biophysical classes in order to better mimic the landscape patterns resulting from natural cycles of disturbance and succession. Like much of the greater Yellowstone ecosystem, the Beaver Creek study area is currently dominated by 120-yr-old coniferous stands and a notable loss of seral aspen. The study area is most similar to Douglas-fir ecosystems of the northern and western portions of the greater Yellowstone ecosystem. For these similar systems, aspen could be restored and stand density of conifers could be reduced through prescribed fire or mechanical removal. Fire might be needed to reduce duff buildup and improve soil quality through nutrient cycling in order to promote the growth of understory herbaceous species and to create standing and downed dead trees for wildlife. Since successful regeneration of aspen depends on availability of viable rootstock, stands that currently include live aspen in the overstory might be targeted first. In the sagebrush/grassland settings, tree encroachment could be halted or reversed by use of prescribed fire or mechanical removal. Fire would have the added advantage of nutrient cycling and reduction of shrub dominance so that growth by herbaceous species would be improved. Human management has probably had the least impact on plant succession at the high elevation sites, and these stands might be targeted for monitoring of tree growth rates, since warmer and more moist conditions have been predicted for the future (Bartlein et al. 1997).

The conversions of cover type and age structure of stands has also undoubtedly affected hydrologic and nutrient cycles. Over the course of a year, water consumption by grasslands is less than by aspens (on comparable sites), which is considerably less than by conifers (Jaynes 1978). In terms of delivery of water to streams, this can have important ramifications. There is greater snow accumulation under aspens, and more sublimation and evaporation of precipitation in evergreen stands. While we did not quantify effects on hydrology, the shift towards coniferous forest occurring throughout the Rocky Mountains has probably had

large effects on rates of evapotranspiration, evaporation, and runoff.

Litter from aspen breaks down rapidly and improves soil fertility (Fowells 1965) and moisture holding capacity, encouraging undergrowth of herbaceous species (Jones and DeByle 1985b). Conifer foliage has much less nutrient content, and decomposition of litterfall and coarse woody debris from conifers is a very slow process. Soils under conifers become progressively more acidic and less nutrient rich with time. Regardless of forest type, though, forage production declines in aging stands (Kuck 1984), as soil nutrient availability decreases and reduced light penetration (through the canopy) persists. So, with a shift towards mature coniferous forests throughout the Rocky Mountains, we might expect a corresponding shift towards increased build-up of duff, increased soil acidity, reduced soil nutrient availability and reduced forage quality throughout the region.

Model assumptions and limitations

The model relied on successional trajectories, which we developed from dendrochronological data and inferences about chronosequences. A strength of this approach is that the data exist, provided directly by field observations of forest stands, and they can be applied for modeling large areas. The rules are easy to modify and the model can be expanded to incorporate new components, such as disturbance (e.g., fire, logging, pest infestation).

Certain limiting assumptions implicit in our model were associated with characteristics of the Beaver Creek study database. For example, the minimum modeling unit was the 1996 stand boundaries, as all field data were collected at the stand level. Thus, stand boundaries were locked into the model. Another limitation of the data is that the recorded stand age is an approximation of the mean age of the dominant overstory trees. Thus, the stand ages may be more indicative of the ages of trees that have filled in stand gaps as older trees have died out. Also our model does not attempt to address effects from pests, which are known to have been a significant factor in forest stands in the Targhee National Forest at various periods in the past. Forest pests can accelerate or retard the rate of succession because of their preferential effect on tree species. Additionally, our model lacks a mechanism for changing trajectories except in cases where logging has occurred. Some stands that currently exhibit a dense overstory may have had sparser overstories in the past. Dense overstories may alter the local environment sufficiently to change a successional trajectory. So, while our model can provide a plausible picture of past vegetation cover by explicitly addressing timber harvest and implicitly addressing fire exclusion, incorporating effects from pests and grazing would yield alternative pictures of the past landscape. Finally, we chose to interpret the model results from the standpoints of veg-

etation cover types and structural classes. The results could also be reanalyzed from other thematic perspectives.

