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Biomass and fire dynamics in a temperate forest-grassland mosaic: Integrating multi-species herbivory, climate, and fire with the FireBGCv2/GrazeBGC system

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ABSTRACT

Landscape fire succession models (LFSMs) predict spatially–explicit interactions between vegetation succession and disturbance, but these models have yet to fully integrate ungulate herbivory as a driver of their processes. We modified a complex LFSM, FireBGCv2, to include a multi-species herbivory module, GrazeBGC. The system is novel in that it explicitly accommodates multiple herbivore populations, inter- and intra-specific spatial forcing of their forage demands, and site-specific dietary selectivity to interactively modify biomass, fuels and fire behavior across a landscape and over time. A factorial experiment with five grazing regimes, three climates and two fire-management scenarios generated interactive influences on undergrowth biomass (shrub, herb, total), surface-fire (fire-line intensity; flame length; scorch height; soil heat; CO, CO_2, CH_4, and $PM_{2.5}$ emissions), and the landscape's fire-return interval. Herbivory's effects increased with biophysical site potential and herbivore forage demand, but its effects were also contingent on climate and fire-suppression. Multi-species grazing modified biomass and fire within stands and biophysical sites, but regimes involving only wildlife or livestock were less effectual. Multi-species herbivory affected the landscape's fire-return interval, but otherwise it did not "scale up" to significantly modify total landscape respiration, primary production, carbon, or the total area burned by individual fires. As modeled here, climate change and the effectiveness of future fire suppression exerted stronger effects on landscape metabolism and carbon than did herbivory.
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1. Introduction

Vegetation pattern reflects interaction among biophysical site potential, plant succession, and disturbance (Keane et al., 2002). Herbivory is among the disturbance agents involved in those interactions (Hobbs, 2006), and in some settings it may be the major driver of an ecosystem's shape and function (Danell et al., 2006). Herbivores "disturb" ecosystems by consuming biomass and by modifying the cycling of nutrients that are in the foods they consume. Those processes potentially involve herbivore populations in the control of biomass and plant succession (Bork et al., 1997; Kelly et al., 2005; Starfield and Chapin, 1996) and thus potentially in the regulation of landscape fire (Zimmerman and Neuenschwander, 1983, 1984). Herbivory is typically selective, density-dependent, and variable across time and space. Those facets of herbivory regimes can be important to understanding their relationships to other processes, but they also are obstacles to prediction (Riggs et al., 2004). Furthermore, models that have been designed principally to provide interaction between episodic disturbance and vegetation (e.g., Keane et al., 2004) apparently remain largely apart from those that have been designed to provide interaction between herbivory and vegetation (e.g., Weisberg et al.,

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2006). More comprehensive understanding of interactions and their significance probably depends on further integration of modeling concepts and approaches.

Landscape fire succession models (LFSMs) have emerged as important tools for exploring relationships between fire and succession (Keane et al., 2004). Advantages of LFSMs include predictions that can be both spatially and temporally explicit, and in some cases management-responsive as well. But developers of LFSMs usually have not attempted to integrate large herbivores with other disturbance agents in their models. Such integration logically requires linking herbivory to plant growth, fuels and disturbance propagation on a common modeling platform. In this paper we describe GrazeBGC, an integrative herbivory module that we have synthesized to run on a prominent LFSM platform, FireBGCv2. The module accommodates multiple herbivore populations, inter- and intra-specific spatial forcing of their herbivory, and it articulates their spatially–explicit removal of biomass to fire behavior, succession, and landscape metabolism. We begin by describing the platform and the grazing module. We then perform a simulation experiment with the integrated system to contrast influences of several grazing regimes on the platform's outputs for biomass and fire dynamics given different expectations for the future climate and fire suppression. We conclude with discussion of herbivory's apparent significance, system benefits and current limitations.

2. Methods

2.1. The simulation platform

GrazeBGC is a module that runs on the FireBGCv2 platform. FireBGCv2 (Keane et al., 2011) is a benchmark revision of Fire-BGC (Keane et al., 1996, 1997, 1999), which previously 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). In what follows we describe its parts that are directly relevant to integrating herbivory.

The platform's landscape structure is hierarchical and similar to that of an "ecosystem diversity" matrix (Haufler, 1994; Haufler and Irwin, 1993; Haufler et al., 1996; Roloff et al., 1999), consisting of "zones", biophysical "sites", "stands" of vegetation, and simulation "plots". Zones are coarse-scale units that help users organize inputs and outputs. Sites define biological potential from historical climate, topography, and soils. Stands represent time- and spatially–explicit plant communities for which composition and structure are calculated in a simulation plot. Sites and zones are static, but stands change as their biomasses grow, change compositionally, and are disturbed over time. Stand spatial resolution is typically 10^2–10^5 m^2. Simulation efficiency is optimized in landscapes 50,000–250,000 ha with 30–100 m pixel resolution.

Plant succession is an emergent property on this platform that is inferred from changes in each stand's biomass composition over time. Each stand's plot simulates a stratum of non-tree undergrowth and may also simulate a stratum of trees if the stand's underlying site potential will support them. The tree stratum is comprised of individual trees and the undergrowth is composed of functional plant guilds (or species). The platform simulates using either a biogeochemical (BGC) or a mechanistic GAP (GAP) approach, and in this paper we use the latter.

Weather combines with site, stand, species and guild attributes to regulate plant growth and contribute to fire behavior. Weather inputs are supplied in streams of daily maximum and minimum temperatures, vapor pressure deficits, precipitation, and solar radiation. Those streams are projected forward in time, and account for local topography (Numerical Terradynamic Simulation Group, 2000; Running et al., 1987).

In mechanistic GAP simulations the platform calculates tree growth in terms of bole diameters and heights, branchwood biomass, and leaf areas, which together are converted into biomass and carbon volumetrically. Tree diameters are simulated at breast height (*DBH*) in annual diameter increments (*DINC*) as reductions from published maxima using four reduction factors (Keane et al., 2011:59–60): shading (*rSHADE*), water (*rWATER*), temperature (*rTEMP*), and crowding (*rCROWD*):

$$DINC = (DINC_{\max})(rSHADE)(rWATER)(rTEMP)(rCROWD) \quad (1)$$

Reduction for shading is based on light interception by trees above. Water-based reduction is calculated from the ratio between actual and potential evapotranspiration (AET/PET). Temperature-based reduction is calculated from the annual number of degree days in relation to the optimum number for growth by each tree species. The crowding factor is calculated from the minimum of two indices (leaf area, stand density) that indirectly assess the effect of crowding on bole diameter growth. Tree height (*HT*) is calculated annually from the following equation wherein *a* and *b* are calculated coefficients (see Botkin et al., 1972 for details),

$$HT = 137 + aDBH - -bDBH^2 \quad (2)$$

Leaf area and branchwood are then calculated from crown biomass equations (Brown, 1978) that use *HT* and *DBH* to calculate light interception from top to bottom canopy layers.

Undergrowth guilds (or species) are grown using site-specific plant models. Each biophysical site is assigned its own plant model, which serves as the repository for state variables that drive and limit biomass growth (*UGROWTH*, kg/ha) by each plant guild in any stand of vegetation growing on the particular biophysical site. Among those variables are the guild's maximum biomass potential on the site ($UBIOMASS_{\max}$) and the maximum rate (η) at which its biomass can accumulate. $UBIOMASS_{\max}$ and η are the ultimate controls on stand biomass and composition, but those variables combine with residual standing biomass from the previous year ($UBIOMASS_{t-1}$), and with shade and water stress (*rSHADE* and *rWATER*) to regulate each guild's growth in the manner of a logistic (modified from Keane et al., 2011:44):

$$UGROWTH = (rSHADE)(rWATER)(\eta)(UBIOMASS_{t-1})\left(1 - \frac{UBIOMASS_{t-1}}{UBIOMASS_{\max}}\right) \quad (3)$$

Here *rWATER* is calculated from growing-season weather as the ratio of precipitation to PET. Daily (i) growth of biomass in each stand (l) is the growth increment (g) of each guild (m) summed over M guilds in each stand:

$$UGROWTH_{il} = \sum_{i=g_{\text{start}}}^{g_{\text{end}}} \sum_{m=1}^{M} g_{ilm} \quad (4)$$

The platform accumulates organic material on the ground in each stand through turnover of stems, leaves, and roots in the simulated trees and undergrowth (Keane et al., 2011:45–47). This material is represented in eight carbon pools (kgC/m^2): four representing fine organic matter (leaffall, litter, duff, and soil C) and four others representing woody ground fuels (1-, 10-, 100-, and 1000-hr time-lag woody fuels; Albini, 1976; Fosberg, 1970). Decomposition dynamics are based on a BGC approach wherein forest floor respiration is influenced by climate, particle size, and species- or guild-specific vegetation inputs that include cellulose, lignin, and C:N ratios for the various components. There is no

detailed nitrogen cycling for the platform's mechanistic GAP simulations that we will use, but its BGC simulations do contain cycling functions that are adaptable to herbivores, which we will address in our discussion.

