

**NEW FIRE SCIENCE INITIATIVE: ARTICULATING THE STRATEGIC ROLE
OF LARGE HERBIVORE GRAZING ON SUCCESSION, FUELS, AND FIRE
DYNAMICS IN A NEW CHANGING CLIMATE**

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ABSTRACT

A simulator was developed to enable prediction of grazing effects on fuels, fire, and vegetation dynamics. The new simulator, *GrazeBGC*, was developed on the proven *FireBGCv2* modeling platform, adding five functions to the platform: 1) static definition of forage biomass demands by multiple herbivore populations; 2) dynamic spatial displacement of wild herbivore forage demands by domestic livestock; 3) dynamic spatial allocation of each herbivore population's forage demands among stands of vegetation across the landscape; 4) stand-level, selective cropping of herb and shrub fuel guilds by herbivores and adjustment of residual fuel loads; and 5) spatially-explicit modification of succession, stand structure, and fuel loads by herbivores over time. With those functions in place, the new simulator predicts effects of user-defined grazing scenarios on succession, fuel, and fire dynamics. The model was applied to a mid-scale sub-watershed (22,000-acre Middle Meadow Creek in northeastern Oregon) in a simulation experiment consisting of 600, 400-year simulations (see next paragraph). Thus far, the project has resulted in 4 public presentations, and one manuscript.

Total project duration was three years (including a 12-month extension). The simulator took most of 2.5 years to formulate, debug, initialize and calibrate. Six more months were required to complete the simulation experiment and summarize its results. The experiment evaluated effects of five different herbivore population levels that were defined by various combinations of cattle, elk, and mule deer. Effects of those five herbivory regimes were compared in a primary experiment under three projections for future climate ("historical" versus "Hadley A2" and "B2" warming scenarios) and under two scenarios for fire suppression ("let burn" versus "95% suppression effectiveness") without any fuels treatment. Those scenarios were crossed with one another and replicated 10 times in a series of 300, 400-yr simulations. A second series of simulations (another 300 simulations) added pro-active fuels treatment as an additional 2-level factor ("none" versus a standardized "fuel reduction" strategy). The experimental design evaluated three types of responses including stand-level structure and fuel-loading (Type I), stand-level fire behavior and effects (Type II); and landscape productivity and fire regime (Type III).

The project's literature review motivated several *a priori* expectations for experimental results: 1) any effects of grazing should increase with the aggregate forage demands of herbivore populations and/or with climate warming; 2) stand-level structure and fuel responses should be sensitive to grazing effects; but 3) fire behavior and landscape responses should be somewhat less sensitive.

BACKGROUND AND PURPOSE

Background: There is a need to incorporate herbivory processes into the logic of landscape fire succession models.

Patterns of vegetation in landscapes reflect interactions between biophysical environments, disturbance regimes, and succession, and herbivory is usually among the

disturbance agents involved. Herbivory (i.e., grazing or browsing) by large herbivores is selective and both spatially and temporally variable, and it influences the pattern of biomass accumulation and the successional pathways in any landscape. In the process, herbivores can influence the progress of any other disturbance process that is mediated by biomass, such as landscape fire. In this interactive context, large herbivores exert contingent influences on how other disturbance agents like fire function in ecosystems.

That logic has become generally accepted in ecosystem science, if not always demonstrated convincingly. Some authors have even argued that large herbivores, despite their relative subtlety, are nevertheless more significant than episodic agents as drivers of forest vegetations. Nevertheless, a quantitative and spatially-explicit understanding of herbivory's significance has remained elusive. A principal difficulty involves modeling interactions through which persistent herbivory regimes might predispose those of other agents, such as landscape fire or silviculture, over extended periods of time. This difficulty compromises our understanding of "how ecosystems work", and it is particularly relevant to ferreting out how much (or if) large herbivore grazing regimes can influence the resilience of forested landscapes under climate stress.

Furthermore, in most landscapes any interactions between herbivory and episodic disturbance regimes can be quite complicated, not merely because herbivores interact with other agents, but also because the herbivory regime is itself multi-faceted. In the western United States, landscapes are typically inhabited by several large herbivore species, each having its own rather unique population dynamics, grazing ecology, and density-dependent influences on vegetation. In theory, effects of different herbivore populations on vegetations may be additive or compensatory, depending on the herbivore species involved and their densities.

Landscape fire succession models (LFSMs) have begun to offer spatially-explicit capabilities for analyzing multi-agent disturbance, including climate, but even these models have remained largely insensitive to the apparent influences of large herbivores. Our purpose is to develop an "herbivore utility" for *FireBGCv2* (Keane et al. 1996, Keane et al. In prep), which is perhaps the dominant process-based LFSM in the western United States. The utility enables *FireBGCv2* to analyze herbivore influences on biomass dynamics at stand or community scale, and to propagate those influences to fire regimes and vegetation mosaics at landscape scale. We illustrate the model in a 400-yr simulation experiment conducted in a typical Inland Northwest grass-tree mosaic (the 22,000 acre Middle Meadow Creek hydrologic unit) in the Upper Grande Ronde River Basin, northeastern Oregon. The experiment explores the extent to which modification of large ungulate populations could condition community structure, stand-level fuel dynamics, fire behavior, and regime characteristics given different scenarios for climate warming, fire suppression effectiveness, and silviculture.

Purpose: Integrate spatially-explicit herbivory processes into the *FireBGCv2* framework

FireBGCv2 is a mechanistic succession model that simulates ecosystem processes across a spatial domain and at multiple scales. It is a second revision of its precursor, *Fire-BGC* (Keane et al. 1996, Keane et al. 1997, Keane et al. 1999), that merged a

process-based, gap-replacement model (FIRESUM; Keane et al. 1989) with a mechanistic biogeochemical model (FOREST-BGC; Running and Coughlan 1988, Running and Gower 1991). FireBGCv2 already contains several utilities for implementing phenology, climate change, episodic fire, and silviculture (Keane et al. In prep.). Within these utilities are redundant modules for implementing different processes such as fire spread, seed dispersal, and succession. The model provides for user-defined queries to periodically evaluate disturbance and vegetation at landscape scale (Keane et al. 1996, Keane et al. in prep).

Therefore, *GrazeBGC* adds several functions to the *FireBGCv2* platform. These include: 1) Non-spatial definition of herbivore biomass demands; 2) Spatial allocation of those demands among stands of vegetation; 3) non-spatial allocation of demand among plant guilds within each stand; 4) herbivore-mediated redistribution and cycling of plant-bound nutrients; and 5) herbivore-induced succession. The purpose of *GrazeBGC* is to enable an analyst to contrast effects of different herbivory regimes by changing the inputs that define those functions, and thereby to simulate their influences on succession, fuel dynamics, and fire behavior across several scales in a landscape. The project's simulation experiment illustrated the model's capabilities by contrasting 5 herbivory regimes under each of 3 different climate-warming scenarios, 2 scenarios for fire suppress effectiveness, and 2 different scenarios for silvicultural fuels management.

