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Temporal patterns of ecosystem processes on simulated landscapes in Glacier National Park, Montana, USA

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Abstract

The mechanistic, spatially-explicit fire succession model, Fire-BGC (a Fire BioGeoChemical succession model) was used to investigate long-term trends in landscape pattern under historical and future fire regimes and present and future climate regimes for two 46 000 ha landscapes in Glacier National Park, Montana, USA. Fire-BGC has two spatial and temporal resolutions in the simulation architecture where ecological processes that act at a landscape level, such as fire, are simulated annually from information contained in spatial data layers, while stand-level processes such as photosynthesis, transpiration, and decomposition are simulated both daily and annually. Fire is spread across the landscape using the FARSITE fire growth model and subsequent fire effects are simulated at the stand-level. Fire-BGC was used to simulate changes in landscape pattern over 250 years under four scenarios: (1) complete fire exclusion under current climate, (2) historical wildfire occurrence and current climate, (3) complete fire exclusion under a possible future climate, (4) future wildfire occurrence and future climate. Simulated maps of dominant tree species, aboveground standing crop, leaf area index, and net primary productivity (NPP) were contrasted across scenarios using the metrics of patch density, edge density, evenness, contagion, and interspersion. Simulation results indicate that fire influences landscape pattern metrics more that climate alone by creating more diverse, fragmented, and disconnected landscapes. Fires were more frequent, larger, and more intense under a future climate regime. Landscape metrics showed different trends for the process-based NPP map when compared to the cover type map. It may be important to augment landscape analyses with process-based layers as well as structural and compositional layers.

Introduction

Background

Landscape pattern is usually quantified from a single thematic data layer that depicts the spatial distribution of an important ecosystem property (Turner and Gardner 1991), most often stand composition or structure described by vegetation-based attributes such as cover types or structural stages delineated at a community level (Forman 19951; Howard 1991). While these characteristics are important, they are usually dynamic and tend to be limited in scope and interpretation when analyzed at the landscape level (Forman 1995). For instance, most cover type maps do not provide insight on how a landscape evolved to its current state, or how these cover types relate to other ecosystem properties such as coarse woody debris and net primary productivity (Pickett and White 1992; Waring and Schlesinger 1985). In addition, the variable rate of successional change across a landscape often makes it difficult to characterize landscape trend and future condition. Most quantitative landscape studies use spatial statistics to describe the pattern of species composition and structure attributes, but very few at-

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tempt to describe the spatial characteristics of the ecosystem processes that influence present and future landscape states (Chen et al. 19961; Turner and Gardner 1991). Perhaps a better approach to quantifying landscape trend and context would be to analyze the spatial pattern of the ecosystem processes important in landscape formation and function, as well as structural or compositional vegetation layers.

Disturbance processes are major forces that shape landscapes, yet these processes are often missing in some landscape analyses and simulation models (e.g., Bossell and Schafer 1988; Bugmann 19961; Hunt et al. 1993; Running and Coughlan 1988). Wildland fire is inherent in many ecosystems and it influences a variety of landscape characteristics in Rocky Mountain forests (Crutzen and Goldammer 1993; Habeck and Mutch 1973; Heinselman 1981; Peet 1988; Turner et al. 1994; Wright 1974; Wright and Bailey 1982). Fire, vegetation, and climate are so intricately connected that a change in one will ultimately result in a change in another (Clark 1990; Fried and Torn 19914; Rundel 1982; Ryan 1991; Overpeck et al. 1990). Therefore, fire dynamics and the pattern of landscape process, structure and composition it creates will be altered as the climate changes and as the vegetation responds to that climate change (Clark 1988; Crutzen and Goldammer 1993; Graham et al. 1990; Fosberg et al. 1993; Ryan 1991; Suffling 1993). Moreover, the exclusion of fire from many terrestrial ecosystems has and will continue to cause shifts in landscape structure and composition that will, in turn, precipitate significant changes in fire dynamics (Baker 1989; Mutch et al. 1993; Marsden 1983). The successful fire suppression efforts of the U.S. Forest Service and other federal agencies, in place since the late 1920s has resulted in high fuel accumulations and an increase in late successional communities on some landscapes in the western United States (Keane et al. 1990; Mutch et al. 1993; Mutch 1994). This, in turn, has caused major changes to the nutrient, water, and carbon cycles that directly affect forest health and landscape structure (Keane et al. 1996b).

Global climate change caused by increasing atmospheric carbon dioxide concentrations is expected to increase growing season length, annual temperatures, large fire occurrence, and fire severity (Ryan 1991; Bolle et al. 1986; Clark 1988; Fried and Torn 1991; Kasischke et al. 1995; Overpeck et al. 1990). Flannigan and Van Wagner (1990) estimated the total land area burned in Canada will increase by 40% under a future climate scenario created by a doubling of atmospheric carbon dioxide. This increase in fire occurrence might favor species adapted to survive fire or those able to quickly colonize postfire landscapes, which will serve to accelerate species migration on the landscape (Crutzen and Goldammer 1993; Ryan and Reinhardt 1988; Ryan 1991). The warmer, wetter climates predicted for the western US may increase net primary productivities (NPP) (McGuire and Joyce 1995), which may result in higher fuel loadings and ultimately in higher fire intensities (Ryan 1991). Longer fire seasons and more intense fires in the future could reduce the effectiveness of suppression efforts to prevent or fight large wildfires (Fried and Torn 1991), and an escalation of fire suppression programs under a changing climate may further elevate fuel loadings and cause fire events of even more extreme intensity, severity, and size.

The problem then is how to evaluate the effects of changing climate and fire regimes on landscape pattern and ecosystem properties over long time spans so that we can develop management strategies to mitigate adverse ecosystem impacts. Long-term responses of landscape processes to fire, fire exclusion, and changing climate have not been studied in detail because comprehensive field studies are problematic, costly, complex, and often inconclusive (Arno et al. 1985). Mechanistic ecosystem process models offer a means to investigate the role of fire and climate in forested ecosystems because they simulate the basic processes that govern vegetation (Bossel and Schafer 1988; Dixon et al. 1990; Kimmins 1993; Reed 1980). Our study uses the mechanistic ecosystem model Fire-BGC (a Fire BioGeoChemical succession model) (Keane et al. 1996a) to simulate the interaction of disturbance processes of fire with stand development processes of succession and landscape processes of weather, species migration, and hydrology to quantify process and structural changes on a landscape.

The main objective of this paper is to compare the pattern of species cover types and ecosystem processes for four simulation scenarios that represent present and future fire and climatic regimes. The spatial and temporal pattern of landscape composition and process are described for two 46 000 ha drainages in Glacier National Park, Montana, USA (Figure 1) using a suite of five landscape metrics (patch density, edge density, contagion, interspersion, and evenness). A chronosequence of tree species cover type layer output every 50 years describe landscape composition over time, while the sequence of NPP layers at 50 year intervals describe landscape process patterns. Unfor-