Conclusions

Modeling and analysis of spatiotemporal changes in vegetation patterns in the East Beaver Creek study area revealed results that are consistent with findings throughout the Rocky Mountains, namely that forest dynamics have shifted from a fire-driven mosaic of cover types and ages to an uninterrupted mature, conifer-dominated landscape. Logging has replaced the natural disturbance mechanism of fire for reintroduction of young stands into the landscape, but the total area, patch size, location, and cover types that are logged do not mimic the vegetation derived from wildfire. This is because, depending upon which species are removed, late seral species may be favored by logging, while wildfire favors early seral species. Reforestation following logging can also eliminate early seral stand types from the successional sequence when species are planted or naturally regenerated that are not early seral species. The net effect is that habitats and processes valuable to many species are not periodically reintroduced.

Stratification of model results by biophysical groups helped us compare how vegetation dynamics and effects from management practices differed among groups and with the landscape as a whole. This type of stratification can provide structure for designing management objectives that are consistent with our understanding of the environmental tolerances of dominant plant species. However, the increasing homogeneity in vegetation cover brought about by more than one hundred years of fire exclusion in these systems has blurred the distinction of vegetation patterns associated with different biophysical settings. The resulting change to a coarser grain of vegetation pattern across the landscape may linger, as disturbances from future fire or pest infestation are also likely to be more areally extensive than in the past. Additionally, as the climate becomes warmer, the potential exists for a more rapid rate for vegetation cover to become more homogenized, should fire exclusion continue.

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LITERATURE CITED

- Arno, S. F., and G. E. Gruell. 1986. Douglas-fir encroachment in to mountain grasslands in Southwestern Montana. *Journal of Range Management* **39**:272–275.
- Barrett, S. W. 1994. Fire regimes on andesitic mountain terrain in northeastern Yellowstone National Park, Wyoming. *International Journal of Wildland Fire* **4**:65–76.
- Bartlein, P. J., C. Whitlock, and S. L. Shafer. 1997. Future climate in the Yellowstone National Park region and its potential impact on vegetation. *Conservation Biology* **11**:782–792.
- Bartos, D. L., W. F. Mueggler, and R. B. Campbell, Jr. 1991. Regeneration of aspen by suckering on burned sites in western Wyoming. USDA Forest Service, Research Paper INT-448.
- Belsky, A. J., and D. M. Blumenthal. 1995. Effects of livestock grazing on upland forests, stand dynamics, and soils of the interior West. Report to the Oregon Natural Resources Council, Portland, Oregon, USA.
- Betz, D. W. 1994. Modeling forest dynamics at the landscape scale: integrating a computer simulation model and geographic information system. Thesis. Utah State University, Logan, Utah, USA.
- Bowerman, T. S., J. Dorr, S. Leahy, K. Varga, and J. Warrick. 1996. Ecological unit inventory of the Targhee National Forest Idaho. Interim report #4. USDA Forest Service, Targhee National Forest, Ashton, Idaho, USA.
- Bradley, A. F., W. C. Fischer, and N. V. Noste. 1992. Fire ecology of the forest habitat types of eastern Idaho and western Wyoming. General Technical Report INT-290. USDA Forest Service, Intermountain Research Station, Ogden, Utah, USA.
- Bridger-Teton National Forest. 1997. Bridger-Teton National Forest PFC assessment. Unpublished report on file at Bridger-Teton National Forest, Jackson, Wyoming, USA.
- Butler, B. R. 1978. A guide to understanding Idaho archaeology, the Upper Snake and Salmon River country. Third edition. Idaho Museum of Natural History, Pocatello, Idaho, USA.
- Caribou National Forest. 1997. Caribou National Forest and surrounding area sub-regional assessment of properly functioning condition (PFC). Unpublished report on file at Caribou National Forest, Pocatello, Idaho, USA.
- Covington, W. W., and M. M. Moore. 1992. Postsettlement changes in natural fire regimes: implications for restoration of old-growth ponderosa pine forests. Pages 81–99 in J. S. Krammes, editor. Effects of fire management of southwestern natural resources. Proceedings of the Symposium, November 15–17, 1988, Tucson, Arizona. General Technical Report RM-191. USDA Forest Service, Fort Collins, Colorado, USA.
- Dieterich, J. H., and A. R. Hibbert. 1990. Fire history in a small ponderosa pine stand surrounded by chaparral. Pages 168–173 in J. S. Krammes, editor. Effects of fire management of southwestern natural resources. Proceedings of the Symposium, November 15–17, 1988, Tucson, Arizona. General Technical Report RM-191. USDA Forest Service, Fort Collins, Colorado, USA.
- Donnegan, J. A., T. T. Veblen, and J. S. Sibold. 2001. Climatic and human influences on fire history in Pike National Forest, central Colorado. *Canadian Journal of Forest Research* **31**:1526–1539.
- Fowells, H. A. 1965. Silvics of forest trees of the United States. Pages 523–534 in Agriculture handbook no. 271. USDA Forest Service, Washington, D.C., USA.
- Fulé, P. Z., W. W. Covington, and M. M. Moore. 1997. Determining reference conditions for ecosystem management of Southwestern ponderosa pine forests. *Ecological Applications* **7**:895–908.
- Gallant, A., A. Hansen, J. Councilman, D. Monte, and D. Betz. 1998. Vegetation dynamics under natural and human drivers during 1856–1996 in the East Beaver Creek Watershed, Centennial Mountains, Idaho. Report to the Targhee National Forest. Montana State University, Bozeman Montana, USA.
- Glenn-Lewin, D. C., and E. van der Maarel. 1992. Patterns and processes of vegetation dynamics. Pages 11–59 in D. C. Glenn-Lewin, R. K. Peet, and T. T. Veblen, editors. Plant succession. Chapman and Hall, London, UK.