Fire is simulated at multiple scales (Keane et al., 2011:25–28). Ignition frequencies and point locations are generated from inputs that include historical fire-return intervals (*fri*), which are defined as the number of years between fire for all land area within each biophysical site. Those historical return intervals are used to compute instantaneous fire-occurrence probabilities that are scaled to individual stands across the landscape (Keane et al., 1989). Any given stand ignites only when its flash fuels exceed a minimum threshold (default is 0.05 kgB/m^2 for litter, twigs, small branches, current-year leaf-fall, or sum of undergrowth). Subsequent fire behavior and spread are simulated from attributes of the individual stands of vegetation (herbaceous and woody fuel loads and moistures) and the attendant biophysical sites on which stands reside (topography, weather). Fire spread can be calculated using vectors, cell automata, or percolation methods; we will use the percolation method, which employs directional vectors for wind and slope to spread fire (Keane et al., 2002, 2006). Fire behavior (e.g., intensity, flame length) and effects (e.g., fuel consumption, smoke) are simulated at stand scale, which can then be aggregated from output to analyze mean responses at site, zone, and landscape scales. New fire return intervals can be tracked from output as well, and among those we will focus on the landscape's fire-return interval average (*fria*), which is a cumulative site-area-weighted average *fri*.

The platform produces stochastic behavior in several ways, but the most important sources are randomization of ignition points from which fires originate and the spatial extent of those fires. Fires interact with weather and fuels to determine the spatial extent of disturbance and to initiate successions. Subsequent growth, decay, and volatilization determine biomass and fuel dynamics over time.

2.2. Formalizing GrazeBGC on the platform

GrazeBGC sensitizes the FireBGCv2 platform to herbivory by adding herbivore functions to the platform's program flow (Figs. 1 and 2). Those functions principally include: (1) non-spatial initialization of herbivore biomass demands; (2) spatial allocation of those demands among stands of vegetation; and (3) partitioning biomass removal among plant guilds in each stand. Together those functions result in spatially–explicit off-take of biomass and adjustment of biomass accrual, which may then influence each stand's future plant growth, succession, fuel profile, fire characteristics, and herbivory. By changing the inputs that drive those functions, investigators can simulate different herbivory regimes and contrast their effects on a landscape's vegetation and disturbance dynamics. In what follows we formalize those functions (variables are indexed in Appendix A).

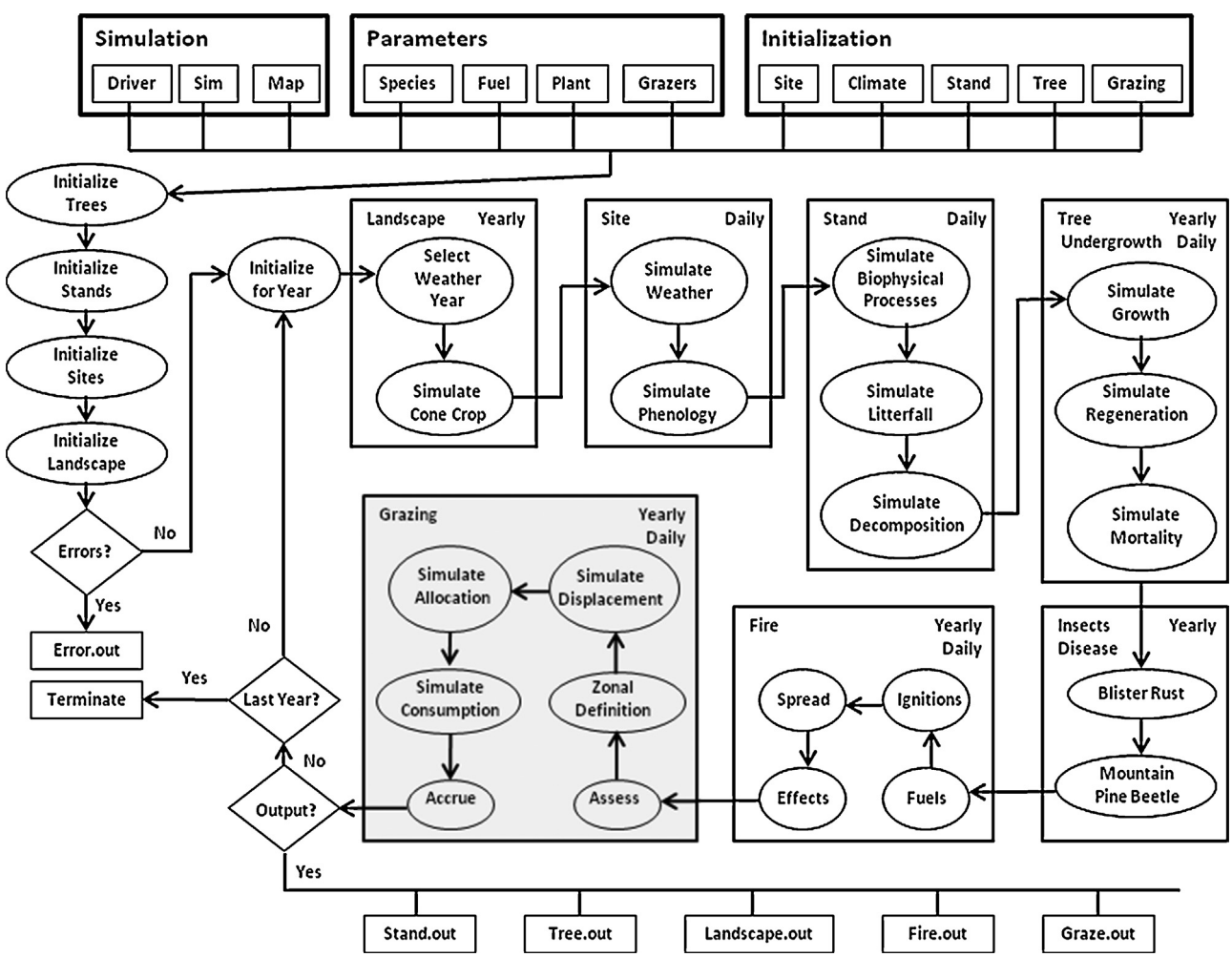

Fig. 1. GrazeBGC calculations are illustrated in the overall context of the FireBGCv2 platform's flow. Shaded boxes indicate major additions that are attributable to GrazeBGC (modified from Keane et al., 2011).

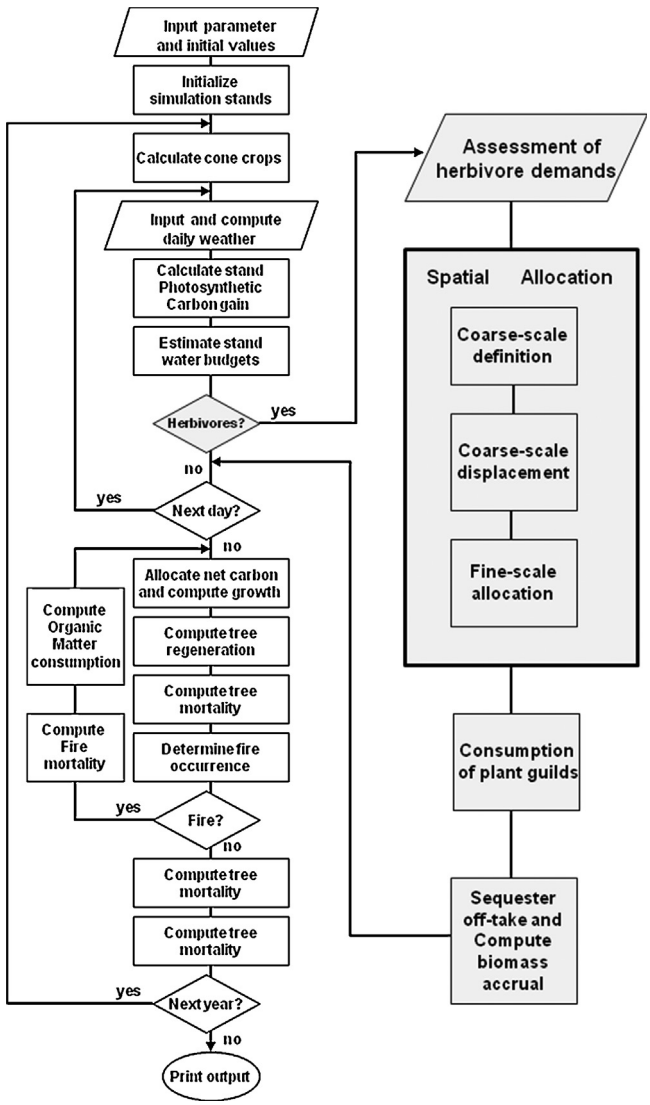

Fig. 2. GrazeBGC modifies FireBGCv2 by adding herbivory processes to the platform's daily calculations. The simulator assesses each population's non-spatial biomass demand from input. Then it spatially allocates that demand, partitions consumption among plant guilds in each stand, and adjusts biomass accrual accordingly (modified from Keane et al., 1996).