STUDY LOCATION AND DESCRIPTION

We illustrate the model in the Middle Meadow Creek (MMC) sub-watershed, a mid-scale hydrological unit in the Upper Grande Ronde River basin of northeastern Oregon, USA. The MMC lies largely within the Starkey Experimental Forest and Range (SEFR) and is of roughly equivalent area (MMC ~ 90 km², SEFR ~ 101 km²). The simulation landscape consisted of a "context" area defined by the entire MMC (9,013 ha) and a surrounding "buffer" extending 1-km beyond the context's periphery on each cardinal direction (an additional 12,187 ha). Processes were simulated over the entire 22,200 hectares, but we limited analysis to the context area.

The MMC landscape is in the maritime-influenced, eastern Blue Mountains ecological province. Climate is severe mid-latitude with Continental and Mediterranean influences (CEC 1997). Maritime weather systems deliver roughly two-thirds of annual precipitation from mid-September through March and most of the remainder in April, May, and early June. Summers, however are typically droughty. From 1966 through 2009, total annual precipitation ranged between 40 cm and 105 cm, the annual maximum temperature between 31° and 39° C, and the annual minimum temperature between -29° and -13° C. Evidence of short-term climate change is not apparent in the MMC's weather station record (which is only about 20 years long), but broader-scale model projections indicate that the ecological province's temperature regime has increased about 1.6° to 2.4° C over the course of the twentieth century. Snow melt is usually complete by May 1 and the growing season is roughly 120 days.

The study area's elevation ranges from 1,067 to 1,524 m, in a mid-elevation mountain range (Blue Mountains) which consists of Miocene (Columbia Basin) basalts overlain with later Pliocene and Pleistocene ash deposits (e.g., Mount Mazama). Over time, the mountain range's ash mantles eroded from extreme topographies and south

slopes, and there Argixerolls (prairie soils) developed in thin loess over the degraded parent material. Ash persisted on gentler terrain, and there Vitrandepts (forest soils) developed from the ash. Aquic alluvials (riparian soils) occur along narrow stream courses. Maximum depths to the root-restrictive layer are typically < 48 cm in Argixerolls, up to 150 cm in Vintrandepts, and as much as 190 cm in Aquics.

Biophysical Sites

This landscape's site-specific vegetation potentials are strongly influenced by soil depth, which limits each site's ability to capture and hold moisture and its ability to support plant growth as the typical summer drought progresses. We defined five biophysical sites (Appendix II), which we synthesized from an operationally mapped vegetation hierarchy, mapped Landfire Environmental Site Potentials, and mapped soil types. The mapped hierarchy was the primary reference, consisting of 21 plant associations which we grouped into 5 closely-related association aggregates: (1) Hot Dry Upland Shrubland, (2) Hot Dry Upland Herbland, (3) Hot Upland Forest, (4) Mixed-conifer Upland Forest, and (5) Riparian Forest. Landfire analogues were used as a secondary reference to fill in areas which had not been mapped from the primary reference. Soil maps were used to establish profile depths and composition for each aggregate. Fire return intervals (number of years between fires) were established from published literature.

Shrubland and herbland aggregates both occur on Argixerolls that do not retain moisture sufficient to support trees through summer drought. The shrubland is defined by the shallowest of those soils, and its vegetation is typified by an association of stiff sagebrush (*Artemisia rigida*) and Sandberg's bluegrass (*Poa sandbergii*). This site is least productive of the five, and it has long fire-return intervals.

Somewhat deeper Argixerolls support the dry herbland. It consists of Palouse prairie variants typically dominated by bunchgrasses including Idaho fescue (*Festuca idahoensis*) and bluebunch wheatgrass (*Pseudoregnaria spicata*). Sandberg's bluegrass is also common, and the introduced annual North Africa grass (*Ventenata dubia*) and the annual forb *Grindelia* (e.g., *Grindelia nana*) may occur as naturalized co-dominants as well. Shrubs are usually unproductive and inconspicuous. Fire-return intervals are typically similar to those in adjacent dry upland forests which are similar in terms of their understory composition.

The dry upland forest occurs on somewhat deeper soils (30 to 83 cm to root-restrictive layer), which often contain some ash. Vegetation is typically considered savanna-like, with sparse, fire-adapted ponderosa pine dominating over an undergrowth of dry herbland species. We mapped this biophysical site to include all juniper and ponderosa pine associations in the Hot Upland Forest and Hot Woodland plant association groups as described by and their respective Landfire analogues. Pre-1900 Fire-return intervals averaged about 6 years on such sites, but within a broad range of 1 and 70 years, with the upper extreme approximating current conditions under aggressive fire control.

Upland mixed-conifer sites are defined by ashy silt loams, which typically exceed 64 cm to their root-restrictive layers (up to 107 cm in this study area). These sites support mixed-conifer associations in the grand fir (*Abies grandis*) and Douglas fir (*Pseudotsuga menziesii*) series. We mapped this biophysical site as the aggregate of all warm, cool, and cold association groups in those two series. Historically, variable- and mixed-

severity fire regimes inter-graded on such sites, with return intervals ranging between 35 and 200 years across the greater ecological province. However this particular landscape's return interval probably was comparatively short within that range (average 37, range 20-67). The forest overstory is typically a multiple-age stratification of grand fir, Douglas fir, western larch (*Larix occidentalis*), lodgepole pine (*Pinus contorta*) and ponderosa pine in various combinations. Undergrowth can be dominated by either shrubs or herbs, depending on fire, herbivory, and silviculture regimes as well as seed source.

None of the upland soil classifications that are typical of the MMC have a water saturation zone above 183 cm in profile, and thus all those soils may dry to their root-restrictive layer each summer in the MMC. In contrast, riparian forests occur on aquatic soils that may remain saturated at depth. However riparian sites occur along narrow stream margins and thus typically have moderate fire regimes and return intervals that are similar to those of their adjacent uplands. Dominant tree species are cottonwood (*Populus balsamifera trichocarpa*), Douglas fir, and grand fir. Twentieth-century anthropogenic disturbance (i.e., logging, livestock grazing, mechanical scarification) reset succession on most riparian sites to herb- or shrub-dominated communities, but their current compositions are nevertheless presumed seral to forest.