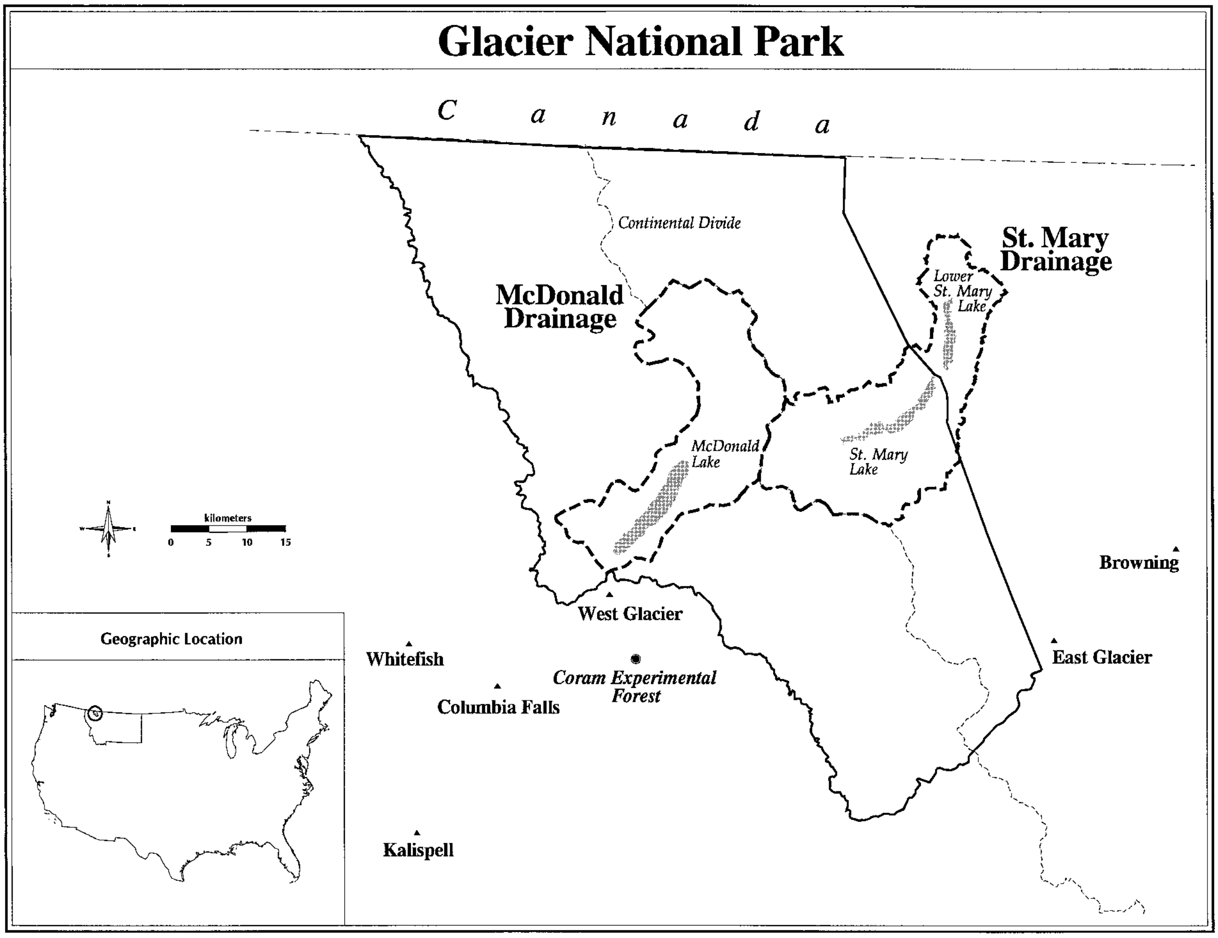

Figure 1. The McDonald and St. Mary watersheds in Glacier National Park, Montana, USA.

tunately, NPP is difficult to estimate in the field, so the structural data layers of leaf area index (LAI) and aboveground standing crop were included in the pattern analysis because they can be estimated by remote sensing and may serve as surrogates for other ecosystem processes such as photosynthesis and respiration (Waring and Schlesinger 1985).

The Fire-BGC model

Fire-BGC is a spatially explicit mechanistic model that simulates primary ecosystem processes at two spatial and temporal scales (Table 1). Five hierarchical levels of organization are implemented into Fire-BGC. The coarsest level is the *landscape*. Nested under the landscape are static polygons called *sites* that have similar topography, soils, weather and potential vegetation. Each site is composed of a number of dynamic *stands* that differ in vegetation composition and structure reflecting past disturbance history. Fire-BGC simulates ecosystem processes on a small portion of the stand called the simulation plot for computational efficiency. Any number of *species* can inhabit a stand and species composition influences many processes such as canopy dynamics and tree regeneration. The finest level of organization is the *tree*. Each tree on a simulation plot is explicitly represented in the Fire-BGC architecture and described by a number of attributes including diameter, height and leaf carbon. Trees are not mapped on the simulation plot. Table 1 lists the ecosystem processes simulated at each hierarchical level.

Fire-BGC is the fusion of two ecosystem models, each developed from very different approaches. The process-based, gap-replacement model FIRE-SUM (Keane et al. 1989, 1990a, b), was merged with the mechanistic biogeochemical simulation model FOREST-BGC (Running and Coughlan 1988; Run-

Table 1. Simulation scales implemented in the Fire-BGC program.

Organizational Scale	Description	Processes Simulated
Landscape	Extent of simulation area	Fire, seed dispersal, ignition
Site	Homogenous biophysical settings	Weather, soils
Stand	Vegetation communities	Photosynthesis, respiration, evapotranspiration, decomposition
Species	Tree, shrub, and grasses species	Regeneration, carbon allocation
Tree	Individual tree components	Mortality, growth, litterfall

ning and Gower 1991) to predict changes in species composition and landscape dynamics in response to changes in various ecosystem processes over long periods. The mechanistic approach of FOREST-BGC improved the level of detail needed to understand those ecosystem processes that govern tree growth and successional dynamics.

Fire-BGC simulates the flow of carbon, nitrogen and water across many ecosystem components to calculate individual tree growth and changes in organic biomass on the forest floor (Figure 2). Carbon is fixed by tree needles via photosynthesis using solar radiation, temperature and precipitation as driving variables. The fixed carbon is then distributed to leaves, stems and roots of individual trees, with a portion lost from each tree component each year to accumulate on the forest floor in the litter, duff, and soil (Figure 2). These forest floor compartments lose carbon through decomposition. Nitrogen is cycled through the system from the available nitrogen pool. The carbon allocated to each tree's stem at year's end is used to calculate diameter and height growth. Daily weather described by temperature, precipitation, and radiation, influence the flux of carbon, nitrogen, and water to and from each component in Figure 2.

The spatially explicit fire simulation model FAIRSITE (Finney 1994) is linked to Fire-BGC to predict the growth of fire across the landscape once it is started by the FIRESTART model which is also linked to Fire-BGC using the Loki system (Keane et al. 1996a). FIRESTART stochastically simulates the occurrence or ignition of a fire on the landscape based on Weibull probability distributions stratified by climate and site fire regime. FARSITE uses the spatial data layers of topography, vegetation, weather and fuels to predict fire behavior characteristics such as fireline intensity and rate of spread (Albini 1976; Rothermal 1972). Another linked program, MAPMAKER, reads a dynamic stand data file created each year from Fire-BGC and maps fuel and plant structure attributes for input to FARSITE (Keane et al. 1996a). Fire-BGC creates new stands in areas where fire intensity calculated by FARSITE is greater than a user-defined threshold taken as 10 kW $^{-1}$ here. Fire effects such as fuel consumption and tree mortality are calculated by Fire-BGC from fire intensity estimates averaged across the burned stand.

Simulation area

The McDonald and St. Mary Drainages of Glacier National Park, Montana, USA (MDSM-GNP) are long, narrow glaciated valleys surrounded by rugged mountains that contain large lakes at the base of the 45 000 ha watersheds. They join at the Continental Divide and flow west and east from Logan Pass (Figure 1). These distinctive landscapes have great diversity in vegetation, topography and climate. Warm, productive western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*) forests dominate low elevation, lakeside settings in the McDonald watershed while subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and lodgepole pine (*Pinus contorta*) forests are common in low areas in the St. Mary watershed (Habeck 1968). Western larch (*Larix occidentalis*), Douglas-fir (*Pseudotsuga menziesii*) and lodgepole pine comprise mixed forests at moderate altitudes in the McDonald-drainage, but most St. Mary moderate elevation stands are composed of lodgepole and subalpine fir (Habeck 1970a; Kessell 1979). Upper subalpine forces consist primarily of subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmanni*) and whitebark pine (*Pinus albicaulis*) in both drainages (Habeck 1970a). Conifer-krummholz and forb communities are found in treeline and alpine environments (2200 to

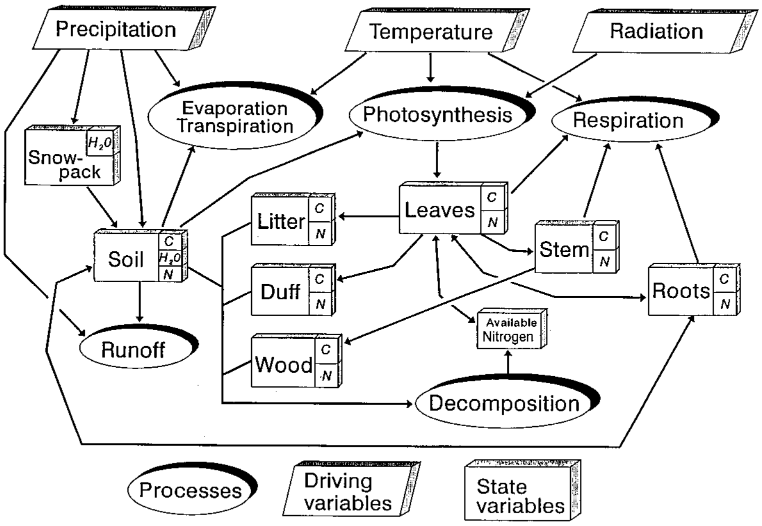

Figure 2. Fire-BGC diagram illustrating the flow of carbon, nitrogen, and water to important ecosystem components.

over 3000 m elevation) (Habeck and Choate 1963; Habeck and Choate 1967). Aspen (*Populus tremuloides*) forests are found primarily at the high prairie and forest interface on the eastern edges of the St. Mary drainage.

Two distinct fire regimes are historically evident on the MDSM-GNP landscape, although relatively little is known of the fire history in the St. Mary drainage. Large, stand-replacement fires have been most common over the last four centuries on moist MDSM-GNP sites with return intervals of l20–150 years (Barrett et al. 1991; Habeck 1970b). Many stands in the higher elevations contain evidence of mixed-severity surface fires (Barrett et al. 1991; Barrett 1986). This fire regime is described by (1) passive crown fires that kill all trees in patches and (2) non-lethal underburns that kill only the smallest and most susceptible trees in other areas (Habeck 1970b). The complex topography of MDSM-GNP has considerable influence on fire pattern, behavior and effects. Since fire behavior is dictated in part by the spatial arrangement of fuels on the landscape, the timberline rocklands and alpine meadows with little woody fuel tend to impede fire spread across and within watersheds. Moist conditions on north-facing slopes also prevent spread of fire from the drier south-facing slopes (Habeck 1970b).