2.2.1. Assessment of herbivore biomass demands

GrazeBGC assesses each herbivore population's biomass demand on a Julian-day schedule from an input file. For each day (incremented by i) and each herbivore population (incremented by j), a biomass demand (F_{ij}, kg) is input at the scale of the landscape without regard to its spatial distribution.

2.2.2. Spatial allocation of herbivory

Spatial allocation partitions each population's initialized biomass demand (F_{ij}) among stands of vegetation. GrazeBGC does this by implementing three sub-processes sequentially each day (Fig. 2): *coarse-scale definition*,*coarse-scale displacement*, and *fine-scale allocation*.

Coarse-scale definition enables the modeling system to represent spatial limitations to grazing that are imposed by barriers. Livestock systems, for example, are often organized into pastures that contain many stands of vegetation. The boundaries of those pastures are barriers that spatially constrain the time-specific, spatially–explicit distribution of livestock grazing functions. GrazeBGC implements such constraints at the relatively coarse scale of the platform's zones. If an herbivore population j (e.g., a livestock herd) is subject to zonal constraint, its input biomass demand on day i within zone k, (F_{ijk}) is defined among the landscape's K zones in proportions p:

$$F_{ijk} = F_{ij}p_{ijk} \tag{5}$$

The usual bounding restrictions apply:

$$F_{ij} = \sum_{k=1}^{K} F_{ijk} \tag{6}$$

And:

$$\sum_{k=1}^{K} p_{ijk} = 1 \tag{7}$$

Coarse-scale displacement enables the system to represent displacement of one herbivore population's foraging by another herbivore population. It implements this displacement at zonal scale as an adaptation of Coe et al. (2001), which described displacement of Rocky Mountain elk (*Cervus elaphus*) as a response to a fixed cattle-stocking rate.

Stocking rates for livestock are commonly denominated in terms of animal-unit-months (*AUMs*). In the terminology of range managers, an *AUM* represents the stocking of one animal unit (*AU*) in pasture for one month (30 days), where the *AU* is usually defined as one mother cow and her calf. Thus some number of *AUM*s represents some number of cow–calf pairs stocked per month. By definition, however, a stocking rate denominated in *AUM* units is density-independent, and therefore it must be converted to a density-dependent equivalent in order to be made spatially relevant (i.e., *AUM* per unit area, *A*). We represent this density-dependent equivalent for a population j in a landscape zone k, with z_{jk}:

$$z_{jk} = \frac{AUM_{jk}}{A_k}; j = 1; k = 1, \ldots, K \tag{8}$$

In Coe et al. (2001), the quantity of AUM_{jk} was 750 = [(500 *AU*) (45 days)/(30 days)] and z_{jk} was 0.316 *AUM*/ha = (750 *AUM*/2,373 ha). Under those conditions elk were apparently displaced from cattle-occupied pastures at rates of 2.1% per day (early season) and 0.6% per day (late-season) or 1.35% per day on average. We develop two formulations for inter-specific displacement from those results.

The first formulation displaces a subordinate population's zonal biomass demand (F_{jk}) at a fixed rate (r, kg/day). Each day the dominant and subordinate populations occupy a common zone, the subordinate's demand is discounted at fixed rate. The general formula for fixed-rate displacement is:

$$F_{(i+1)jk} \leftarrow F_{ijk} - F_{ijk}r \tag{9}$$

Wherein we constrain r within bounds observed by Coe et al. (2001): $0.006 \leq r \leq 0.021$.

If the dominant population's density-dependent equivalent is not fixed over time, then r becomes a function of that population's variable density equivalent. Three assumptions apply: (1) the subordinate population's displacement rate, r, is a Type I functional response (Holling, 1959a,b,b) to the dominant population's density-dependent equivalent and thus r increases linearly with z; (2) r is density-dependent on the dominant population and not on the subordinate; and (3) r originates at zero when the dominant's density equivalent is zero. Using the average displacement rate

from Coe et al. (2001), and indexing $j = 1$ for the dominant population and $j = 2$ for the subordinate, the variable-rate calibration for r is:

$$r_{i2k} = 0.04272(z_{i1k}) \tag{10}$$

Wherein r_{i2k} is the daily rate by which the subordinate population's biomass demand is displaced from the zone k by the dominant's stocking rate in that same zone (z_{i1k}). The formula for variable-rate displacement is thus:

$$F_{(i+1)2k} \leftarrow F_{i2k} - F_{i2k}\left(0.04272\left(\frac{AUM_{i1k}}{A_k}\right)\right) \tag{11}$$

In Eq. (11) the dominant population's density-dependent demand on day i (AUM_{i1k}) modifies the subordinate's demand in the same zone on the following day ($F_{(i+1)2k}$). The dominant's demand can be calculated from animal units (AU_{1k}), its number of days in-zone ($\sum_{i=d_{\text{in}}}^{d_{\text{out}}} i$,

where d_{in} is the entry date and d_{out} is the exit date) and its daily zonal demand (F_{i1k}) summed over those days on a 30 days (i.e., 1 month) base:

$$AUM_{lk} = \frac{\sum_{i=d_{\text{in}}}^{d_{\text{out}}} F_{i1k}}{30 \times \left[\left[\sum_{i=d_{\text{in}}}^{d_{\text{out}}} F_{i1k}/AU_{i1k}\right]/\sum_{i=1}^{N} i\right]} = \frac{N \times \sum_{i=d_{\text{in}}}^{d_{\text{out}}} F_{i1k}}{30 \times \left[\sum_{i=d_{\text{in}}}^{d_{\text{out}}} F_{i1k}/AU_{i1k}\right]} \tag{12}$$

Wherein N is the total number of days spent in the common zone by the dominant population. Thus, the full model for variable-rate displacement is:

$$F_{(i+1)2k} \leftarrow F_{i2k} - 0.04271(F_{i2k})\left[\frac{N\sum_{i=d_{\text{in}}}^{d_{\text{out}}} F_{i1k}}{A_k(30)[\sum_{i=d_{\text{in}}}^{d_{\text{out}}} F_{i1k}/AU_{i1k}]}\right] \tag{13}$$

Regardless of method, displacement of a subordinate population's forage demand begins when the dominant population enters the common zone (on day = d_{in}) and continues until either its demand is zeroed (on day = d_{out}) or until the subordinate's demand has been completely displaced. Each day the subordinate's demand ($F_{i2k}r$) is subtracted from its a priori demand (F_{i2k}):

$$F_{(i+1)2k} \leftarrow F_{i2k} - (F_{i2k}r_{i2k}) \tag{14}$$

Then the displaced quantity is re-allocated among adjacent landscape zones that are not occupied by the dominant population:

$$F_{(i+1)2k_r} = F_{i2k_r} + (F_{i2k}r_{i2k}), k_r \in \{\text{zones}|k_r \neq k\} \tag{15}$$

As described above, *coarse-scale definition* and *coarse-scale displacement* assign and then adjust the biomass demands zonally. *Fine-scale allocation* re-distributes those adjusted zonal demands among the individual stands of vegetation within each zone. This sub-process may be implemented through either purely nutritional predictor variables or through combinations of nutritional and non-nutritional predictors.