- Gruell, G. E. 1983. Fire and vegetative trends in the Northern Rockies: interpretations from 1871–1982 photographs. General Technical Report INT-158. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, USA.
- Hansen, A. J., and J. J. Rotella. 2000. Bird responses to forest fragmentation. Pages 201–219 in R. L. Knight, F. W. Smith, S. W. Buskirk, W. H. Romme, and W. L. Baker, editors. Forest fragmentation in the southern Rocky Mountains. University of Colorado Press, Boulder, Colorado, USA.
- Harrington, M. G., and S. S. Sackett. 1992. Past and present fire influences on Southwestern ponderosa pine old growth. Pages 44–50 in M. R. Kaufmann, W. H. Moir, and R. L. Bassett, editors. Old-growth forests in the Southwest and Rocky Mountain Regions. Proceedings of a Workshop, March 9–13, 1992, Portal, Arizona. General Technical Report RM-213. USDA Forest Service, Fort Collins, Colorado, USA.
- Houston, D. B. 1973. Wildfires in northern Yellowstone National Park. *Ecology* **54**:1111–1117.
- Hutto, R. L. 1995. Composition of bird communities following stand-replacement fires in northern Rocky Mountain conifer forests. *Conservation Biology* **9**:1041–1058.
- Jaynes, R. A. 1978. A hydrologic model of aspen–conifer succession in the western United States. USDA Forest Service, Research Paper INT-213.
- Jones, J. R., and N. V. DeByle. 1985a. Fire. Pages 77–81 in *Aspen: ecology and management in the western United States*. USDA Forest Service, General Technical Report RM-119.
- Jones, J. R., and N. V. DeByle. 1985b. Soil. Pages 65–76 in *Aspen: ecology and management in the western United States*. USDA Forest Service, General Technical Report RM-119.
- Knight, R. L., F. W. Smith, S. W. Buskirk, W. H. Romme, and W. L. Baker. 2000. Forest fragmentation in the southern Rocky Mountains. University of Colorado Press, Boulder, Colorado, USA.
- Kuck, L. 1984. Impacts of phosphate mining on mule deer, elk, and moose in southeast Idaho. Volume 1. Southeast Idaho wildlife studies. Idaho Federal aid to wildlife restoration Pittman-Robertson Project W-160-R. Idaho Department of Fish and Game, Boise, Idaho, USA.
- Landres, P. B., P. Morgan, and F. J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecological Applications* **9**:1179–1188.
- Littell, J. S. 2002. Determinants of fire regime variability in lower elevation forests of the northern greater Yellowstone ecosystem. Thesis. Montana State University, Bozeman, Montana, USA.
- Lyon, L. J., M. H. Huff, R. G. Hooper, E. S. Telfer, D. S. Schreiner, and J. K. Smith. 2000. Wildland fire in ecosystems—effects of fire on fauna. USDA Forest Service, RMRS-GTR-42, Vol. 1. Ogden, Utah, USA.
- Mast, J. N., P. Z. Fulé, M. M. Moore, W. W. Covington, and A. E. M. Waltz. 1999. Restoration of presettlement age structure of an Arizona ponderosa pine forest. *Ecological Applications* **9**:228–239.