Methods

Input data

The site, stand and tree input spatial data layers and data files needed to parameterize and initialize the simulation landscape for the MDSM-GNP Fire-BGC application were quantified from field data, the literature, existing spatial data layers, and satellite imagery (Keane et al. 1996b). An extensive ecological inventory of the two drainages was conducted during the 1993–1995 summer field seasons, when many ecological characteristics of plant communities were assessed from 110, 0.04 ha circular, geo-referenced plots (i.e., releves) located in stands representative of common plant associations (Keane et al. 1996b). Site descriptions; tree age and size information; duff, litter and woody necromass; soil depth and texture; and undergrowth canopy cover were measured on each plot using ECODATA methodology described by Keane et al. (1990b) and Jensen et al. (1993). In addition, 98 ground-truth plots were established across both drainages during the summer of 1995 to identify plant community type characteristics for validation of satellite imagery classifications discussed next.

Fire-BGC sites (polygons having similar environmental attributes) in the simulation study area were delineated as potential vegetation types (Kessell 1979; Pfister et al. 1977) using satellite imagery, topography (Way 1973) and plant autecology information (Minore 1979). A potential vegetation type (similar to a habitat type but at a coarser scale) is a site classification based on the assumption that a plant community will eventually become a stable 'climax' community in the absence of disturbance and this stable community will uniquely describe a biophysical setting (Pfister et al. 1977). Kessell's (1979) gradient model and the mentioned field data were used to map 'climax' tree species distribution across the study area from several environmental gradients including elevation, aspect, landform position and slope (Keane et al. 1996b; Way 1973) using GRASS GIS software (USA CERL 1990) (Table 2). These potential vegetation types were refined using field data and then mapped as sites in this Fire-BGC application.

Satellite imagery from a July 15, 1990 Thematic Mapper (TM) scene was used to develop a cover type map. This image was classified to several forest, shrub, herb and rock land cover categories using a supervised approach with MDSM-GNP field data used as training areas and ground-truth (Howard 19919; Jensen 1986). Species topographical range information coupled with the site map were used to refine the cover type predictions. This cover type raster map was combined with the site layer to produce the Fire-BGC input raster layer of stands hierarchically nested within the sites (Keane et al. 1996b). The cover type map and associated field data were also used to refine site delineations by identifying permanent shrubfields, herblands, glaciers, lakes and rocklands (Habeck 1970a). The final Fire-BGC site and stand maps were compared to georeferenced field data to compute a validation accuracy of 74 and 66% correct, respectively.

Fire-BGC parameters that describe various ecological processes and conditions within a site were quantified from summaries of the field data (Table 2). Stand-level input parameters for fuel, tree, and understory species components were also estimated from field data. We sampled fuel information using Brown (1970) intersect techniques and tree data from fixed-radius circular plot tree tallies by diameter class and species for every stand-site combination in the MDSM-GNP study area.

Simulation methods

Consequences of fire and climate change were evaluated from the following Fire-BGC simulation scenarios implemented on the MDSM-GNP landscape (Keane et al. 1997).

(1) No Fires: Current Climate (NFCC – A fire exclusion scenario where all fires are suppressed within the study area. Only the process of succession affects plant community composition and structure. This scenario simulates potential impacts of a fully successful fire suppression program. Weather data from 1950 to 1994 were used to simulate the current climate.

(2) Historical Fire Occurrence: Current Climate (HFCC) – Fires are stochastically simulated on the study area at approximately the same frequency as they occurred prior to European/American settlement (ca. 1900) with weather data from 1950 to 1994. This attempts to mimic current 'natural' fire processes in MDSM-GNP study area.

(3) No Fires: Future Climate (NFFC) – A fire exclusion scenario using weather compiled from Ferguson's (1996) climate warming data set (described below). This scenario attempts to describe differences in landscape pattern as the climate warms and all fires are suppressed, even though it is unrealistic to assume that no fires will occur.

(4) Future Fire Frequency: Future Climate (FFFC) – Fires are stochastically simulated at approximately the frequency expected under the future climate (Ferguson 1996). Future 'natural' ecosystems are characterized with this scenario.

All scenarios were simulated for 250 years using the same initial conditions as discussed above. No insect and disease epidemics were simulated in this application. Some model parameters, primarily maximum stomatal conductance, leaf turnover, and decomposition rates, were adjusted during the initialization process to produce more reasonable simulation results based on preliminary model outcomes (Keane et al. 1996a). Annual simulation results were written to various spatial data layers and output files for subsequent analysis.

The current climate for each site was quantified from 44 years (1950–1994) of weather data taken from nearby West Glacier (McDonald Drainage) and Babb (St. Mary Drainage) National Weather Service weather stations. Unfortunately, this was the longest weather record available without long periods of missing data. Daily observations of temperature, humidity, solar radiation, and precipitation were extrapolated to each Fire-BGC site from daily base station data using the MTCLIM climate model (Hungerford et al. 1989) and adjusted using data from Finklin (1986). Fire-BGC cycles the 44 years of weather data in sequence during the 250 years of simulation.

A generalized global warming scenario was constructed by Ferguson (1996) for the Interior Columbia River Basin (Quigley and Arblebide 1997) from sum-

Table 2. Topographic and fire regimes description used to map Fire-BGC sites on the MDSM-GNP landscape.

Site Num	Site Name[1]	Aspects (°)	Slopes (%)	Elevation Range (m)	Fire Frequency (years) Historic	Future
1	TSHE/THPL	270–120	<70%	915–1370	300	250
2	TSHE/THPL	120–270	10 to 70%	915–1525	250	208
3	Lower Subalpine ABLA North	270–120	<70%	1370–1830	150	125
4	Lower Subalpine ABLA South	120–270	10 to 50%	915–1980	150	125
5	Upper Subalpine ABLA North	270–120	10 to 50%	1830–2285	200	167
6	Upper Subalpine ABLA South	120–270	10 to 50%	1980–2440	200	167
7	Dry PSME	220–270	0-90%	1340–1465	70	58
8	ABLA/CLUN	All	All	1340–1705	250	208
9	ABLA/XETE	120–270	5-90%	1705–1980	200	167
10	ABLA/MEFE	270–120	5-90%	1705–1920	250	208
11	ABLA/LUHI	120–270	All	1980–2135	300	250
		270–120	All	1920–1075		
12	ABLA-PIAL	120–270	All	2135–2410	500	417
		270–120	All	2075–2380		
13	Shrub	All	All	All	200	167
14	Herb	All	All	All	500	417
15	Alpine	All	All	1980+	500	417
16	Rock	All	All	All	1000	833

[1]Site names are taken from Pfister et al., (1977). Species abbreviations are: ABLA-*Abies lasiocarpa*, TSHE-*Tsuga heterophylla*, THPL-*Thuja plicata*, PIAL-*Pinus albicaulis*, PSME-*Pseudotsuga menziesii*, CLUN-*Clintonia uniflora*, XETE-*Xerophyllum tenax*, MEFE-*Menziesia ferruginea*, LUHI-*Luzula hitchcockii*.

marized outputs of three Global Circulation Models (GCM's). This scenario was implemented in a C program that modified the 1950 to 1994 daily weather record to portray a possible 44-year future climate. This climate change data file has warmer and wetter summers (approximately 2–5 °C increase in temperature, 30% increase in precipitation) and winters (approximately 2– 4 °C increase in temperature, 25% increase in precipitation). This is only one possible warming scenario and does not represent a prediction of future weather conditions.

Historical fire intervals were computed for each site from fire chronologies by Barrett et al. (1991), Davis (1981), Fischer and Bradley (1987), and Barrett (1986) (Table 2). Since fire history studies have not been conducted on many MDSM-GNP ecosystems such as the subalpine, fire size and frequency other parameters needed by FIRESTART were estimated from studies done elsewhere (Baker 1989; Clark 1990; Johnson 1979; Reed 1994; Veblen et al. 1994), and also from fire atlases compiled by Glacier National Park. Stand age distributions and fire scar information collected in the field were also used to estimate site fire frequency. Future fire regimes (Table 2) under the Ferguson (1996) climate change scenario were taken mostly from the global change literature where an increase in fire occurrence of 8 to 48% is speculated for the northern latitudes (Balling et al. 1992; Clark 1988; Fried and Torn 1991; Kasischke et al. 1995; Overpeck et al. 1990; Flannigan and Van Wagner 1990; Peters 1990; Ryan 1991). An analysis of the differences in fire weather for the summer months in both the current and future weather files indicated that a 20% increase in fire frequency may be the most appropriate for MDSM-GNP sites. Fire history data from hundreds of sites compiled by Barrett (1997) were used to refine future fire occurrence estimates (Table 2). This is only one possible portrayal of future wildfire dynamics and does not predict fire occurrence under new climatic conditions.

Fire-BGC output layers of tree species cover type (COV), leaf area index (LAI, m^2m^{-2}), net primary productivity (NPP, Mg ha^{-1}), and aboveground standing crop (ASC, Mg ha^{-1}) (total aboveground tree and shrub carbon loading) were created every fifty simulation years (simulation years 1, 50, 100, 150, 200 and 250). The COV map category for a polygon (i.e., stand) is selected as the tree species with the majority of basal area, or if no trees present, a shrub, herb or barren category was assigned depending on the site. The continuous values of LAI, NPP, and ASC for each map pixel were reclassified to five ordinal map categories based on five even divisions between the maximum and minimum values of each simulated attribute. Five classes best described the distribution of the data for all continuous maps for all years.