For a purely nutritional approach we adapt matching law from Senft (1987), wherein the spatial distribution of foraging is driven by an herbivore population's relative community preference (*RCP*):

$$RCP_l = \frac{G_l}{A_l} = \frac{B_l}{\sum_{l=1}^{L} A_l B_l} \tag{16}$$

In Senft et al., 1987 notation $\hat{G}_l$ represents the proportion of grazing time allocated to a stand l. A_l represents the area (m^2) of stand l, and B_l the biomass (kg) of preferred plants in stand l. The denominator on the right sums areas and preferred biomasses (A_l and B_l) over all stands in the landscape. The currency that denominates effort is represented by $\hat{G}_l$ and relative community preference by the ratio $\hat{G}_l$ to A_l. That quantity is "matched" by the ratio between B_l and the area-weighted sum of all preferred biomass in the landscape.

Given that "community" and "stand" are equivalent terms for our purpose, and assuming that grazing time or effort allocated to a stand and the biomass demanded of it have equivalent relationship to preferred biomass in the stand, we substitute the equivalent biomass demand, f_i (kg), for grazing effort $\hat{G}_l$ and adapt the equation spatially to a specific stand that is nested within a specific FireBGCv2 landscape zone:

$$RCP_{ikl} = \left(\frac{\hat{G}_{ikl}}{A_{kl}}\right) = \left(\frac{f_{ikl}}{A_{kl}}\right) = \left(\frac{B_{ikl}}{\sum_{l=1}^{L_k} A_{kl}B_{ikl}}\right) \tag{17}$$

We now allocate demand among all stands in each zone according to each herbivore population's matching relationship:

$$\left(\frac{f_{ijkl}}{A_{kl}}\right) = \left(\frac{B_{ijkl}}{\sum_{j=1}^{N_k}\sum_{l=1}^{L_k} A_{kl}B_{ijkl}}\right), j = 1, \ldots, N_k \tag{18}$$

Wherein N_k represents the number of herbivore populations in the zone.

We now isolate proportional demands for the various stands in a zone by multiplying each side of the previous equation by A_{kl}:

$$f_{ijkl} = \left(\frac{A_{kl}B_{ijkl}}{\sum_{j=1}^{N_k}\sum_{l=1}^{L_k} A_{kl}B_{ijkl}}\right) \tag{19}$$

Then we solve for absolute demand allocations by products of those proportions and corresponding zonal demands:

$$F_{ijkl} = f_{ijkl}F_{ijk} = \left(\frac{A_{kl}B_{ijkl}}{\sum_{j=1}^{N_k}\sum_{l=1}^{L_k} A_{kl}B_{ijkl}}\right)F_{ijk} \tag{20}$$

As a check, each herbivore population's total daily demand in-zone (F_{ijk}) must equal the sum of its spatially–explicit demands therein:

$$F_{ijk} = \sum_{l=1}^{L_k} F_{ijkl} = \sum_{l=1}^{L_k}\left(\frac{A_{kl}B_{ijkl}}{\sum_{j=1}^{N_k}\sum_{l=1}^{L_k} A_{kl}B_{ijkl}}\right) \tag{21}$$

Eqs. (19) and (20) provide a potentially useful mechanism for allocating the biomass demands of several herbivore populations among stands of vegetation. Nonetheless, the relative preferences that underlie B for each herbivore population must be relative across all stands in the zone and thus may be quite difficult to obtain (Clark et al., 2013; Cruz and Ganskopp, 1998; Darambazar et al., 2014; Johnson, 1980; Walburger et al., 2007). To circumvent that obstacle, plant nutritional metrics may also be used to spatially allocate those biomass demands. As a practical matter, nutritional metrics are more easily estimated than preferences, and furthermore, the underlying basis for B is relative preference (*RP*), which may be conceptualized as an exponential function of

relative nutritive quality (*RNQ*, from Senft, 1987):

$$RP = e^{k(RNQ-1)} \tag{22}$$

We now assume that an adaptive herbivore can prefer only biomass that on average meets or exceeds some threshold for nutritional quality (*NQT*). Given that assumption, the quantity of preferred biomass, *B*, is substitutable by a corresponding quantity, $\underline{B}$, which satisfies that threshold:

$$F_{ijkl} = F_{ijk}\left(\frac{A_{kl}\underline{B}_{ijkl}}{\sum_{j=1}^{N_k}\sum_{l=1}^{L_k}A_{kl}\underline{B}_{ijkl}}\right) \tag{23}$$

Either Eq. (20) or Eq. (23) might be used to allocate herbivore demands among stands. If Eq. (20) is used, the allocation must be driven by inter-stand variation in the aggregate biomass of those plant guilds which are preferred by the herbivore population. If Eq. (23) is used, then the allocation is driven by inter-stand variation in the aggregate which meets a nutritional threshold. Neither Eq. (20) nor Eq. (23) limits spatial allocation based on foraging efficiency per se (but see Wickstrom et al., 1984; Spalinger and Hobbs, 1992). Each stand's guild biomasses are developed during simulation from platform Eqs. (3) and (4) above, which can render each stand to contain a unique quantity of relevant biomass. Preference or nutrition coefficients, as the case may be, are accounted for by the modeler in an input file.

Because the platform partitions each stand's undergrowth biomass among plant guilds, the value of *B* in Eq. (20) and that of $\underline{B}$ in Eq. (23) each represent an aggregate biomass that satisfies each term's condition: "preferred" in Eq. (20), or "nutritionally adequate" in Eq. (23). The amount of biomass the modeling system considers satisfactory is controlled by the analyst. For example, if Eq. (20) is used the value of *B* may be conditioned using a dietary selection index (e.g., Ivlev, 1961) so that *B* is constrained to include only the aggregate biomass of those guilds that are preferred by herbivores (i.e., those for which Ivlev's $\alpha > 0$). To illustrate this constraint, we assume that a stand of vegetation includes some number of functional plant guilds, *M*, each having biomass b_m. On any given day the amount of the stand's biomass that is relevant to allocating the herbivore population's grazing is a function of each guild's selection coefficient, α_{jm}. Since a non-positive α for a given *b* logically implies that *b* must be zero, we have the following conditions for biomass relevancy in the stand:

$$B_{ijkl} = \sum_{m=1}^{M} b_{ijklm} = \left\{\begin{matrix} 0, & \alpha_{jm} \le 0 \\ b_{ijklm}, & \alpha_{jm} > 0 \end{matrix}\right\} \tag{24}$$

If Eq. (23) is used, then the value of $\underline{B}$ can be constrained on a nutritional metric such as digestible energy (*DE*, kcal/g) so that the allocation among stands responds to the aggregate biomass of only those guilds that yield *DE* sufficient to meet some critical physiological requirement, such as minimum body maintenance, $\min_j$:

$$\underline{B}_{ijkl} = \sum_{m=1}^{M} b_{ijklm} = \left\{\begin{matrix} 0, & DE_{jm} < DE_{\min j} \\ b_{ijklm}, & DE_{jm} \ge DE_{\min j} \end{matrix}\right\} \tag{25}$$

Alternatively, $\underline{B}$ may be further constrained to include only biomass that is both consumable and digestible. If herbivores will consume only the portion of any plant guild's biomass that is current year's growth (*CYG*,g), then the quantity of any guild's biomass that is relevant to spatial allocation is the product of its *CYG* quantity and its coefficient for dry-matter digestibility (*DMD*, g/g):

$$\underline{B}_{ijkl} = \sum_{m=1}^{M} b_{ijklm} = \left(\frac{CYG_{iklm}}{b_{iklm}}\right)(DMD_{jm}) \Rightarrow \underline{B}_{ijkl} = \sum_{m=1}^{M}(CYG_{ijklm})(DMD_{jm})$$

Other assayable criteria might also be applied to further condition the relevance of plant biomass for allocating grazing among stands (e.g., metabolizable energy or protein, concentrations of secondary metabolites, etc.).