Overstory and understory calibration

We calibrated forest overstory on growth (site index) and stocking limits on closely-related aggregates: Hot Upland forest was calibrated on average ponderosa pine/bunchgrass sites (*Pinus ponderosa/Pseudoregnaria spicata*, *P. ponderosa/Festuca idahoensis*); mixed-conifer forest on average grand fir sites (*Abies grandis/Linnaea borealis*, *A. grandis/Vaccinium membranaceum*); and riparian forest on maximally productive grand fir sites (*A. grandis/V. membranaceum*). Ecophysiology for individual tree species was defaulted from earlier versions of *FireBGCv2* but with each species' morphological limits (maximum height, girth, age, etc.) and site-specific growth potential calibrated from online databases and regional literature. Each site's maximum biological potential for tree stocking (i.e., maximum basal area) was calibrated by compounding basal area at "full stocking" by a factor of 1.25. Maximum seedling establishment rates were limited to maximum seedling densities at a stand quadratic mean diameter (QMD) of 2.54 cm, given upper-management-zone and uneven-age density index assumptions.

Undergrowth plant models were calibrated for the 16-guild structure described in Table 1. State variables most relevant to herbivory in those plant models include the number of guilds, their respective guild-specific growth constants (η), maximum heights (ht), and maximum attainable biomass (bio_max) (Table 3). For consistency we defaulted guild growth constants from earlier applications of *FireBGCv2* unless empirical evidence suggested otherwise. Height maxima were defined from an on-line plants database. Guild-specific biomass maxima were not available in published literature, and so we used unpublished data to synthesize guild-specific estimates for that parameter

We synthesized biomass potential for guilds in the shrublands from fuel loads reported for structurally comparable sagebrush-grass types in the digital photo series. The maximum biomass loading for *A. Rigida* in the MMC was set to 510 kg/ha (~17% live growth and ~83% dead), herbs to 420 kg/ha of which graminoids accounted for 170 kg/ha (~40%) and forbs 250 kg/ha (~60%). Thus the maximum total biomass load for dry shrublands was 930 kg/ha. All shrub biomass was attributed to *A. rigida* (SIES

guild). Herb biomass was partitioned among the eight herb guilds in proportion to their canopy coverages reported in true *A. rigida* associations.

Published biomass estimates were also lacking for the study area's dry herblands, but two previous studies had estimated current year productivity (*CYP*) of individual plant species in nearby analogues. We ordered those plant species and aggregated their *CYP* estimates according to guild membership, and then projected each guild's maximum biomass load from its CYP_{max} in the data set. Maximum biomass loads for shrub guilds were projected from their respective CYP_{max} assuming a common growth constant (η) of 1.14.¹ Maximum biomass loads for herb guilds were projected equal to CYP_{max} , thereby assuming no year-to-year carry-over in the standing biomass from the previous year. The maximum loading for all guilds in aggregate was 3,640 kg/ha (3.9x that attainable on the shrubland site), with aggregate CYP_{max} limited to 1,545 kg/ha (3.4x that of shrubland).

To project maximum biomass on dry upland forest sites we plotted aggregate *CYP* (all species, y) against stand overstory density (canopy cover of trees, x) in the analogue sample of ponderosa pine sites. Plotted *CYP* values were then grouped according to 10% overstory increments, and the greatest *CYP* value in each increment was selected to represent an incremental maximum. Then, *CYP* values in the selected subsample were regressed on overstory canopy coverage to project maximal *CYP* as a function of canopy cover: $CYP = 1917.058 - 18.583x$; $p = 0.009$, $r^2 = 0.656$, $n = 8$. From that regression's y-intercept we inferred CYP_{max} for all guilds in aggregate: $CYP_{max} = 1917$ kg/ha at 0% overstory canopy cover (roughly 1.2x that of the herbland and 4.3x that of the shrubland). Maximum biomass loads were then projected for the various guilds from CYP_{max} using the same procedures described above for dry herblands. The maximum biomass for all plant guilds in aggregate was set to 3,310 kg/ha (91% of herbland, and 3.6x of shrubland). Notably, the dry forest site projection was somewhat lower than that for dry herbland, probably because of non-random error in the empirical data available that was available. We nevertheless used the calculated projections.

Using the same procedures described above for dry upland forest, we projected biomass maxima in moist upland forest to be 12,490 kg/ha (roughly 3.8x that of dry forest), with CYP_{max} of 2,654 kg/ha (i.e., 1.4x, 1.7x, and 5.9x that of dry forest, herbland, and shrubland, respectively). By adjusting the maximum biomass recorded in their 27th year to the maximum canopy cover recorded over the entire time stream², and then partitioning the adjusted biomass among plant guilds in proportion to their CYP_{max} in the analogous clip-plot samples, the result for the aggregate biomass maxima would be somewhat lower (10,783) with life-form maxima temporally distributed between 10 and 20 years: 9600 kg/ha for shrubs in year 20; 858 kg/ha for graminoids in year 10; and 1095 kg/ha for forbs in year 10. Biomass maxima for minor guilds (those which did not appear in clip-plot samples but were nevertheless represented in canopy data) were arbitrarily set to the minimum among the other guilds.

¹ Given that: $CYP_{max} = (B_{t-1} \cdot \eta) - B_{t-1} = B_{t-1}(\eta - 1)$, and $B_t = B_{t-1} + CYP_{max}$, then $B_{t-1} = CYP_{max}/(\eta - 1)$, and $bio_max = B_{t-1} + CYP_{max}$. For example, if $CYP_{max} = 14$ kg and $\eta = 1.14$, then $bio_max = 14/.14 + 14 = 114$ kg.

²For example, the maximum shrub biomass recorded in that study was estimated inside an herbivore enclosure in year 27, but that same enclosure's canopy-cover chronology indicated that its shrub canopy had actually peaked 7 years earlier (in year 20); therefore, we adjusted the shrub bio_max upward in proportion to the difference in canopy cover between the 20th and 27th year.

We partitioned the recorded maximum biomass in those two life forms among their respective, nested guilds, in proportion to CYP_{max} recorded in the most productive clip-plot analogues to project a maximum aggregate biomass loading of 11,300 kg/ha. Then, after arbitrarily setting maxima for minor guilds equal to the minimum among other guilds, the resulting aggregate bio_max was 13,090 kg/ha, with CYP_{max} equal to 2,806 kg/ha (the highest productivity reported among analogue stands at 0% overstory canopy cover).

Landscape fire regime

We calibrated the landscape fire regime (landscape fire rotation and return interval) to the current climate as reflected in the previous 44-yr weather record, and to mimic historical regimes from a documented composite of historical fire frequencies and fire sizes. For dry and moist upland forests those variables were calibrated on averages reported from closely-related analogue sites. For the riparian site and non-forests, return intervals were calibrated from literature and the study landscape's own records (fire starts and fire sizes for the period 1964-2007). Ignition and perimeter maps for the study landscape were sourced from Forest Service GIS (<http://www.fs.us/r6/data-library/gis/umatilla/index.shtml>. Accessed February 26, 2009).