All maps were imported into ARC/INFO for display and analysis, and then exported to the FRAGSTATS analysis program (McGarigal and Marks 1995) to compute the landscape metrics of patch density (number 100 ha^{-1}), edge density (m ha^{-1}), Modified Simpson's Evenness Index (MSEI, dimensionless), contagion (%), and Interspersion-Juxtaposition Index (IJI, %). Patch density is the number of patches divided by the land area and converted to number per 100 ha, and edge density is the sum of the lengths of all edge segments divided by landscape area converted to m ha^{-1}. Values of MSEI approach a value of 1.0 as the observed diversity approaches perfect evenness or equal distribution between patch types (McGarigal and Marks 1995). Contagion measures the extent to which landscapes are aggregated or clumped at the pixel level with high contagion values describing landscapes having few large, continuous patches. The IJI is essentially the same as contagion, but it is evaluated at the patch level to reduce the influence of the number, size, contiguity, or dispersion of patches. It is the sum of the length of each unique edge type involving the corresponding patch type divided by the total length of edge of the same type, multiplied by the logarithm of the same quantity, summed over each unique edge type, then divided by the logarithm of the number of patches minus 1 then scaled to 100 (McGarigal and Marks 1995). These indices were selected because of their simplicity and because they are frequently used in land management applications (Li and Reynolds 1994).

Table 3. Fire characteristics for the historical fire-current climate (HFCC) and future fire-future climate (FFFC) simulation scenarios.

Fire Characteristic	Historical fire scenario (HFCC)	Future fire scenario (FFFC)
Number of fires years	15	18
Average fire size (ha)	4551	6050
Average fireline intensity (kW m^{-2})	903	3056
Percent area in crown fire (%)	33	67
Landscape burned (%)[1]	54	60
Area with multiple burns (%)[2]	17	38
Total area burned (ha)	68273	108896

[1]Percentage of the simulation area that experienced at least one fire over 250 simulation years
[2]Percentage of the simulation area that burned more than once.

Results

Wildland fire simulations

Over the 250 years of simulation, FIRESTART started 24 fires in 15 fire years under the historical fire occurrence (HFCC) scenario and 22 fires in 18 fire years under the future fire occurrence scenario (FFFC) (Table 3). Fires simulated by FARSITE from fire starts under the current climate (HFCC were generally moderate intensity, surface fires that burned a much smaller portion of the landscape (Table 3) because their size was limited by fuel contagion. Crown fires were prevalent under the future fire scenario (FFFC), resulting in high fireline intensities and large fire sizes (Table 3). Fires often burned into the tree canopy and were more intense in productive, low-elevation GNP sites because of higher fuel loadings and the greater amounts of crown biomass relative to those stands at higher elevations. Simulated scorch heights were rarely small enough to allow the survival of fire-tolerant trees, so most wildfires killed most trees in a stand (stand-replacement) and created non-forest patches on the landscape. This was especially true for the future fire (FFFC scenario (Table 3). The simulated fire rotation of 315 years for the historical scenario agreed well with Glacier National Park fire histories (Barrett et al. 1991, Barrett 1986). Under FFFC scenario, the simulated fire rotation was 213 years, shorter than the expected 276 years but within the range of variation based on fire return intervals (Barrett et al. 1991). Some areas (l7% of the simulation area) were burned more than once under the HFCC scenario, while this proportion more than doubled to 37% under the future fire scenario (FFFC).

South-facing, low elevation sites in the St. Mary Drainage (Sites 7 and 8) tended to have more multiple surface fires that did not kill all trees, especially under the FFFC scenario, and resultant fire return intervals of 50 years (five fires over 250 years) corresponded well to the input fire frequency of 58 years (Table 2). Fires simulated under the FFFC scenario burned many non-forested areas, such as alpine and upper timberline, that rarely burned under current climate conditions. This was probably because the high productivity under a future climate regime resulted in greater biomass on the landscape, thereby allowing fire to spread across areas that otherwise would not have had enough fuel to burn, and the warmer climates tended to dry alpine fuels enough to carry a fire.

Landscape patterns

The continuous values of NPP, LAI and ASC for each patch were classified into five categories to perform the landscape metric analysis with FRAGSTATS so results would compare with landscape metrics computed for species cover type maps (see Figure 3 for example). These five categories are even divisions of the range of values recorded for each continuous attribute for the entire layer. These layers, such as the LAI layer shown in Figure 3, were reformatted for input to FRAGSTATS for landscape metric analyses.

Patch density tends to decrease or remain somewhat stable for the compositional and structural landscape maps (COV, LAI, ASC) (Figure 4), especially for both fire scenarios (Figure 4a). However, the number of patches actually increases for the NPP layers indicating increasing spatial heterogeneity of productivity, especially for landscapes subject to fire (Figure 4b). There is very little difference in patch density between climate scenarios for COV, LAI, and ASC maps, but there is a great disparity for all scenarios in the NPP map. By year 250, the density of NPP patches differs greatly across scenarios with NFFC having the lowest patch density, perhaps because of high respiration rates of late seral communities, and FFFC having the highest patch density because of more fires and higher productivities for entire landscape (Figure 4b). Patch density trends are similar within the fire (HFCC and FFFC) and no-fire (NFCC and NFFC) scenarios (Figure 4a, 4c, 4d) with the exception of the dip in ASC at year 250. LAI patch density converges at around 10.0 per 100 ha for all scenarios probably because most stand LAI's range from 1.0 to 3.0 causing an uneven distribution across LAI categories.

Trends in edge density appear similar to patch density changes over the 250-year simulation time (Figure 5). However, there is a greater distinction between the fire and no-fire scenarios for the COV, LAI, and ASC maps (Figures 5a, 5c, and 5d). The NPP layer edge density is somewhat stable over all scenarios and simulation years and does not show the great differences between fire and no-fire scenarios compared to patch density (Figure 5b). Edge density decreases with fire for the COV and LAI maps probably because of the large, stand-replacement fires experienced in both scenarios. The drastic rise in ASC edge density for all scenarios is probably a result of inadequate quantification of BGC parameters to compute standing biomass (see Keane et al. 1996b).

Productivity (NPP) categories are evenly distributed across the landscape throughout time for the fire scenarios (Figure 6b) but unevenly distributed for the no-fire scenarios and also unevenly distributed for structural and compositional maps of COV, LAI, and ASC based on trends in modified Simpson's Evenness index (MSEI) (Figures 6a, 6c, 6d). The most marked difference in MSEI is between fire and no-fire scenarios where fire reduces evenness by half or a third for all but the NPP map because of the predominance of crown fire. Moreover, the downward trends in the ASC map for fire scenarios indicate more uneven representations of biomass categories, while no-fire scenarios are trending upwards to greater evenness by the end of simulation.

Contagion for COV, LAI, and ASC maps increases under fire scenarios, with indices nearly doubling for the fire versus no-fire scenarios by the end of the 250-year simulation (Figures 7a, 7c, 7d). In contrast, contagion for the NPP layer remained relatively stable for all but the NFFC scenario (Figure 7b) because many simulated patches on future landscapes without fire tended to converge to a constant NPP around 1.0 Mg ha^{-1}. The Interspersion-Juxtaposition index (IJI) index did not show major differences between fire and climate scenarios for any but the LAI map (Figures 8a, 8b, 8d) where fire scenarios were highly interspersed when compared with no-fire scenarios (Figure 8c). There were very few consistent differences between climate scenarios for IJI (except for LAI) (Figure 8), but future climate causes some major differences in contagion for NPP map (Figure 8b).

Additional insights emerge when the landscape metrices are interpreted together. The greatest con-