Purely nutritional approaches like those illustrated above may not always be sufficiently realistic. Non-nutritional factors can also modify the spatial distribution of foraging, thus requiring terms to account for those factors as well (Senft et al., 1985). Resource selection probability functions (RSPFs) provide one means of implementing multiple drivers on this platform. To explain, we modify from Manley et al. (2010) the general form for an RSPF:

$$w^*(X_i) = \exp(\beta_0 + \beta_1 x_{i_1} + \ldots + \beta_p x_{i_p}) \tag{27}$$

In Manley et al. (2002) notation, $w^*(X_i)$ is the absolute probability that the *i*th resource unit (e.g., a stand of vegetation) will be selected for use (i.e., foraged) given a constant, β_0, and $\beta_1 x_{i_1} + \ldots + \beta_p x_{i_p}$), the estimated value produced by the random variant $X_i = (x_{i1}, \ldots, x_{ip})$. The x_i predictor variables may each be either nutritional or non-nutritional in character. Eq. (27) provides the template for an expanded version using FireBGCv2/GrazeBGC notation for days (*i*), herbivore populations (*j*), landscape zones (*k*), and individual stands of vegetation (*l*):

$$w^*(X_{ijkl}) = \exp(\beta_0 + \beta_1 x_{ijkl_1} + \ldots + \beta_n x_{ijkl_p}) \tag{28}$$

With the solution from that equation, each herbivore population's daily biomass demand can be allocated among stands in each landscape zone:

$$F_{ijkl} = F_{ij}(w^*(X_{ijkl})) \tag{29}$$

2.2.3. Consumption of plant guilds

FireBGCv2/GrazeBGC grows and crops biomass from each stand's plant guilds in daily increments. In what follows we review how the FireBGCv2 platform calculates biomass growth in each stand, and then we explain how the GrazeBGC module selectively crops that growth on behalf of each herbivore population.

Eqs. (3) and (4) above showed how the platform accumulates each stand's undergrowth biomass guild-specifically. Those equations also show that the platform's accrual of UGROWTH is not sensitive to herbivory because there is no term for consumption or removal. When running GrazeBGC, however, each guild's accrual of *UGROWTH* is discounted through daily consumption by herbivores.

To calculate the consumption of each guild, each stand's allocated forage demand (F_{ijkl}) is partitioned among *M* guilds in each stand according to biophysical-site-specific dietary preferences. To acknowledge the distinction between "biomass demanded" and "biomass consumed", GrazeBGC tracks both metrics denoting the latter as *UCROPPED*, which is cropped in guild-specific daily increments (*c*) for each herbivore population:

$$UCROPPED_l = \sum_{i=c_{\text{start}}}^{c_{\text{end}}}\sum_{j=1}^{N}\sum_{m=1}^{M} c_{ijlm} \tag{30}$$

When computing actual values, *N* and *M* are refined to account for the dependency of *N* on each herbivore population's biomass demand in a particular zone each day, and for the dependency of *M* on those guilds that are available for cropping in each stand.

On any day, a plant guild's net accrual of biomass in any given stand ($NETGROWTH_{ilm}$) is the difference between the platform's growth output and the module's consumption output:

$$NETGROWTH_{ilm} = UGROWTH_{ilm} - UCROPPED_{ilm} \tag{31}$$

We use preference logic (Chesson, 1978; Riggs et al., 2000; Smith, 1965) to partition each herbivore population's consumption of $NETGROWTH_{ilm}$ among plant guilds in each stand of vegetation. Each population's site-specific guild preferences (α) can be defined in a vector ($A_j^{(0)}$):

$$A_j^{(0)} = \begin{bmatrix} \alpha_{j,1} \\ \alpha_{j,2} \\ \alpha_{j,3} \\ \cdots \\ \alpha_{j,M} \end{bmatrix} \left(\sum_{m=1}^{M} \alpha_{j,m} \right)^{-1} \tag{32}$$

Once again, j indexes herbivore populations and m indexes plant guilds. Each preference vector is normalized over guilds. In practice, several seasonal vectors are usually input for each herbivore population to account for changes in its site-specific dietary preferences over the course of the year.

The algorithm crops each population's biomass demand from the plant guilds in each stand in proportion to normalized preference. If a population's demand for a particular guild's growth biomass exceeds the amount available in a stand, then the unmet quantity is re-allocated among remaining guilds in a re-normalized vector $A_j^{(0)}$. For example, if m_{ϕ_1} is the index of the guild for which the herbivore demand exceeds supply, then the re-normalization for herbivore population j is:

$$A_j^{(1)} = \begin{bmatrix} \alpha_{j,1} \\ \alpha_{j,2} \\ \cdots \\ \alpha_{j,\phi_1} = 0 \\ \cdots \\ \alpha_{j,M} \end{bmatrix} \left(\sum_{m \neq m_{\phi_1}}^{M} \alpha_{j,m} \right)^{-1}, \sum_{m \neq m_{\phi_1}}^{M} \alpha_{j,m} = 1 \tag{33}$$

and so on, given further depletions.

The modeling system cycles through all stands in each zone daily, first accruing growth then selectively cropping each population's partitioned biomass demand in descending hierarchical order (i.e., for the dominant population first in each stand). As used in this paper, the module crops those demands from available plant growth of the current year (*CYG*) and is constrained from cropping biomass grown in previous years. If all *CYG* is cropped from all guilds in any given stand, then the unsatisfied demand is reported in output as unmet, and no further adjustments are made until the following day after plant growth has been accrued again across the landscape.

2.2.4. Modification of succession and disturbance

Any disturbance agent's behavior can be regulated by factors that are extrinsic to the agent itself. Fire behavior, for example, is regulated by several factors that prominently include fuel loading, which in-turn is regulated by plant growth and herbivory that occurs prior to the fire. Previous growth within the same year and growth in prior years are both relevant. GrazeBGC can link fire behavior to prior plant growth and herbivory in two ways.

The first of those is by tracking guild-specific growth, consumption, and net growth in each stand of vegetation over the course of each year. Without the grazing module, the platform's accrual of undergrowth biomass is insensitive to herbivory and all of *UGROWTH* is available to support fire until leaf-fall each year. With the grazing module, however, only *NETGROWTH* remains available and thus fire in any given stand is affected by prior grazing up to the date of ignition.

Fire can also be linked to prior herbivory by modifying biomass accumulation across years, which may be accomplished in two ways. The first is inherent to the platform and does not involve any modification of plant vigor by herbivores. As explained in Eq. (3), the platform accrues undergrowth biomass by adding each guild's annual growth biomass ($UGROWTH_y$) to the guild's biomass residual from the previous year ($UBIOMASS_{y-1}$). The accrued quantity is a function of the guild's intrinsic growth rate η in relation to the guild's biomass potential, as modified by stress factors (shading, water stress). This formulation is important for simulating succession because it suppresses biomass accumulation by those guilds that are consumed by herbivores, since in Eq. (3), the base from which future *UGROWTH* is calculated will be suppressed by herbivory. Moreover, those guilds having relatively low intrinsic growth rates will be suppressed to greater extent than those which have high intrinsic rates, all other factors being equal. Thus the platform enables a direct effect of herbivory on the realized rate of each guild's biomass accrual. This effect does not depend on lowering the guild's intrinsic growth rate, and it does not necessarily reduce annual growth.

Nevertheless, heavy grazing may reduce root biomass or carbohydrate reserves, thereby reducing plant vigor and a plant population's intrinsic ability to produce biomass. Moderate grazing may apparently enhance vigor as well under some circumstances (Peek et al., 1978). These effects are over and above the function of Eq. (3), requiring some explicit mechanism for modifying intrinsic rates during simulation. This may be achieved by allowing any guild's intrinsic rate to be modified as a function of the guild's prior utilization by herbivores. The value of η in a future year may be modulated given its initialized maximum value (η_0), the speed of the intrinsic rate's modification (λ), and the utilization level at which its modification begins (u_0):

$$\eta_{t+1}(u_t) = \frac{\eta_0}{\left(1 + e^{\lambda(u_t - u_0)}\right)} \tag{34}$$

Recasting that equation with the module's indexing for specific guilds, m, and with expansion of the utilization term, u, into spatial components gives the following:

$$\eta(t+1)lm = \frac{\eta_{0m}}{\left(1 + e^{\lambda\left(\left(1 - \frac{(UGROWTH_{tlm} - UCROPPED_{tlm})}{UGROWTH_{tlm}}\right) - u_0\right)}\right)} \tag{35}$$

2.3. An experiment

2.3.1. Biophysical setting

We conducted our experiment in a landscape context defined by Middle Meadow Creek (MMC; see "Context" in Fig. 3), a sub-watershed segment that is mostly contained within the Starkey Experimental Forest and Range (SEFR) in the Blue Mountains ecological province (Franklin and Dyrness, 1973). Elevation ranges between 1067 and 1524 m. Climate is severe mid-latitude with maritime and continental influences. Maritime weather delivers roughly two-thirds of annual precipitation from mid-September through March, and most of the remainder in April, May and early June. Summers are droughty. Annual precipitation (1966–2009) ranges from 40 to 105 cm, annual maximum temperature 31–39 °C and minimum from −29° to −13 °C.