Herbivore biomass demands

We spatially allocated herbivore biomass demands using the nutritional-threshold-based approach described previously. For cattle and elk, each stand's nutritional biomass (β in equation 21) was calculated daily during simulation as the sum of its guild-specific products of net current annual undergrowth (i.e., $NETGROWTH_i$) and the respective guild-specific dry matter digestibilities (DMD). For mule deer, β was defined as the product of net leaf accumulation and DMD , assuming 50:50 leaf:stem ratio (i.e., $\beta = ((NETGROWTH_i \cdot 0.50) * DMD)$). $NETGROWTH_i$ was read directly from the simulator's intermediate output (i.e., daily), and the various guild-specific DMD values were input in six seasonal vectors that were defined on Julian dates spanning the annual presence of herbivores on the landscape: Spring (03/16-06/15: JD75-166); Early Summer (06/16-07/15: JD167-196); Middle Summer (07/16-08/15: JD197-227); Late Summer (08/16-09/15: JD228-258); Early Autumn (09/16-10/15: JD259-288); and Late Autumn (10/16-12/31: JD289-365). All herbivores were assumed absent during the intervening winter months (January 1 through March 15 inclusive) because the landscape is a summer range.

Seasonal digestibility vectors (DMD) for cattle and elk were calibrated on laboratory assays of current year's growth. Initial estimates used in model development were based on *in vitro* digestion using cattle inocula, but ultimately those estimates were re-calibrated for the simulation experiment using species-specific fiber fractionations. Coefficients for evergreen shrub guilds were conditioned *a priori* to reduce the relevance of evergreen growth biomass to spatial allocation. Evergreens typically contain secondary metabolites, which variously include phenolic alkaloids (*Mahonia repens*, STES; *Ceanothus velutinus*, SIET), monoterpenoids (*Artemisia rigida* SIES; *Juniperus sp.* STET), and/or benzenoids (*Linnaea borealis*; STES). These metabolites are not well reflected in either *in vitro* or in fiber assays, yet collectively these compounds tend to render foliage unpalatable in comparison to plant tissues that do not contain them. Monoterpenoids in particular depress dietary intake when consumed *in vivo* despite having relatively high digestibility *in vitro* and thus digestibility coefficients, when used alone, will over-estimate the relevance of evergreen growth biomass. In lieu of any clear

understanding of metabolite concentrations or their quantitative influence in our particular study area, we arbitrarily conditioned the *DMD* of evergreen shrub guilds by 90% (i.e., $DMD \times (1 - 0.90)$).

For mule deer, we discounted net leaf growth (i.e., $NETGROWTH_i \times 0.50$) on *DMD* coefficients in literature: evergreen shrubs (0.55); immature deciduous shrubs (0.73); mature deciduous shrubs (0.47); immature graminoids (0.91); mature graminoids (0.47); immature forbs (0.70); and mature forbs (0.40). On dry upland sites (shrubland, grassland, and dry upland forest), we arbitrarily defined herbs (graminoids and forbs) to be immature prior to June 16 (approximate summer solstice) and mature thereafter, and deciduous shrub growth to be immature prior to August 16 (approximate date of earliest winter-hardening of twig tissues) and as mature thereafter. On moist upland and riparian forest sites, those maturity dates were retarded 1 month, to July 16 and September 16, respectively. For deer, evergreen shrub coefficients were held constant throughout simulation on all sites.

Elk and deer precede cattle onto this landscape each spring and remain there longer each autumn. We implemented fixed-rate spatial displacement (equations, 8, 11, 12) to displace elk away from cattle when both species were present. Deer were not displaced from either cattle or elk.

Within-stand dietary demands were based on herbivore-specific dietary preferences (equations 33-36) and initialized in seasonal vectors defined on the same Julian dates used to condition nutritional adequacy.

We limited our implementation of herbivore-induced succession to the model's inherent retardation of growth (equation 29) without modifying intrinsic growth constants (as in equations 37-38). Nutrient cycling was addressed nominally as described previously (see 2.1.2.2.4.)

Landscape Initialization

The landscape contained 2,831 stands of vegetation (34 shrublands, 1,024 herblands, 73 dry forests, 1,696 moist upland forests, and 4 riparian forests). However, despite the fact that much of the landscape existed within an experimental research forest, none of these stands had a record of stand-based inventory. To circumvent this problem we initialized forest overstory using the Forest Vegetation Simulator and Most Similar Neighbor processes in the U.S. Forest Service's Integrated Forest Management System (INFORMS). This process used satellite imagery and a GIS to locate spectral-analogue stands for which plot-based tree lists had been recorded on surrounding national forests as part of their operational forest inventories ($N = 1,936$). Those tree lists were grown in the FVS to a common base year (2010). Then their resulting output lists were imputed to their most-similar-neighbor stands in the simulation landscape. This provided every forest stand's simulation plot with an estimated tree list, but the MSN process can result in erroneous lists (i.e., attributable to non-random error) when the most similar neighbors actually represent site potentials that differ from those of stands to which the lists are imputed. Sixteen of the imputed tree lists for dry upland forest stands (22%) were obviously erroneous because their lists contained grand fir, western larch and/or lodgepole pine; each of those species is uncharacteristic for the that particular biophysical site, which is too dry to support them. So, we reassigned those particular stands to the site of their nearest neighbor for which their species lists were appropriate.

Undergrowth biomass was initialized for shrubland guilds at each guild's biological maximum multiplied by a factor of 0.33 (i.e., to 551.66 kg/ha for all guilds in aggregate). Dry herbland biomass loads were initialized by scaling their projected bio_{max} (established from CYP_{max}) to reported average CYP values (i.e., to 773.7 kg/ha, or roughly their biological maximum times 0.326457). Dry forest undergrowth guilds were initialized in the same way, and without respect to the density of forest overstory. Thus, stands in each of those three biophysical sites contained redundant biomass loads, and so to enhance simulation efficiency we delineated stand groups that shared unique combinations of elevation class (1300-1400; 1400-1500), slope class (0-20%; >20%) and aspect class (45°-135°; >135°-225°; >225° – 315°; >315°-45°). When initializing moist upland and riparian understory, however, the suppressive effect of each stand's imputed overstory canopy was accounted for by interpolating guild-specific CYP from the relationship between each guild's CYP_{max} (i.e., y-intercept at 0% overstory) and the guild's CYP_{min} (i.e., 0.0 kg/m² at 100% canopy).