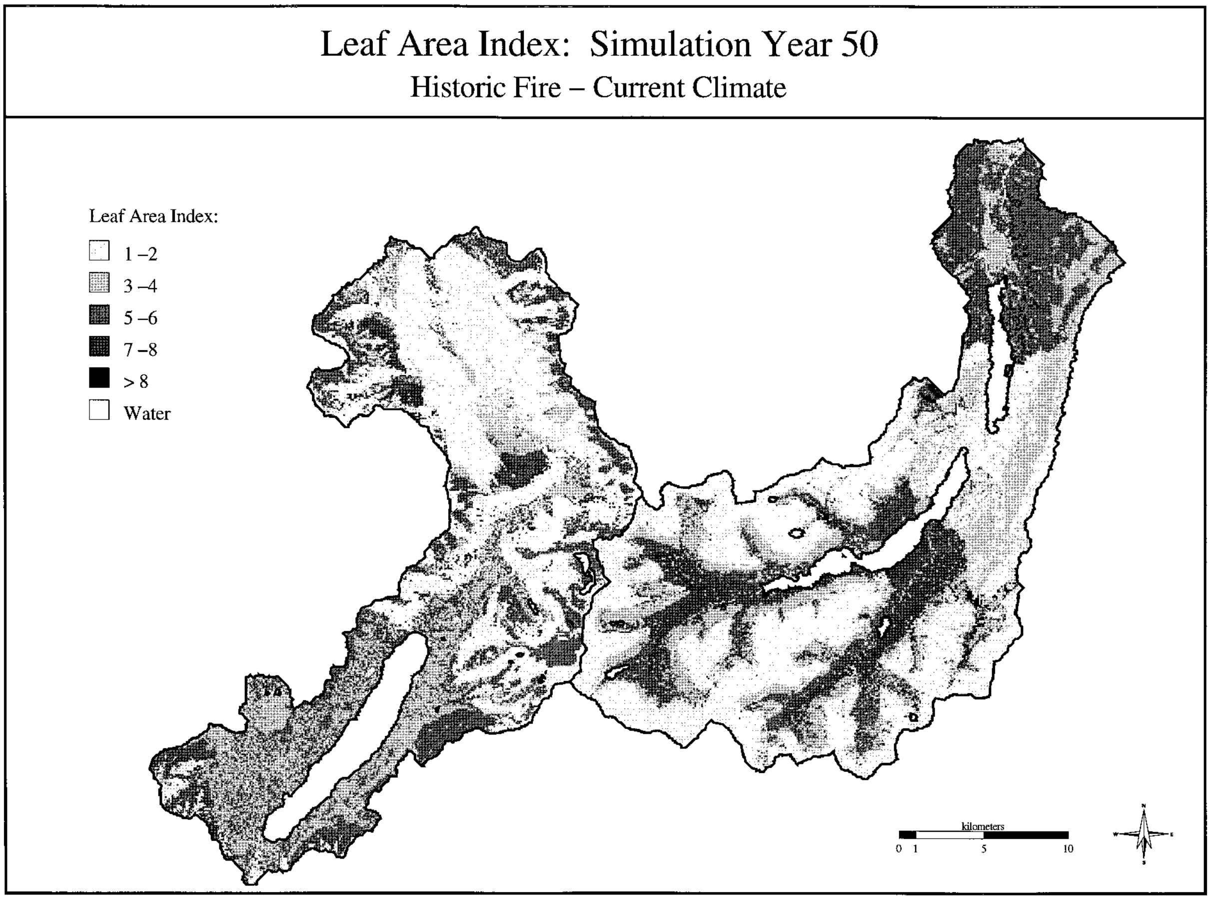

Figure 3. Fire-BGC output map of Leaf Area Index (LAI, m^2m^{-2}) reclassified to five categories at simulation year 50 for the historical fire current climate scenario (HFCC).

trasts in trends of landscape metrics are consistently across the fire and no-fire scenarios, and landscape metric trends differ little between current and future climate. After 250 years with fire, the simulated landscapes are locally diverse, with a fine scale mosaic of many patches. Diverse patches are highly interspersed, and patches of the same type are contagiously distributed across the landscape. This makes sense, as there is a strong influence of elevation and aspect on the vegetation in the MDSM-GNP. These trends are most pronounced for NPP and least so for ASC and COV.

Discussion

Landscape and fire dynamics

Simulated fires burned over 55% and 67% of the MDSM-GNP landscape under the current and future climate scenarios, respectively, after 250 years of simulation (Table 3). These fires tended to be mostly lethal surface fires and crown fires that created more productive and diverse landscapes when contrasted to landscapes that developed without fire (Keane et al. 1997). Fires created patchy landscapes, where stands in various stages of succession were unevenly distributed in space, resulting in high edge density and less contagion. Fires in warmer, wetter climates (FFFC scenario) were larger and more intense (Table 3) because of greater fuel accumulations (Keane et al. 1998), and they probably will be more difficult to fight with conventional suppression technology.

Changes in landscape pattern over time appeared to be more influenced by fire than by climate alone over the 250 years of simulation (Figures 4–8). Landscape metrics for nearly all maps tended to be similar and remain somewhat constant for the no-fire scenarios (NFCC and NFFC) throughout the simulation, and

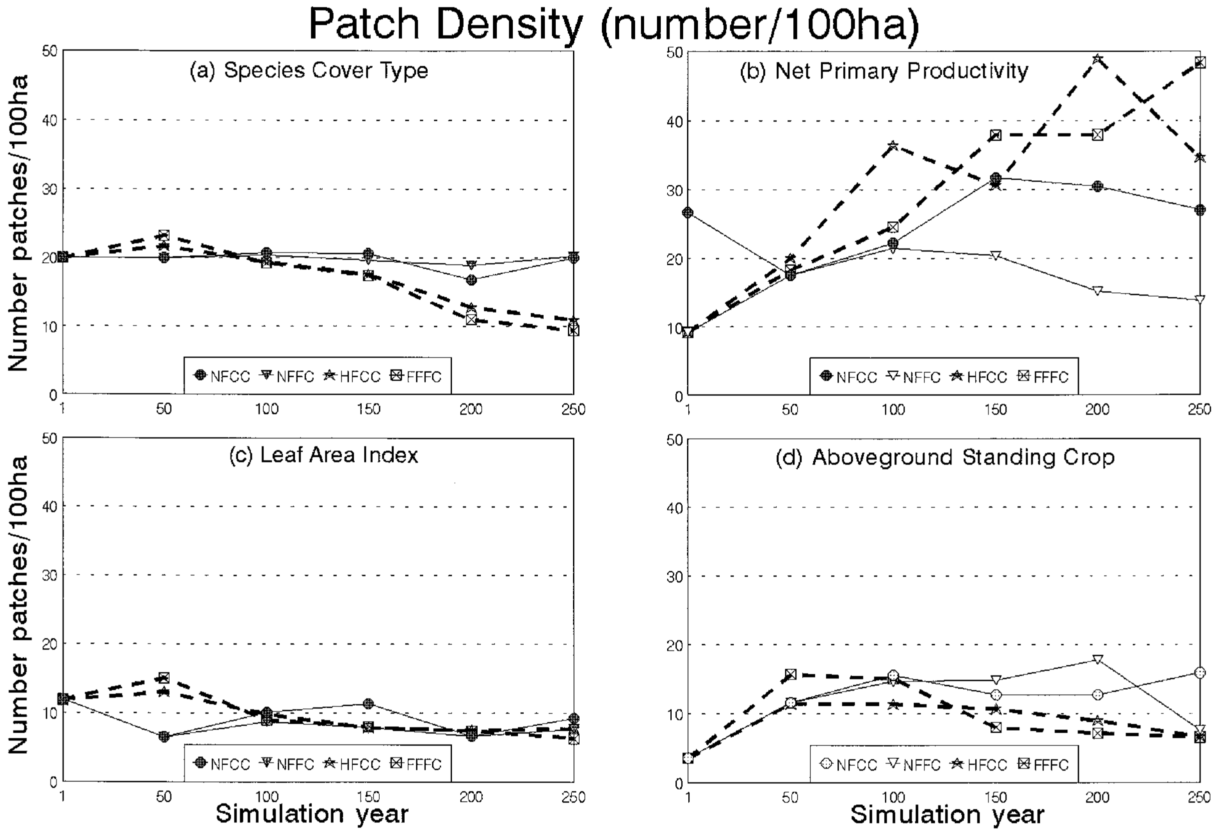

Figure 4. Patch density (patches per 100 ha) trends over 250 years of simulation contrasted across the four simulation scenarios by the four spatial data layers of (a) species cover type (COV), (b) net primary productivity (NPP), (c) leaf area index (LAI), and (d) aboveground standing crop (ASC). Dashed lines indicate fire scenarios HFCC (Historic Fire, Current Climate) and FFFC (Future Fire, Future Climate), and solid lines are no-fire scenarios NFCC (No Fires, Current Climate) and NFFC (No Fires, Future Climate).

when climate and fire interact, as in the FFFC scenario, their joint influence is more pronounced than climate change alone (Baker 1995; Gardner et al. 1996). Landscape pattern trends for fire scenarios (HFCC, FFFC) appear to be inversely proportional to trends for no-fire scenarios: there is a strong downward trend for patch density, edge density, and MSEI for the fire scenarios, but only a minor upward or level trend in the same metrics for the no-fire scenarios (Figures 4–6). Many spatial metrics were quite similar between the two fire scenarios for all but NPP maps indicating that even though fires are larger and more intense under future climates (Table 3), their effect on landscape pattern is approximately the same as historical fire regimes (Figures 4–8) which might mean the complex topography of MDSM-GNP may influence fire growth and pattern more than fuel contagion (Barrett et al. 1991; Swanson et al. 1990). The NPP metrics did show a difference between future and current fire landscapes probably because of the increased productivity under the warmer climate scenario.