Parent geology is Miocene basalt, which has been overlain by Pliocene and Pleistocene ash, and by wind-blown loess. Depths of

ash and loess vary spatially and interact with precipitation and the summer drought to define the landscape's biophysical sites. We identified five biophysical sites from soil surveys, literature and online databases (Powell et al., 2007; United States Geological Survey, 2009): (1) hot dry upland shrubland, (2) hot dry upland herbland, (3) hot dry upland woodland, (4) upland mixed-conifer forest, and (5) riparian forest.

Shrubland and herbland each occur on thin Argixerolls (priairie soils ≤28 cm in depth) that developed mostly from loess over partially degraded basalt. Natural vegetation of the shrubland is an association of stiff sagebrush (*Artemisia rigida*) and Sandberg's bluegrass (*Poa sandbergii*), and that of the herbland is Palouse prairie dominated by Idaho fescue (*Festuca idahoensis*) and bluebunch wheatgrass (*Pseudoregnaria spicata*). The shrubland is least productive of the five sites, and it has a historic fire-return interval (*fri*) of at least 44 years (Agee, 1994; Johnson and Simon, 1987). The herbland is more productive and its historic *fri* is about 3 years.

The woodland site occurs on deeper Argixerolls (≤48 cm) that may also contain substantial ash. Its natural vegetation is savanna-like, fire-adapted ponderosa pine (*Pinus ponderosa*) with an undergrowth of mostly dry herbland species, but it does not necessarily require fire for maintenance. Its pre-1900 fire-return interval averaged about 5 years, but within a broad range of

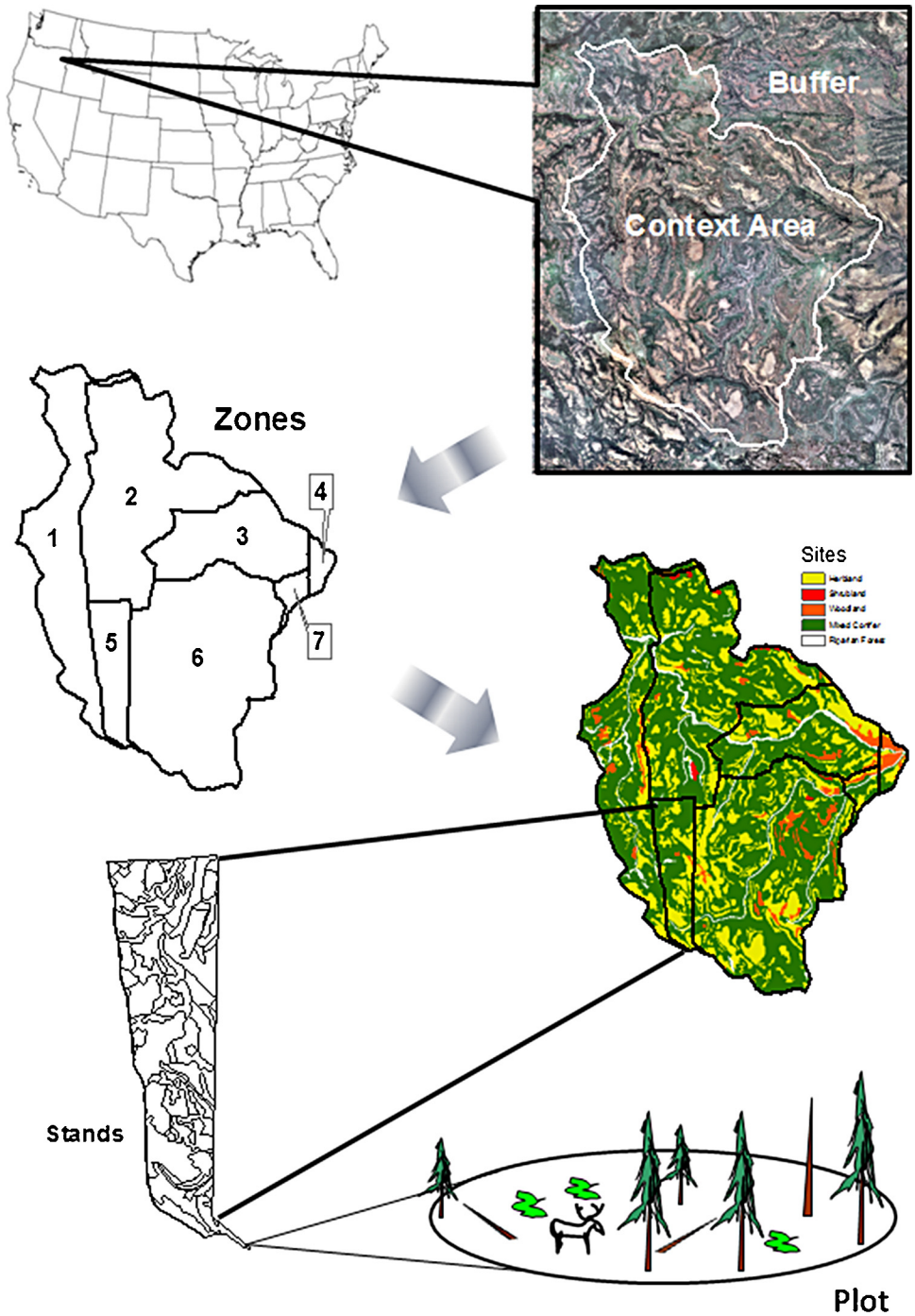

Fig. 3. Middle Meadow Creek (MMC) is a 6th order hydrologic unit (sub-watershed segment) in the Grande Ronde River basin, in northeastern Oregon, USA. Ecological processes were simulated across the entire landscape, but herbivory and its analysis was limited to the MMC context area.

1–70 years (Arno, 1980; Brown and Smith, 2000; Heyerdahl et al., 2001; McIver and Weatherspoon, 2001) wherein the upper extreme approximates current conditions under aggressive fire suppression.

Upland mixed-conifer occurs on Vitrandepts (ashy silt-loams, 64–107 cm deep) developed principally from ash on protected terrain. Its vegetation includes a limited variety of associations in grand fir (*Abies grandis*) and Douglas fir (*Pseudotsuga menziesii*) forest series (Powell et al., 2007). Variable- and mixed-severity fire regimes intergraded historically here, with return intervals up to 200 years regionally (Powell, 2011) but probably about 37 years on average in the MMC (range 20–67; see Heyerdahl et al., 2001).

Soils of those four upland sites do not have permanent water-saturation zones and commonly desiccate to root-restrictive layer during the summer drought. Plant growth is thus truncated temporally across the uplands according to the timing of site-specific moisture stress each year (shrubland, herbland, woodland, upland mixed-conifer, in that order). Riparian forests, however, occur on aquic alluvium that may remain saturated at depth. There dominant trees are cottonwood (*Populus balsamifera trichocarpa*), Douglas fir, and grand fir. This site occurs on narrow stream margins and its *fri* is only modestly longer than that of adjacent upland forest (roughly 44 years; see Olson, 2000).

We built five plant models to drive undergrowth (one model for each biophysical site). Each model defined 16 functional guilds by first dichotomizing plant taxa according to growth form (shrub, herb); then dichotomizing shrubs according to shade tolerance (intolerant, tolerant), foliage persistence (evergreen, deciduous), and potential height at 20 years of age (tall >1 m, short $\leq$1 m); and then dichotomizing herbs according to shade tolerance, life cycle (annual, perennial), and class (graminoid, forb). We synthesized each guild's $UBIOMASS_{max}$ from species-specific data (Ottmar et al., 2007; Young et al., 1967; Johnson and Simon, 1987; Riggs et al., 2000; Case, 1995; Sheehy et al., 1999; R. Cook and J. Cook unpublished data). From those sources we limited each site's total undergrowth biomass (kg/ha, summed across all 16 guilds) as follows: 930 (shrubland); 3640 (herbland); 3310 (woodland), 12,490 (upland mixed-conifer); and 13,090 (riparian forest). We also limited the current annual growth by all guilds in aggregate to recorded maxima for current year production (CYP_{max}, kg/ha): 454 (shrubland), 1545 (herbland), 1917 (woodland), 2654 (upland mixed-conifer), and 2806 (riparian forest). Intrinsic growth rates (η) for herbs were defaulted from earlier FireBGCv2 applications (5.48 for perennials, 10.86 for annuals; Keane et al., 1997, 1999; Sampson, 1944), and for shrubs we synthesized $\eta = 1.14$ from literature (Riggs et al., 2000; Young et al., 1967). All other state variables for undergrowth were defaulted from earlier FireBGCv2 applications.