The SEFR is located on typical, mid-elevation summer range, and its herbivore populations have been managed to approximate those across the surrounding landscape. Livestock have been managed in a grazing system that includes the MMC as well as the SEFR, and so we initialized the livestock population from both SEFR and non-SEFR pastures in the MMC. Elk and deer populations are sequestered within the SEFR by a 2.4-m high perimeter fence (since 1989), and we initialized those populations from SEFR records, which we then extrapolated to the rest of the MMC simulation landscape on an equivalent-density basis. Each herbivore population's biomass demand was initialized as a daily flux to mimic seasonal migrations on and off the summer range landscape and to account for both seasonal growth and mortality of individuals in each population. Annual biomass demands were scaled to each herbivore population's average demography for the year, and the daily flux calculated by applying mass-specific demands to daily demography.

Simulation Design and Analysis

We designed a multi-factor simulation experiment with repeated measures. Main factors were herbivory with five regimes ($H = 5$), climate ($C = 3$) and fire-suppression ($F = 2$). Main factors were crossed with one another (i.e., $5 \times 3 \times 2 = 30$ factor combinations), and each combination was simulated in 10, 400-year simulations to produce a total of 300 runs ($N_{sim} = 300$). We analyzed simulation outputs in SAS v9.3 using generalized linear mixed-model procedures (GLIMMIX procedure). We extracted output data for analysis on an even 25-year interval to preclude temporal autocorrelation, and with respect to the direction of the livestock grazing rotation, so that every 25-year interval yielded an even-year and an odd-year result.

Main-factor regimes were formulated principally to provide insight to the model's sensitivity to herbivory. The five herbivory regimes imposed different biomass demands based on differences in each population's number of animals. Regime H1 set all herbivore demands to zero to simulate an herbivore-free landscape and to mimic results that could be expected from comparable *FireBGCv2* simulations (which do not account for herbivory). Regime H2 set elk and deer demands to reflect recent population sizes, while setting livestock demands to zero to simulate removal of domestic livestock from the landscape. Regime H3 reversed H2, setting wild herbivore demands to zero and livestock demands to reflect recent levels, and thereby simulating extirpation of the

landscape's native ungulates. Regime H4 set both wild and domestic demands to recent historical levels, and H5 set wild herbivore demands to recent levels while doubling livestock demands to nominally mimic densities that prevailed closer to the mid-20th century. Non-spatially-explicit biomass demands (i.e., total population demands) were held static across simulations, although each regime's spatial distribution varied depending on the other factors and their effects on plant biomass. Climate regimes included: re-iteration of a previous 44 year historical record by projection from the nearest permanent weather station using MT-CLIM; and warming scenarios based on B2 (moderate) and A2 (extreme) family assumptions. Each warming regime was ramped-up over the course of the first 100 years and then stabilized. Finally, fire suppression was dichotomized between S1 (no suppression) and S2 (90% suppression effectiveness). Suppression was implemented by random deletion of fire starts at the nominal rate. The landscape's livestock grazing rotation was accommodated in the design by tracking responses zonally (i.e., by pasture) and by the direction of the livestock grazing rotation. The directional effect was examined by contrasting responses in even-numbered years (clockwise rotation through pastures) with those of odd-numbered years (counter-clockwise rotations), and then by interaction between zone and rotation.

We evaluated responses of three general types. Type I responses reflect various aspects of stand structure and fuels at the end of each simulation year. These included stand total vegetation carbon (vegC, variable 730 in *FireBGCv2* documentation) tree basal area stocking (*ba*, v107), average tree height (*ht*, v108), average height to base of tree canopy (*hbc*, v109), number of trees (*nt*, v114), coarse woody debris (logload, v485), fine woody debris (fuelload, v486), shrub biomass (shrubB, v490), and herb biomass (herb, v491). Type II responses reflected fire behavior and its immediate effects including fire-line intensity (kW/m²), a crown fire index (*crwnI*), scorch height (m), flame height (m), dead carbon burned (deadC, kg/m²), live carbon burned (liveC, kg/m²), fuel consumption (%), tree mortality (%), soil heat (°C), and releases of fine particulate matter (PM_{2.5}, g/m²), methane (CH₄, g/m²), carbon monoxide (CO, g/m²), and carbon dioxide (CO₂, g/m²). Type III responses profiled the entire landscape's carbon-based dynamics in terms of respiration, primary production, carbon sequestration, and fire dynamic. These responses included annual fire carbon loss (*fireC*, kgC/m²), tree mortality (*mort*, kgC/m²) maintenance respiration (*mr*, kgC/m²), heterotrophic respiration (*hr*, kgC/m²), growth respiration (*gr*, kgC/m²), gross primary production (*gpp*, kgC/m²), net primary production (*npp*, kgC/m²), net ecosystem production (*nep* = *npp* - *hr*), net ecosystem exchange (*nee* = *nep* - *fireC*), stand total carbon (*totC*, kgC/m²), above-ground carbon (*abC*, kgC/m²), average fire return interval (*fri*, years), and landscape fire rotation (*fro*, years).

KEY FINDINGS

1. Overall, to what general extent are modeled ecosystem responses sensitive to large-herbivore grazing regimes?

Simulations evaluated the study landscape's responses to five static herbivore regimes: 1) no herbivores; 2) recent historic elk and deer populations, but without any cattle; 3) recent cattle density but without any elk or deer; 4) recent levels of cattle,

elk, and deer; and 5) recent levels of elk and deer plus a doubling of recent cattle numbers. This particular mix of herbivore regimes provided a spectrum of herbivore densities ranging from none at all to higher densities that approximated mid- to late-20th century populations in the study landscape.

The first three herbivory regimes produced unremarkable effects either at stand or landscape scale. Simulations implementing only recent elk and deer populations produced results similar to those implementing only recent cattle populations, and in either case (wildlife only or cattle only) results were similar to those produced by simulations that did not implement any herbivore populations at all. However, herbivore effects became evident under those regimes that mimicked historical, multi-species grazing regimes (regimes 4 and 5), which both involved all three herbivore species at mid- to late-20th century densities. Influences of multi-species grazing were modestly evident under the current climate and intensified when the climate was warmed in the A2 and B2 scenarios.

Management implications

These results suggest generally that current *FireBGCv2* simulations (i.e., without the new *GrazeBGC* functions) may adequately represent succession and fire in landscapes where expectations for herbivore populations are low and where the climate can be assumed to approximate a historical regime. However, when herbivore populations are expected to be at least moderately diverse and/or where climate warming is anticipated, implementation of the platform's grazing functions provided by *GrazeBGC* can provide useful sensitivity to herbivory processes.