- McGarigal, K., and B. J. Marks. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. General Technical Report PNW-GTR-351. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- McGill, R., J. Q. Tukey, and W. A. Larsen. 1978. Variations of box plots. *The American Statistician* **32**:12–16.
- Meagher, M., and D. B. Houston. 1998. Yellowstone and the biology of time: photographs across a century. University of Oklahoma Press, Norman, Oklahoma, USA.
- Miller, R. F., and J. A. Rose. 1995. Historic expansion of *Juniperus occidentalis* (Western juniper) in southeastern Oregon. *Great Basin Naturalist* **55**:37–45.
- Miller, R. F., and J. A. Rose. 1999. Fire history and western juniper encroachment in sagebrush steppe. *Journal of Range Management* **52**:550–559.
- Millsbaugh, S. H., C. Whitlock, and P. J. Bartlein. 2000. Variations in fire frequency and climate over the past 17 000 yr in central Yellowstone National Park. *Geology* **28**:211–214.
- Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. *Ecological Monographs* **52**:199–221.
- Schier, G. A. 1975. Deterioration of aspen clones in the Middle Rocky Mountains. USDA Forest Service, Research Paper INT-170.
- Schier, G. A. 1981. Aspen regeneration. Pages 15–21 in N. V. DeByle, editor. Situation management of two intermountain species: aspen and coyotes. Volume 1. Proceedings of Symposium, April 23–24, 1981. Utah State University, Logan, Utah, USA.
- Schier, G. A., W. D. Shepperd, and J. R. Jones. 1985. Regeneration. Pages 197–208 in N. V. DeByle and R. P. Winokur, editors. *Aspen: ecology and management in the western United States*. USDA Forest Service, General Technical Report RM-119.
- Steele, R., S. V. Cooper, D. M. Ondov, D. W. Roberts, and R. D. Pfister. 1983. Forest habitat types of eastern Idaho–western Wyoming. USDA Forest Service, General Technical Report INT-144.
- Swetnam, T. W. 1990. Fire history and climate in the Southwestern United States. Pages 6–17 in J. S. Krammes, editor. Effects of fire management of southwestern natural resources. Proceedings of the Symposium, November 15–17, 1988, Tucson, Arizona. General Technical Report RM-191. USDA Forest Service, Fort Collins, Colorado, USA.
- USDA Forest Service. 1995. Draft. Camas Creek watershed landscape analysis. USDA Forest Service, Targhee National Forest, St. Anthony, Idaho, USA.
- Veblen, T. T. 1992. Regeneration dynamics. Pages 152–187 in D. C. Glenn-Lewin, R. K. Peet, and T. T. Veblen, editors. *Plant succession*. Chapman and Hall, London, UK.
- Veblen, T. T., T. Kitzberger, and J. Donnegan. 2000. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. *Ecological Applications* **10**:1178–1195.
- Wadleigh, L., and M. J. Jenkins. 1996. Fire frequency and the vegetative mosaic of a spruce-fir forest in northern Utah. *Great Basin Naturalist* **56**:28–37.
- Whitlock, C. 1993. Postglacial vegetation and climate of Grand Teton and southern Yellowstone National Parks. *Ecological Monographs* **63**:173–198.