The temporal and spatial pattern of the process-based variable NPP differed greatly from the other three structural and compositional mapped entities of COV, LAI and ASC across all landscape metrics (Figures 4–8). This is probably because the ecological processes, other than disturbance, that govern vegetation such as climate, soils, and species dispersal, cause short term changes in NPP while COV, LAI, and ASC changes occur over the long term. This is also why landscape metrics for NPP across all scenarios did not differ as dramatically as the other thematic layers. Fire events instantaneously alter landscapes and create new plant communities with entirely different leaf areas, biomass, and species composition. However, NPP can be the same before and after a fire because it depends on many factors acting in concert such as daily weather, leaf area, living biomass (respiration), and available water. Given that the response

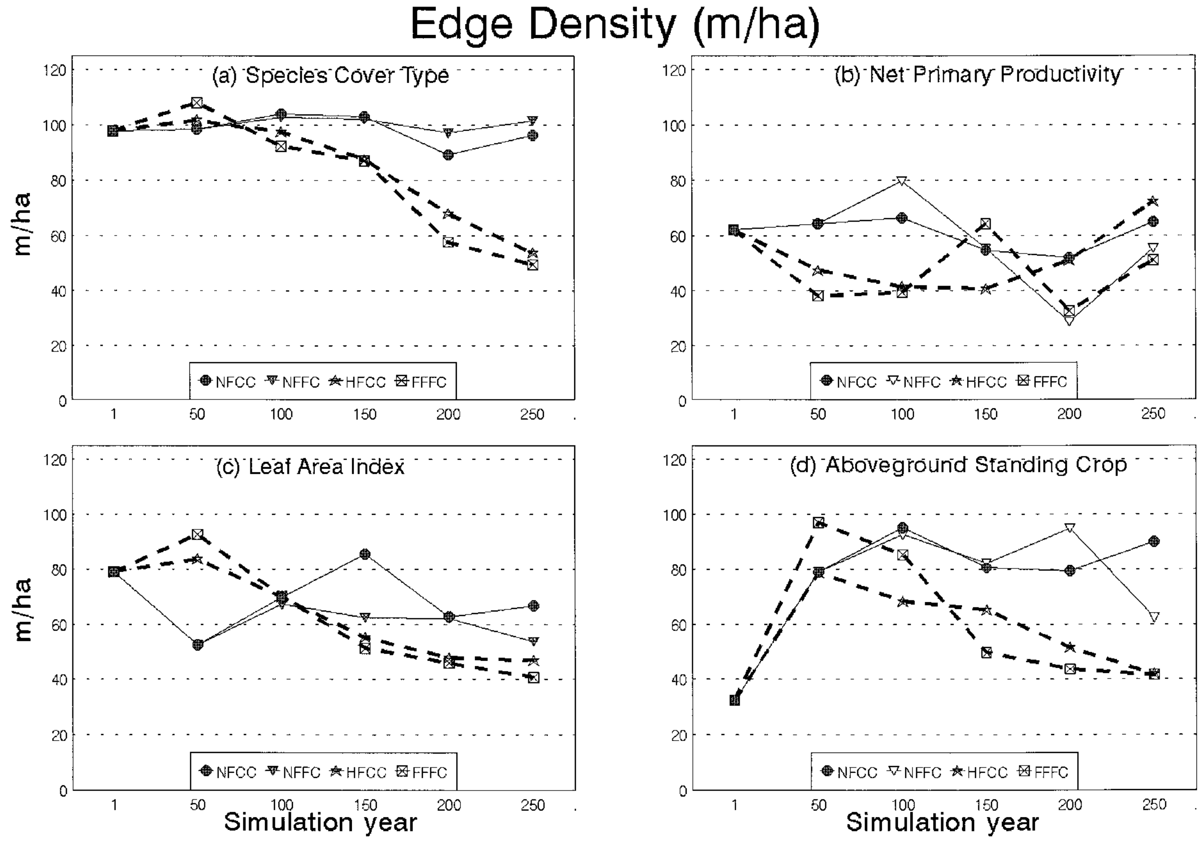

Figure 5. Edge density trends over 250 years of simulation contrasted across the four simulation scenarios by the four spatial data layers of (a) species cover type (COV), (b) net primary productivity (NPP), (c) leaf area index (LAI), and (d) aboveground standing crop (ASC). Dashed lines indicate fire scenarios HFCC (Historic Fire, Current Climate) and FFFC (Future Fire, Future Climate), and solid lines are no-fire scenarios NFCC (No Fires, Current Climate) and NFFC (No Fires, Future Climate).

of NPP patterns at a landscape level is quite different from cover type or LAI, it would follow that NPP and other process-based attributes may be important to include in landscape structural analyses. The response of important organisms such as bark beetles, birds, and bears may be more correlated to patterns of process such as NPP than patterns of cover or structure during certain times of the year (Heinrichs 1988; Bormann and Likens 1979; Chen et al. 1996).

It is interesting that landscape metric trends for the LAI and ASC maps were more similar to trends observed for the COV map than for the process-based NPP map. LAI and ASC maps were included in this study because we assumed they would act as surrogates for other process-based attributes because LAI correlates well with gross primary production and ASC (total aboveground biomass) compares well with autotrophic respiration (Waring and Schlesinger 1985). However, the behavior of landscape metrics computed from these maps was similar to metrics computed for compositional maps (COV). Apparently, LAI and ASC are more related to successional species composition while NPP seems to be more dependent on biophysical environment than community composition.

Contagion and IJI indices computed from LAI maps uniquely differed from those computed from NPP or COV maps. Moreover, edge and patch density values from the ASC maps were quite different from NPP or COV values, especially for no-fire scenarios. This seems to be related to stand development with aboveground living biomass reaching maximum values during mid-to-late seral stages while greatest NPP occurs during early seral stages. However, cover type will change from early to mid-seral to late climax stages unlike NPP.

Trends in diversity and patch density across fire and no-fire scenarios for this study generally agree

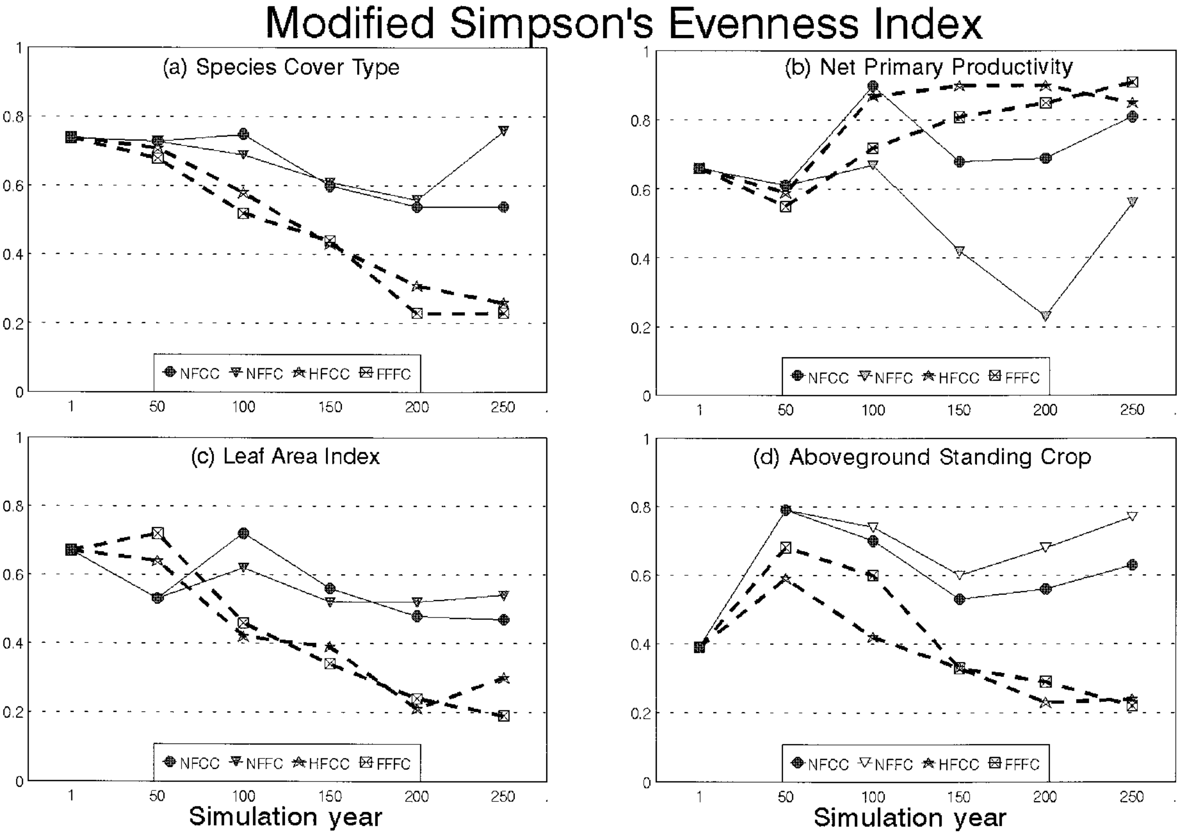

Figure 6. Modified Simpson's Evenness Index (MSEI) trends over 250 years of simulation contrasted across the four simulation scenarios by the four spatial data layers of (a) species cover type (COV), (b) net primary productivity (NPP), (c) leaf area index (LAI), and (d) aboveground standing crop (ASC). Dashed lines indicate fire scenarios HFCC (Historic Fire, Current Climate) and FFFC (Future Fire, Future Climate), and solid lines are no-fire scenarios NFCC (No Fires, Current Climate) and NFFC (No Fires, Future Climate).