2. To what extent are modeled stand structure and fuel loads responsive to grazing and browsing by large herbivores?

The simulation experiment evaluated responses of several structural variables to herbivory: (1) total vegetation carbon, (2) tree basal area stocking, (3) tree height, (4) height to base of tree canopy, (5) coarse- and (6) fine-woody debris, (7) shrub biomass and (8) herb biomass. As expected, shrub and herb biomasses were sensitive to herbivory regimes (see Table 2 in manuscript). Shrubs and herbs were reduced by multi-species grazing regimes (i.e., cattle, elk, and deer), and those reductions were particularly evident under the severe A2 climate-warming scenario. Woody fuel load dynamics were also sensitive to modification of the herbivory regime. Whereas herbivory's effects on shrub and herb biomasses were directly related to grazing, apparent influences on woody fuels were more likely an indirect effect of grazing on fire behavior which was mediated by shrub and herb biomass. Results for total vegetation carbon and tree overstory metrics were inconclusive.

Management implications

Simulation results were congruent with prior field experiments in industrial plantations and herbivore exclosures over the previous 30 years. Although herbivores consumed relatively small proportions of total annual biomass production in most stands, their grazing nevertheless retarded the accrual of understory biomass. Effects on shrub and herb biomass intensified under warming climates, probably because the ratio of herbivore dietary demand to plant production increased as climate warming stressed primary production. Nonetheless, those effects were (a) site-specific, (b) realized only under the two multi-species grazing regimes examined, and (c) were contingent upon the fire suppression regime as well.

3. To what extent is fire behavior influenced by herbivory at stand level?

The experiment evaluated 13 response variables representing various aspects of fire behavior: (1) fire-line intensity, (2) a crown fire index, (3) scorch height, (4) flame length, (5) dead carbon burned, (6) live carbon burned, (7) fuel carbon burned, (8) tree mortality, (9) soil heating, (10) particulate emissions, (11) methane emissions, (12) carbon monoxide emissions, and (13) carbon dioxide emissions. Effects of herbivory on stand biomass translated broadly into fire behavior and its effects. Results were consistent with *a priori* expectations that grazing would suppress fire behavior. But, as with structural responses, effects of grazing on fire behavior varied with both grazing and climate regimes, and were both site- and time-specific. Tree mortality was the only fire-related response that was not influenced by herbivory to a significant extent. All other fire-related responses examined were sensitive to herbivory regime at some level in the experimental design (see Table 3 in manuscript).

Fire-line intensity, scorch and flame heights were each sensitive to grazing regimes. However, those effects were (a) largely limited to the multi-species grazing regimes, (b) site-specific, and (c) time-specific. Multi-species grazing (among the scenarios we explored) imposed greater biomass demands and spread those demands across more plant guilds, and this resulted in greater suppression of understory fuels than under the wildlife-only or livestock-only regimes. Site-specificity was a straightforward function of differences in site productivity among the various biophysical sites in this landscape. Time specificity was related to secondary succession which was, in turn, influenced by herbivores over the course of the experiment. Persistent suppression of understory plant guilds throughout the course of secondary succession truncated undergrowth height and biomass accrual, and thereby suppressed fire behavior. As fire recurred and grazing persisted over the course of the 400-yr simulations, the frequency of crown fires decreased and ground fires became dominant.

The amount of dead carbon burned, particulate emissions, and gaseous emissions each responded to herbivory over time as well. Emissions were strongly dependent on the repeated measure (i.e., on year), and were sensitive to biophysical site as well, reflecting the varied biomass dynamics among biophysical sites (grassland, shrubland, forest, etc.) Furthermore, fire emissions from any particular biophysical

site were contingent upon the climate regime and the effectiveness of fire suppression ($P < 0.01$) as well. In comparison, the response of dead carbon consumption by fire was not strongly time-dependent while nevertheless being contingent upon the climate, fire suppression and biophysical site as well as on the herbivory regime ($P < 0.01$). These results probably reflect that any particular stand of vegetation's secondary succession is less important in determining the amount of dead carbon burned (when there is a fire) than is the specific fuel, climate, and suppression effectiveness at the time of a burn. However, the amount of live carbon burned and the total woody fuel consumption were each time-dependent and contingent on fire suppression effectiveness and biophysical site as well as on the herbivory regime. Thus it appears that succession dynamics did interact with other factors to influence average consumption of total and live fuels despite the apparent lack of such interaction in the regulation of dead fuels.

Fire-line intensity, scorch height, flame length, and the crown fire index each differed among biophysical sites on average. However, these responses also exhibited site-independent differences that were both time-dependent and contingent upon the climate and herbivory regime ($P < 0.01$).

All stand-level fire responses, including even tree mortality, were to some extent sensitive to the landscape's zonal characteristics and to its related livestock grazing rotation. Effects of herbivory on fire behavior were: 1) influenced by the zone in which burned stands were located, 2) sensitive to the direction of livestock rotation through zones, or 3) sensitive to interaction between zone and the direction of livestock rotation ($P < 0.05$). All non-emission responses were sensitive to either zone, rotation, or both but without an interactive effect of zone and rotation together. Emission responses were all subject to interaction between the zone and rotation.

Management implications

Managers can expect that grazing by large herbivores will influence fire behavior to substantial extents when the grazing regime is sufficiently intense to modify shrub and herb fuel loadings at the time of ignition. The longer the pre-fire time period over which grazing persists in a particular zone or pasture, and the more intense the grazing regime in that zone, the more likely that prior grazing will contribute to modulating fire behavior there. However, any influences of grazing on fire behavior and spread are likely to be negated when fuel and weather conditions facilitate ignition into overstory canopies. Much of the difference observed in this simulation was attributable to interactions between sites, their successions and fuel loads, and herbivory rather than to herbivory alone.

- 4. To what extent do stand-level effects of herbivory translate (i.e., "scale up") to differences in fire regimes at landscape scale?**

The experiment evaluated 13 variables representing various aspects of vegetation dynamics at landscape scale: (1) fire carbon loss, (2) tree mortality, (3) maintenance respiration, (4) heterotrophic respiration, (5) growth respiration, (6) gross primary production, (7) net primary production, (8) net ecosystem production, (9) net ecosystem exchange, (10) total carbon, (11) above-ground carbon, (12) fire return interval, and (13) landscape fire rotation.

Climate, fire suppression, and herbivory were each implicated in driving simulated responses at landscape scale, but the climate and fire suppression regimes dominated (in that order, see Table 4). Despite herbivory's influence on multiple Type I and Type II responses at the stand level, its over-all influence at the landscape scale was limited to the fire return interval alone, and that influence was rather-strongly time-dependent ($P_{YH} = 0.03$). In general terms increasing the herbivory regime resulted in the landscape developing longer fire return intervals over time. Differences began to emerge between the lower herbivory regimes (H1, H2, H3) and multi-species regimes (H4, H5) from 150 to 200 years in simulation, and by 400 years most herbivory regimes had developed statistically unique fire return intervals. This probably reflects that variation in stand-level conditions across the landscape at any particular time produce a range of fuel and fire responses, which nevertheless are not reflected in landscape-level fire dynamics until herbivory regimes have sufficiently modified successional trajectories. This could mean that herbivory's annual influence on fuels is less important to the development of fire and vegetation dynamics than are its long-term influences on succession and fuel bed dynamics.