Woodland and forest inputs included conifer site indices, basal-area and seedling-density limits, and lag times for seedling establishment. We calibrated site index on forest associations from Powell (1999, 2009),) as follows: dry woodland on average ponderosa pine/bunchgrass (*Pinus ponderosa*/*Pseudoregnaria spicata*, *P. ponderosa*/*Festuca idahoensis*); upland mixed-conifer on average grand fir (*Abies grandis*/*Linnaea borealis*, *A. grandis*/*Vaccinium membranaceum*); and riparian forest on maximally-productive grand fir (*A. grandis*/*V. membranaceum*). Each site's maximum basal-area stocking was calibrated to "full stocking" (Powell, 1999) compounded by a factor of 1.25. Seedling density was limited to published maxima at stand quadratic-mean diameter (QMD) of 2.54 cm using upper–management-zone and uneven-age density assumptions (Powell, 1999). Tree morphology and shade tolerance were calibrated from databases (Gymnosperm, 2011; United States Department of Agriculture, 2011) and tree growth parameters from published literature (Barrett, 1979; Cochran, 1979a,b; Cochran and Seidel, 1999; Powell, 1999; Seidel and Cochran, 1981). All other tree inputs were defaulted from the earlier FireBGCv2 applications.

We simulated processes across the MMC context area (9013 ha) and a buffer extending 1 km beyond it on cardinal directions (an additional 12,187 ha). The entire simulation landscape initially contained 2044 stands (11 shrublands, 85 herblands, 61 dry woodlands, 1883 upland mixed-conifer forests, and 4 riparian forests). The MMC context alone contained 944 stands: 9 shrublands (7.76% of area); 71 herblands (23.79%); 17 dry woodlands (1.00%); 846 upland mixed-conifer stands (67.42%); and 1 riparian-forest stand (0.03%). Woodland and forest plots were populated with trees using the U.S. Forest Service's Integrated Forest Management System (INFORMS) by imputing inventoried tree lists from nearest-neighbor analogue stands ($N_{list} = 1936$; Crookston et al., 2002; Justice, 2011) that were identified from satellite imagery (National Agriculture Imagery Program, 2006) and grown to a common base year (2010) in a forest vegetation simulator (FVS, Dixon, 2002). We arbitrarily initialized biomass of undergrowth guilds in shrublands, herblands, and woodlands at 33% of each guild's site-specific maximum. The suppressive effect of imputed tree canopy on undergrowth in forests was accounted for by interpolating each guild's initial biomass between maximum potential at 0% overstory canopy and minimum at 100% overstory canopy.

2.3.2. Simulation design and analysis

We conducted a factorial experiment with four fixed factors (Table 1), each having from two to five treatment levels: herbivory ($H = 5$), climate ($C = 3$), fire-suppression ($F = 2$), and biophysical site ($S = 5$). Three of those factors (H, C, and F) were crossed to produce 30 factor combinations ($5 \times 3 \times 2 = 30$), and each combination was replicated with 10, 400-year simulations ($N_{sim} = 300$).

The five herbivory regimes were variants of the landscape's recent historical regime, 1989–2010, as estimated from archives of the Oregon Department of Fish and Wildlife and the U.S. Forest Service (Fig. 4), accounting for recorded population sizes and sex/age

Table 1
The simulation design included four fixed factors: herbivory ($H = 5$), climate ($C = 3$), fire suppression ($F = 2$), and biophysical site ($S = 5$). Herbivory, climate, and fire suppression were crossed to formulate 30 factor combinations, which were each replicated in 10,400-year simulations.

Factor levels	Experimental factors			
	Herbivory	Climate	Fire suppression	Biophysical site
1	No-herbivore[a]	Historical	None	Shrubland
2	Wildlife-only[b]	A2 (warm, dry)	90%	Herbland
3	Livestock-only[c]	B2 (warm, moist)		Woodland
4	Historical (Wildlife + livestock)[d]			Upland mixed conifer forest
5	Historical 2*x* (wildlife + 2*x* livestock)[e]			Riparian forest

[a] Herbivore-free mimics FireBGCv2 without the GrazeBGC module.
[b] From level no. 4, simulates only Rocky Mountain elk and mule deer.
[c] From level no. 4, simulates only livestock.
[d] Average multi-species regime, 1989–2010, estimated from archives. Livestock composition approximates 70% black Angus and 30% Angus *x* Hereford breeds.
[e] From level no. 4, doubles livestock to approximate mid-20th century herbivory.

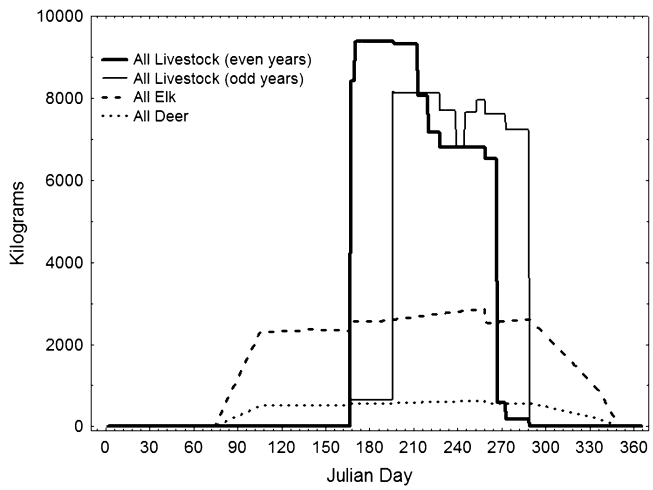

Fig. 4. Historical, daily biomass demands simulated for livestock, elk, and deer are displayed for the MMC context area. Difference between even-year and odd-year livestock demands are attributable to alternate-year rotation between MMC pastures that are within the SEFR and those that are outside the SEFR rotation. Documented biomass demand by livestock in even years (771,110 kg) has been roughly 93% of that in odd years (825,675 kg). Livestock breed composition has averaged roughly 70% black Angus and 30% black Angus *x* Herford. We simulated four other herbivory regimes by variously deviating from the historical regime shown (see Table 1).

composition (average number of animals), intra-year fluxes attributable to seasonal migration (elk, deer), anthropogenic forcing (livestock rotation), births and deaths, and interpolated body size dynamics. We implemented those regimes with inter-specific displacement of elk by cattle (Eq. (9)), nutritionally-driven fine-scale allocation (Eqs. (23) and (26)) and preference-driven guild consumption (Eqs. (32) and (33)). Nutrition coefficients (*DMD*, for calculating $\underline{B}$) and preference coefficients (α, for calculating consumption within stands) were input seasonally: spring (03/16–06/15: julian day (JD) 75–166); early summer (06/16–07/15: JD 167–196); middle summer (07/16–08/15: JD 197–227); late summer (08/16–09/15; JD 228–258); early autumn (09/16–10/15: JD 259–288); and late autumn (10/16–12/31: JD 289–365). Nutritional biomass ($\underline{B}$) for livestock and elk was tracked in each stand by summing guild-specific products of *NETGROWTH* (leaf + stem) and its *DMD*. For mule deer we defined $\underline{B}$ on leaf accumulation and its *DMD*, assuming 50:50 leaf:stem ratios. Those vectors were calibrated for elk and livestock from site- and season-specific fiber fractionations (J. Cook, unpublished data; DelCurto et al., 2014a,b,b). For mule deer, those vectors were calibrated from literature (Blank, 1984; Short, 1981; Welch, 2005) assuming that herbs and deciduous shrubs were phenologically immature: (1) on shrubland, herbland, woodland sites until June 16 (approx. summer solstice) and August 16 (earliest winter-hardening), respectively; and (2) until July 16 and September 16, respectively, on upland and riparian forest sites. We discounted evergreen shrub *DMD* 90% in all seasons to nominally acknowledge the depressive effect of foliage secondary chemistry on digestive function and intake (e.g., Bergström, 2007; Cates and Orions, 1975; Li, 1974; Nagy et al., 1964; Nagy and Tengerdy, 1967; Roscoe and Hall, 1960).

Table 2
Climate warming was implemented with regionally down-sized GCM family projections based on IPCC assumptions for greenhouse gas emissions (scenarios A2 and B2). Temperature increases were implemented as offsets (°C) and precipitation as multiples of historical average.