with results simulated by Baker (1992) and Ratz (1995), even though landscape complexity was significantly higher in this study. Patch sizes tend to become smaller and diversity generally increases on simulated landscapes with fire (Baker 1992; Roberts 1996). Gardner et al. (1996) found simulated drier climates produced more but smaller fires on the Yellowstone landscape than nominal or wetter climates, and these fires increased patch density and decreased patch size. However, Baker et al. (1991) found landscape structure, described by patch age, can fluctuate as the climate changed with disturbance. Baker (1995) and Gardner et al. (1996) also found significant changes in landscape metrics as a warming climate changed the fire regime which do not agree with a comparison of metrics for HFCC and FFFC scenarios from this study. This is probably a result of the complex MDSM-GNP landscape regulating fire pattern by the patchy and static nature of unburnable land types such as rocklands, water, and glaciers. It could also be due to differences in simulation approaches. They simulated climate change by modifying the fire regime and did not model the effect of climate change without fire on the landscape. Moreover, they modeled only stand-replacement fires by setting patch age to zero with no direct simulation of the effect of climate change on successional rate. We simulated climate effects directly on vegetation and on fire regime independently, and then computed fire effects from FARSITE fire intensity maps and stand characteristics which created diverse post-fire patterns depending on fire boundaries, pre-fire vegetation structure, and species composition. Ratz (1995) noticed large system fires occurred in all of his simulation scenarios without explicit weather influences which supports these simulation results indicating the important role fire plays in shaping landscapes. Roberts (1996) simulated increases in patch diversity and fragmentation with in-

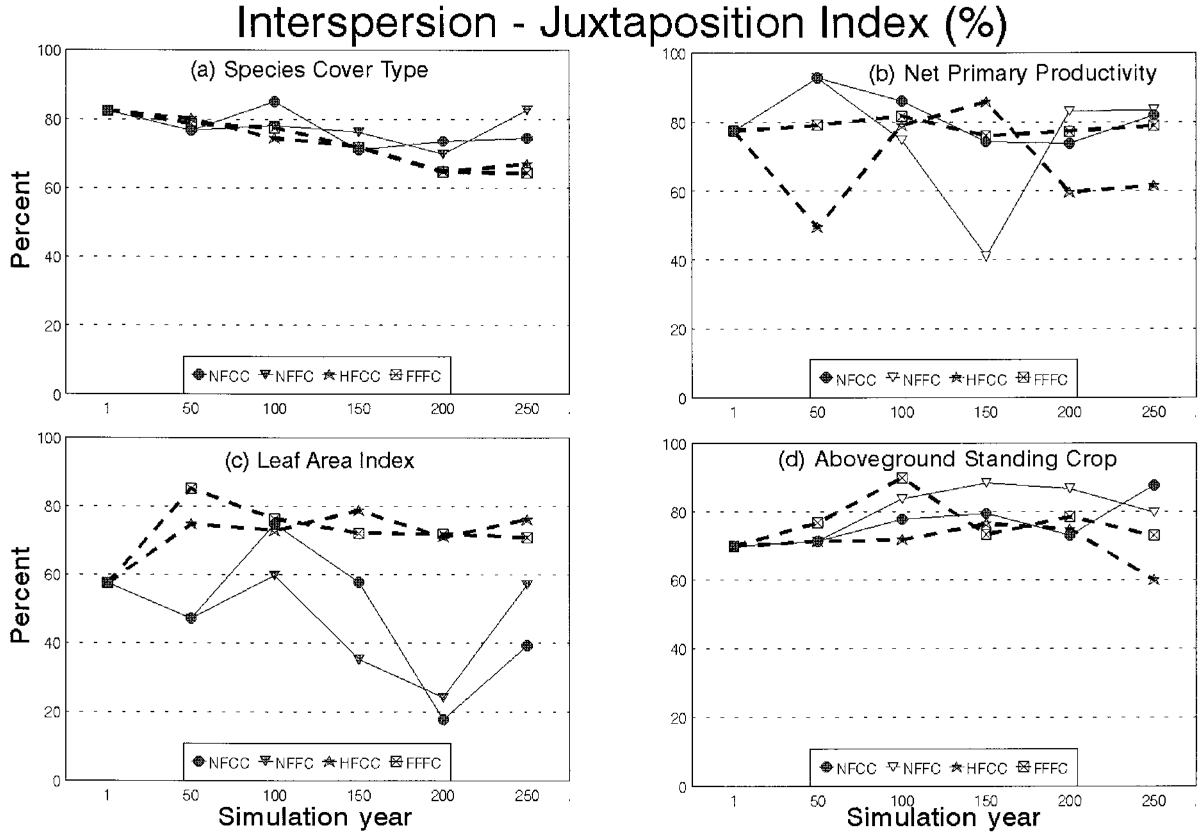

Figure 7. Contagion trends over 250 years of simulation contrasted across the four simulation scenarios by the spatial data layers of (a) species cover type (COV), (b) net primary productivity (NPP), (c) leaf area index (LAI), and (d) aboveground standing crop (ASC). Dashed lines indicate fire scenarios HFCC (Historic Fire, Current Climate) and FFFC (Future Fire, Future Climate), and solid lines are no-fire scenarios NFCC (No Fires, Current Climate) and NFFC (No Fires, Future Climate).

creases in fire frequency which also agrees with this study.

Comparisons of continuous data layers such as ASC, LAI and NPP with categorical data layers are difficult with these landscape metrics. Five classes for the continuous layers best represented the three maps when consistency and range of data were considered, even though this did not match the seven categories of cover type. New metrics are needed so spatial structure of continuous data layers can be consistently compared with spatial structure of categorical maps for evaluation of landscape trend.

Model limitations

The simulation of the HFCC and FFFC scenarios required over 600 hours (25 days) of computer time on a Sun SPARC 10 workstation. At times, FARSITE simulated the spread of fire slower than the fire would have spread in real time. This intensive use of computer resources necessitated simplification of Fire-BGC input data and simulation strategy. To increase simulation speed, the initial MDSM-GNP simulation landscape was classified to only 60 stands over the 16 sites on 92 000 ha which probably does not accurately portray the diversity and structure of this complex landscape. Also because of their long run times, the FARSITE and FIRESTART programs were executed only once for each fire and their output was stored so that Fire-BGC simulation runs could be repeated as parameters were adjusted. This meant that fire ignitions couldn't be linked with changes in vegetation and FARSITE could not use the same weather year as Fire- BGC. It was also obvious from the simulation results that 250 years was not long enough to adequately describe fire and landscape dynamics in the MDSM-GNP study area. Ideally, the model should have simulated several fire rotations (600 to 1000 years) to obtain more comprehensive changes

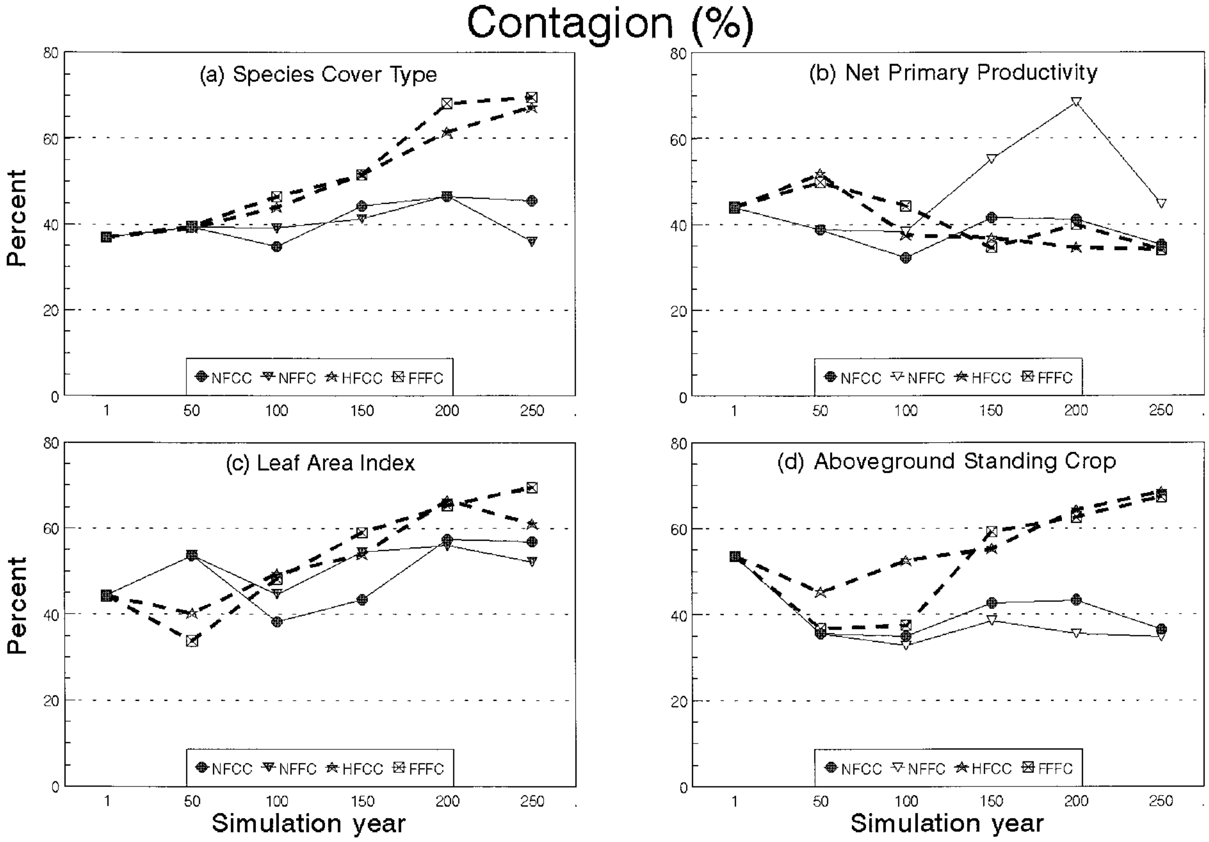

Figure 8. Interspersion-Juxtaposition Index (IJI) trends over 250 years of simulation contrasted across the four simulation scenarios by the spatial data layers of (a) species cover type (COV), (b) net primary productivity (NPP), (c) leaf area index (LAI), and (d) aboveground standing crop (ASC). Dashed lines indicate fire scenarios HFCC (Historic Fire, Current Climate) and FFFC (Future Fire, Future Climate), and solid lines are no-fire scenarios NFCC (No Fires, Current Climate) and NFFC (No Fires, Future Climate).