Management implications

These results are congruent with speculation that late 19th and early 20th century herbivory regimes suppressed fire spread and lengthened fire return intervals, thereby contributing to high present-day fuel loading in similar ecosystems. It may be notable that the 150-yr time span required for emergence of effects on fire return (in our simulations) is approximately equal to the time elapsed from initial European settlement to the present day. Nevertheless, large herbivores consume relatively small amounts of any landscape's primary production, and are thus unlikely to affect long-term metabolic or carbon balances at landscape scale. This may not be adequately reflected in the model's current version because of its limited capability to accelerate nutrient cycling (via herbivores). However, if confirmed with further simulations (and enhanced program coding for recycling), then herbivory's implications may be perceived as more salient for managing fuels and fire behavior (operationally or strategically) but less so for strategic management of long-term carbon sequestration.

5. Does fuels management "trump" the apparent influences of herbivory on fuel and fire dynamics?

In theory, effects of herbivory on vegetation, fuels, and fire are ultimately regulated by balances (or imbalances) between herbivore biomass demands and

biomass production: The greater is the supply of forage biomass relative to herbivore demands, the less likely is a given herbivory regime to influence system dynamics. To the extent that other disturbance agents modify that supply:demand relationship, any influences that herbivores may have on fuels or fire are theoretically contingent upon the regimes of those other disturbance agents. Fuels treatment regimes stand out in this regard because such treatments, which typically involve thinning and fire, almost always will increase early-succession forage biomass while at the same time reducing woody fuels. Therefore, fuels treatment programs may be able to "trump" or over-ride herbivore effects when herbivore populations are held stable. We attempted to evaluate how an aggressive fuels reduction program might be expected to modify the various effects of herbivores we observed in the primary experiment, but that effort was inconclusive.

The secondary set of simulations included a dichotomy of fuels treatments to nominally explore this issue. Half of all simulations implemented no fuels treatment and the other half implemented an automated fuels-treatment scenario that was broadly based on US Forest Service practice. The treatment scenario was implemented with the *FireBGCv2* management utility, and it coupled selective thinning of forest overstories (thinning from below) with subsequent broadcast burning at specified fire intensity. The management utility parameterized limits on tree size and species for thinning, but it did not contain a parameter for defining a minimum re-entry interval between sequential stand thinning. The utility simulated fuels treatments automatically when thinning criteria were satisfied, but it did so without regard to the number of years which had passed since any previous fuels treatment in the same stand. The practical effect was that individual stands were sometimes re-treated on intervals shorter than 5 years, whereas "real-world" operational constraints would normally force longer intervals (perhaps 10-25 years).

Management implications

The question of whether or not herbivory effects are likely to be "trumped" by fuel management programs is probably one of the most important questions that must be answered in order to reconcile herbivore populations with other objectives in landscape management. In theory fuels management programs can dominate, but the relationship is also certainly scale-dependent on the size of the herbivore populations and on the scale of the fuel management program (in any particular setting). There is probably a threshold for effective fuels treatment in this regard, below which herbivore populations may have substantial influences on fuel accrual and fire behavior, but above which managed herbivore populations may become largely irrelevant to fuel or fire dynamics. Further simulation experiments will be required to address this issue. Realism of those additional simulations will be aided by simple modification of the simulator to allow limiting intervals between fuel treatments.

RELATIONSHIP TO OTHER FINDINGS

The development of *GrazeBGC* constitutes a rather substantial step toward integration of spatial herbivory concepts into the logic of landscape fire succession models. Developed specifically to run on the *FireBGCv2* platform (Keane et al. 2011), the new model now provides mechanistic, and dynamic allocation of biomass removal (i.e., removal of flash fuels) across landscapes by herbivores, and in both time- and spatially-explicit fashion. Furthermore, the new model uses these mechanisms to modify biomass accrual rates and the species composition of stands over longer-term secondary succession, thereby enabling study of herbivory's long-term influences on disturbance and system dynamics.

Results of our particular, 400-yr simulations for northeastern Oregon are congruent with earlier conceptual and empirical work which suggested that 20th century herbivore grazing regimes contributed to modifying pre-settlement fuel and fire dynamics. That our simulation experiment roughly doubled the study landscape's fire return interval under historical multi-species grazing (compared to that under no grazing or wildlife-only grazing) lends credence to those arguments, and in doing so the experiment (and the model itself) provide insight to some of the specific mechanisms through which long-term herbivory influences are created. In doing so, however, the simulation experiment's results also suggested that those impacts may not be attributable to 20th century livestock grazing alone, but rather are more likely to represent cumulative effects of grazing by multiple species that included native herbivores as well as domestic livestock.

Much debate and concern focus on the likely rate and severity of global climate change (see Loehle and Scaffetta 2011), as well as on that regionally in the Interior West (Hansen et al. in review). Until now, there were no spatially-explicit models capable of articulating herbivory effects to that of the climate on vegetation or episodic disturbance. However, *GrazeBGC* now provides an architecture in which herbivore populations can interact with climate and with other episodic disturbance agents in simulations based on the *FireBGCv2* modeling platform. No other model can perform this function.

FUTURE WORK NEEDED

Despite its advantages, the *GrazeBGC* platform, and our simulation experiments in particular, suffer from some deficiencies which should be addressed in future work. From the standpoint of modeling succession and fire, the principal deficiencies concern: 1) rudimentary nutrient-cycling capability, 2) interactions with other disturbance agents, and 3) static herbivore populations.

1) Rudimentary nutrient cycling

A major short-coming of *GrazeBGC*, in its current state of development, may be its rudimentary treatment of herbivore-mediated nutrient cycling, which we admit is patently naïve. Currently, the model removes nutrients in consumed biomass from the standing crop daily, thereby making it unavailable as fuel for fire, but it neither begins to immediately cycle those ingested nutrients, nor does it explicitly allocate their metabolic bi-products (nitrogen in dung and urine) spatially among stands or variously among plant guilds. Instead, the model simply banks the plant-bound nutrients that are consumed by

herbivores and then cycles them at the end of the year as if they were litterfall. Others have observed evidence that herbivores do indeed accelerate nutrient cycling, and thereby increase productivity and the rate of succession. The project's scant resources precluded us from incorporating that degree of elegance, and we chose to focus on the greater problem of spatially allocating the grazing itself.

Consequently, *GrazeBGC* implements herbivore-induced succession by retarding biomass accrual, but that function is not facilitated by accelerated nutrient cycling in the model's current formulation. We suspect that one consequence of this short-coming is that the apparent influences of herbivory on forest succession, and on landscape fire return intervals, in particular (in our simulations) is probably conservative. Were the model able to accelerate and re-allocate plant growth on herbivore-cycled nutrients, its representation of stand dynamics would be somewhat different. Further refinement of the modeling platform's nutrient cycling functions (for herbivores) would be very useful.

2) Interactions with other disturbance agents:

We chose to exclude, or were unable to adequately consider, interactions with other disturbance agents. Silviculture, insects and disease vectors each stand out in this regard. Our experiment's consideration of silviculture was hampered by an inability to specifically limit the re-entry interval between fuel-reduction treatments in the same stand. This problem arose from the *FireBGCv2* platform, which contained parameters to qualify stands for fuels reduction in simulation, but which did not also contain a parameter that could limit the frequency of re-entry in a particular stand. This problem should not be too difficult to fix in *FireBGCv2*, and doing so would enable re-simulation of herbivory and our fuels strategies with more realistic re-entry intervals (see manuscript for details). This would result in nearly instantaneous production of a second publication focused on interactions between fuels management and herbivory effects.

Similarly, insect infestations and plant diseases affect plant vigor, composition, and fuel loads, and thus potentially fire behavior as well (Hicke et al. 2012). These agents are able to influence succession and fuels even in the absence of any interaction with large herbivores, but in combination (with or without silviculture) they also present disturbance sequences that modify the range of forage choices that will be available to herbivores, thereby influencing the spatial dynamic of herbivory, and thus its effects potentially as well (Riggs et al. 2004). Resources limited our ability to address these agents and their interactions with herbivory with rigor, despite the fact that the *FireBGCv2* modeling platform does contain utilities for implementing timber harvest and some pathogens (Keane et al. 2011).

Consequently, the veracity of our experiment's conclusions depends on an assumption that our omission of those factors contributed only random error – an unlikely prospect in our opinion, but we were at a loss to do otherwise. More simulations will be required to ferret out the various extents to which herbivory's influences are likely to be contingent on silviculture and pathogenic factors.

3) Static herbivore demands:

We did not introduce annual variation in herbivore biomass demands, rather choosing to assume static herbivore populations throughout the course of our 400-year simulations. This was a reasonable strategy for our purpose here, which was simply to illustrate the

model's ability to render sensitivity to herbivory regimes. Clearly, however, static populations would be an unrealistic long-term expectation for problem-oriented simulations (i.e., management applications). Climate and weather variation will periodically flux relationships between herbivore biomass demands and biophysical-site productivity in any landscape, and those relationships will be further modified by episodic disturbance agents (e.g., fire, logging, pathogens). Particularly under extreme warming (e.g., our A2 climate scenario), reduced landscape productivity in this ecosystem would cause rather profound destabilization of its herbivore carrying capacity (Hansen et al. in review), and thereby destabilize any herbivore optima that may develop at stand level over short periods of time. *GrazeBGC* begins to provide a framework in which such questions can be addressed through simulations that exceed the domains of short-term, small-scale field experiments, but enabling the model to integrate dynamic herbivore populations would be beneficial for that purpose.

DELIVERABLES

Publications (manuscripts):

Riggs, R.A., R. Keane, M. Vavra, N. Cimon, R. Cook, L. Holsinger, J. Cook, T. Delcurto, D. Justice, and B. Naylor. **Conditioning Landscape Fire and Succession Dynamics on Large Herbivore grazing regimes: Simulations with the *GrazeBGC* model.** Manuscript attached (106pp). (probable outlets include Ecological Modeling, Ecological Monographs, or Wildlife Monographs)

Additional deliverables:

Riggs, R.A. **Modeling multi-agent disturbance regimes with FireBGCv2 and GrazeBGC.** Presented to:

Washington Forest Protection Association, Vancouver, Washington, April 21, 2011.

Oregon Forest Resource Council, Corvallis, Oregon, May 17, 2011.

Wallowa Board of Commissioners, Natural Resource Advisory Committee, Enterprise, Oregon, May 23, 2012

Riggs et al. **Can spatial herbivory concepts usefully inform landscape fire succession models (or not)?** 5th International Fire Ecology Congress, Dec 3-7, 2012, Portland, Oregon (pending).

LITERATURE CITED

Hicke, J.A., M.C. Johnson, J.L. Hayes, and H.K. Preisler. 2012. Effects of bark beetle-caused tree mortality on wildfire. *Forest Ecology and Management* 271(2012):81-90.

- Keane, R.E., R.A. Loehman, and L.M. Holsinger. 2011. A research simulation platform for exploring fire and vegetation dynamics: the *FireBGCv2* landscape fire and succession model. General Technical Report RMRS-GTR-255. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, 137 pp.
- Keane, R.E., R.A. Parsons, and P.F. Hessburg. 2002. Estimating historical range and variation of landscape patch dynamics: limitations of the simulation approach. *Ecological Modeling* 151:29-49.
- Keane, R.E., P. Morgan, and S.W. Running. 1996. FIRE-BGC--a mechanistic ecological process model for simulating fire succession on coniferous forest landscapes of the northern Rocky Mountains. USDA Forest Service, Research Paper INT-RP-484, Intermountain Forest and Range Experiment Station, Ogden, UT, USA.
- Keane, R.E., C. Hardy, K. Ryan, and M. Finney. 1997. Simulating effects of fire management on gaseous emissions from future landscapes of Glacier National Park, Montana, USA. *World Resource Review* 9(2):177-205.
- Keane, R.E., P. Morgan, and J.D. White. 1999. Temporal pattern of ecosystem processes on simulated landscapes of Glacier National Park, USA. *Landscape Ecology* 14(3):311-329.
- Keane, R.E., S.F. Arno, and J.K. Brown. 1989. FIRESUM -- an ecological process model for fire succession in western conifer forests. USDA Forest Service, General Technical Report INT-266.
- Loehle, C., and N. Scafetta. 2011. Climate Change Attribution Using Empirical Decomposition of Historical Time Series. *Open Atmospheric Science Journal* 5:74-86
- Riggs, R.A., J.G. Cook, and L.L. Irwin. 2004. Management implications of ungulate herbivory in Northwest forest ecosystems. *Transactions of the North American Wildlife and Natural Resources Conference* 69:759-784.
- Running, S.W., and J.C. Coughlan. 1988. A general model of forest ecosystem processes for regional applications I. Hydrologic balance, canopy exchange and primary production. *Ecological Modeling* 42:125-154.
- Running, S.W., and S.T. Gower. 1991. FOREST-BGC, a general model of forest ecosystem processes for regional applications II. Dynamic carbon allocation and nitrogen budgets. *Tree Physiology* 9:147-160.