in landscape pattern. Differences in NPP, COV, LAI, and ASC across scenarios probably would have been more dramatic if simulation periods were longer based on the trends over the last 100 years of simulation in this effort. Unfortunately, the time required to simulate multiple 1000 years on the current computer system would have probably been in excess of three to five months for each scenario. These millennia simulation intervals will be possible as computer speeds increase and data storage media improve.

Because of the stochastic properties of Fire-BGC, we would have liked to simulate multiple runs of all scenarios so that we could quantify the variation associated with each point in Figures 4 to 8, but we did not have the computer resources or time to perform this task. However, we did execute Fire-BGC 10 times each for the NFCC and HFCC scenarios to quantify variability for only the LAI output maps. The NFCC scenario was used to evaluate stand-level stochasticity because polygon boundaries were static due to the absence of fire. The HFCC scenario simulated 15 fires with random starts across the 250 years using FARSITE.

We found stochastic processes simulated at the stand level by the NFCC scenario, such as tree regeneration and cone crop abundance, resulted in very little variation (1–3%) in landscape metrics computations across any simulation year. This variation was greatest at the end of the simulation period. However, landscape-level fire growth processes in the IHFCC scenario caused a wide variation of landscape metrics across simulation runs (Figure 9a–d). By the end of the simulation period, the standard deviation was largest in the MSEI index (0.159 or 35% of the mean, Figure 9c) and smallest for contagion (8.755 or 15% of the mean, Figure 9d). The upward trend in contagion was generated for every simulation run in the HFCC scenario. These variations are not as large as those

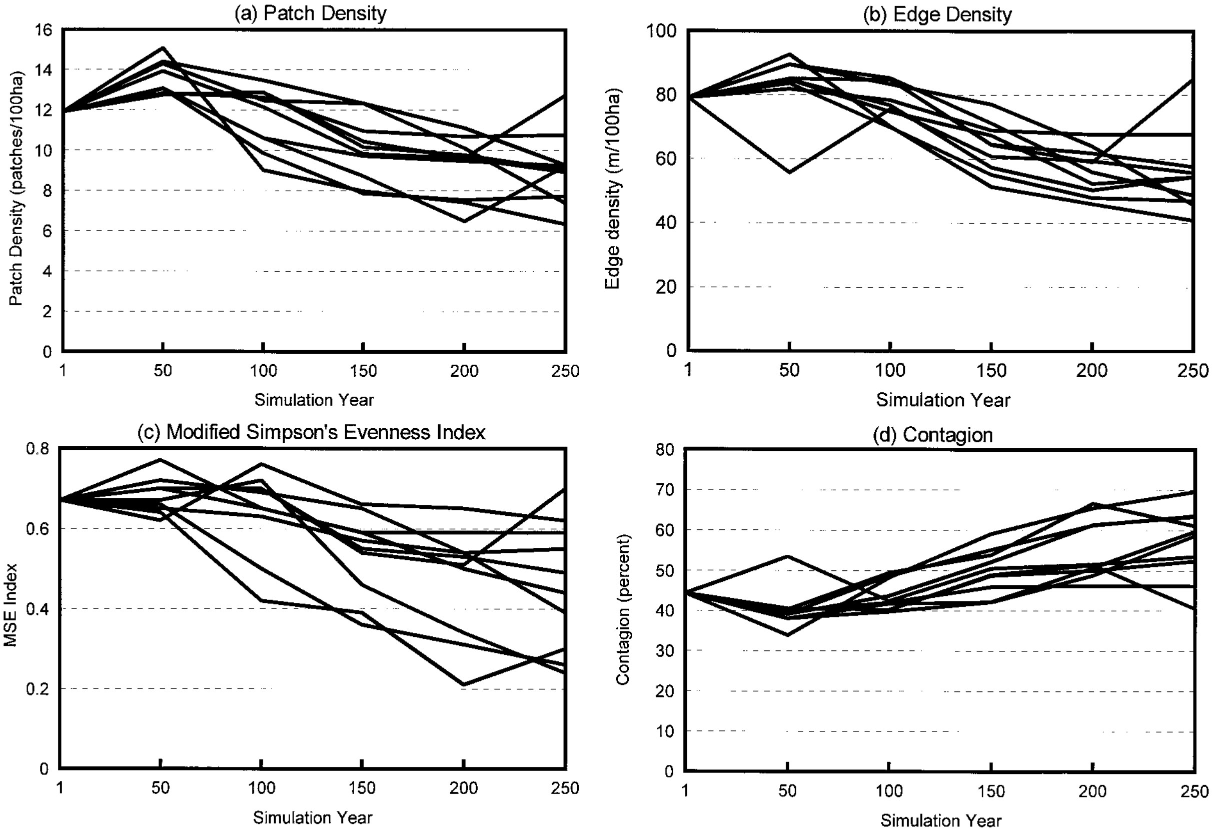

Figure 9. Computed landscape metrics for 10 executions of the HFCC scenario for the LAI spatial data layer. (a) Patch density (patches/100 ha), (b) Edge density (m/100 ha), (c) Modified Simpson's Evenness Index (MSEI), and (d) Contagion (percent).

simulated by Baker (1992, 1995) probably because of the mechanistic simulation of fire spread using FARSITE. These results show the influence of the highly stochastic nature of fire ignition on landscape patch dynamics.

Fire-BGC input data sources have many limitations. All simulations used general weather and fire regime information, some of which were taken from sources outside the study area that may not be representative of Glacier National Park. Daily weather files for both future and present climates consisted of only a 44 year record (18% of the 250 year simulation period) which obviously does not encompass the entire range of climatic variability contained in the fire regime input data. The use of current weather data to represent historical fire regimes may be inappropriate but the only source of data we had available. Extrapolations of daily weather from base stations to simulation sites using the MTCLIM program do not accurately predict fine-scale micrometerological phenomenon like frost pockets or warm-air drainages that directly influence vegetation patterns (Habeck 1968, 1970; Hungerford et al. 1989). Inadequate initialization of some tree, stand and site parameters in Fire-BGC often created discordant states within the model. Many initial conditions, such as available nitrogen and soil carbon, are difficult and expensive to measure in the field so they must be estimated from other sources of data. This resulted in some initial simulation stand conditions that were in direct disagreement with other site and landscape conditions. For example, it was difficult to match the amount of available nitrogen in the stand to current stand conditions because it was not directly measured in the field. As a result, the model required a number of years before available nitrogen pools corresponded with simulated stand conditions. It probably would have been more appropriate to summarize results for only the last 100 years of simulation because of some suspect initial conditions, but then results would have been less robust because they would have only encompassed a fraction of the MDSM-GNP fire rotation.

Conclusions

Fire-BGC is a useful tool for investigating landscape pattern dynamics under changing climate and fire regimes. Fire-BGC simulations provide the level of detail needed to understand and interpret differences in predicted future landscapes because its mechanistic design integrates ecophysiological processes of tree growth, regeneration and mortality with the processes of fire, weather, and forest floor dynamics.

Simulation results show wildfire will continue to play a major role in the development of landscapes in Glacier National Park even as our climate changes. Both fire and climate are important to landscape dynamics but it is their interaction that will dictate future landscape structures and influence subsequent management strategies. Our results support Ryan's (1991) contention that landscape dynamics under changing climates are likely to be mediated by disturbance, such as fire. Judging from simulation results in this study, future landscapes may be more diverse and patchy if fires are allowed to burn, and these fires will tend to be larger and more intense. Prescribed fire could be an important tool for controlling the intensity, severity, timing and smoke emissions for future fires.

The inclusion of process-based variables like NPP in evaluations of landscape change will help us understand the causal mechanisms that form landscapes and influence species distribution and composition. The use of surrogate variables for NPP are useful when maps of ecosystem process are difficult to produce or validate using field data, but these surrogates are usually are better correlated with species cover type.

Results of this simulation study represent only one execution of Fire-BGC for each scenario that describes only one landscape trajectory of the thousands that could possibly occur. Until we have adequate computer resources for executing Fire-BGC many times to quantify variation, results should be interpreted in this context. However, multiple runs of one fire scenarios show that, although the variation between simulation runs is sometimes large, the trends in landscape metrics over time rarely changes across nearly every run.

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