Regime parameter	Climate scenarios		
	Historical	A2 (warm, dry)[a]	B2 (warm, moist)[a]
Atmospheric CO_2[a]			
Start	287	369	369
End	287	856	621
–			
T_{max} and T_{min} offsets			
Winter	0	2.5	1.8
Spring	0	3	1
Summer	0	6.7	2.1
Autumn	0	4.6	1.6
–			
Precipitation multiple			
Winter	1	1.11	0.99
Spring	1	1.02	1.17
Summer	1	0.66	1.24
Autumn	1	0.93	1.05

[a] http://www.grida.no/publications/other/ipcc_sr/?src=/climate/ipcc/emission/.

The three climate scenarios contrasted the historical climate record against warm–dry (A2) and warm–moist (B2) scenarios. The historical climate was a site-adjusted, forward-projected, 44-year sequence developed from the daily weather record at La Grande, Oregon. The other two scenarios were developed from regionally down-sized General Circulation Model (GCM) averages based on Intergovernmental Panel for Climate Change (IPCC) scenarios for greenhouse emissions. Those scenarios modified historical temperature and precipitation seasonally (Table 2) and were ramped in over the course of the first 100 years. Landscape nitrogen deposition and fixation were held constant in all scenarios ((0.842 kgN/m^2)/year).

The two fire regimes dichotomized fire-suppression effectiveness (Keane et al., 2011). The first regime (N) implemented no suppression. The second regime (S) randomly suppressed 90% of ignitions each year, but without suppressing the spread of those fires that were allowed to burn.

Table 3
Twenty-three outputs were analyzed to encapsulate biomass, surface fire (thermal behavior and emissions), and landscape (respiration, production, carbon, and fire) responses.

Stand	Surface fire		Landscape			
Biomass[a]	Thermal[b]	Emissions[c]	Respiration[d]	Productivity[e]	Carbon[f]	Fire[g]
shrubB	*flame*	CO_2	*mr*	*gpp*	*totC*	*fria*
herbB	*int*	*CO*	*hr*	*npp*	*abC*	*area*
underB	*scorch*	CH_4	*gr*	*nep*	*bgC*	
hbc	*soilH*	$PM_{2.5}$				

[a] Above-ground biomass of shrubs (*shrubB*, kg/m^2), herbs (herbB, kg/m^2), and total understory (*underB* = *shrubB* + *herbB*; kg/m^2) were analyzed across all sites. Height from ground to base of live tree canopy (*hbc*, m) was analyzed only on woodland and forest sites.
[b] Flame height (*flame*, m), fire-line intensity (*int*, kW/m), scorch height (*scorch*, m), and soil heat (*soilH*, oC).
[c] Surface-fire emissions of carbon dioxide (CO_2), carbon monoxide (*CO*), methane (CH_4), and particulate matter ($PM_{2.5}$), respectively (g/m^2).
[d] Maintenance (*mr*), heterotrophic (*hr*), and growth respiration (*gr*), respectively (kgC/m^2).
[e] Gross primary (*gpp*), net primary (*npp*), and net ecosystem production (*nep* = *nppn* − *hr*), respectively (kgC/m^2).
[f] Total (*totC*), above-ground (*abC*), and below-ground carbon (*bgC*), respectively (kgC/m^2).
[g] Fire-return-interval average (*fria*, years) and total area burned by individual fires (*area*, ha).

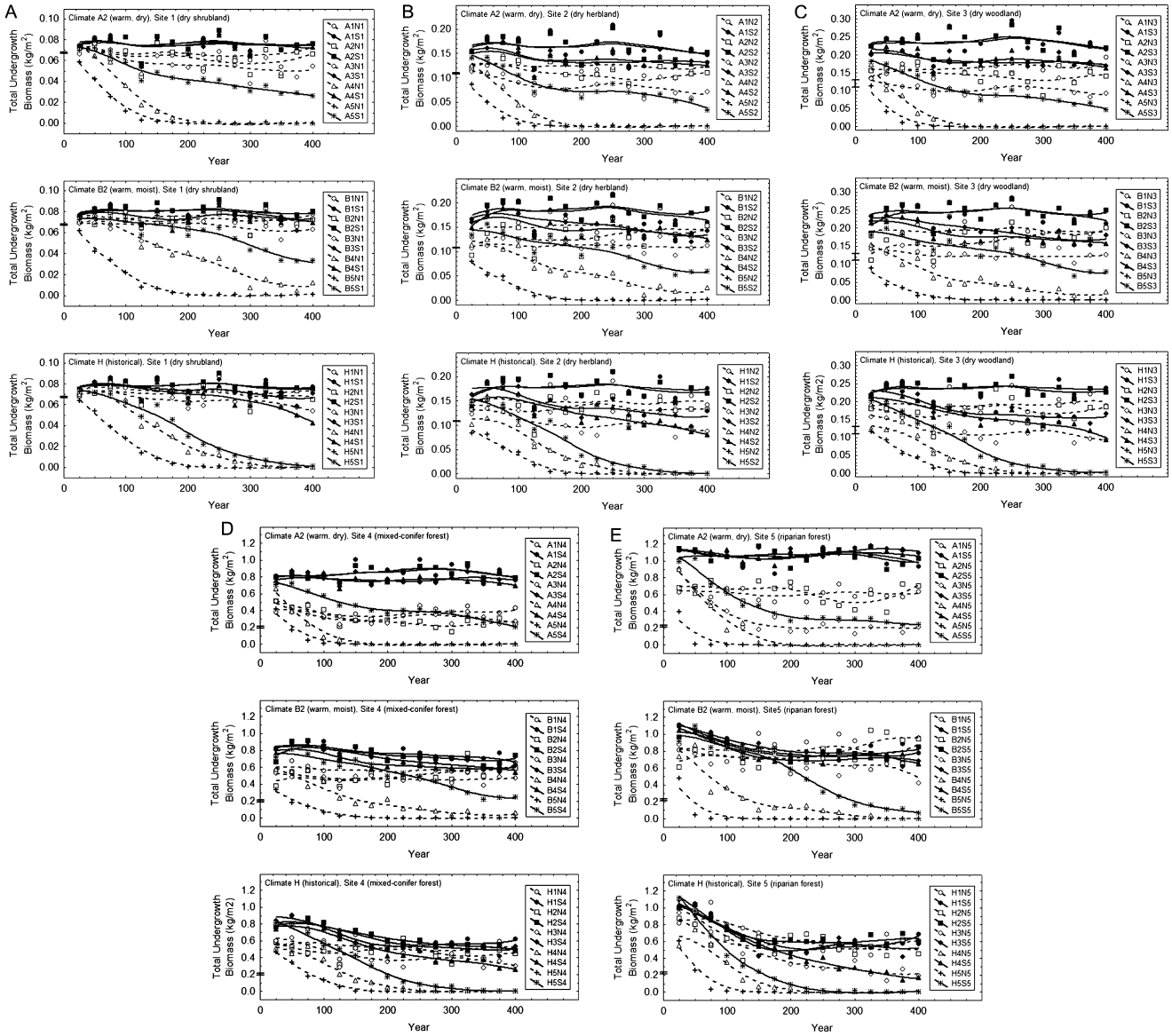

Fig. 5. Unadjusted raw means for total undergrowth biomass (kg/m^2) are paneled by biophysical site: (A) dry shrubland, (B) dry herbland, (C) dry woodland, (D) upland mixed-conifer, and (E) riparian forest. Outputs are graphed in each panel by climate scenario in descending order: A2, B2, and H. Mean responses are plotted in each graph on a 25-year sample interval. Graph legends code factor combinations according to climate (A = A2, B = B2, H = historical), grazing regime (1, 2, 3, 4, or 5), fire suppression (S = suppression, N = none), and biophysical site (1, 2, 3, 4, or 5). For example, "H5N4" codes the biomass dynamic estimated under the historical climate (H), with sustained heavy multi-species grazing (grazing regime 5), without fire suppression (N), in stands of upland mixed-conifer site potential (site 4). Results were calculated from 10 replicate, 400-year simulations of each multi-factor regime. Initial loadings are represented by horizontal bars (95% family) on the *Y*-axis. Note that *Y*-axis scaling increases across biophysical sites a through d.

We analyzed 23 output variables (Table 3), which we sampled from each 400-year output stream at 15-year interval so that the analyzed output from each of our 300 replicates contained 26 records. Each output was analyzed with a semi-parametric mixed-effects model (Wand, 2003). We addressed observed heteroscedasticity with optimized power transformation (Box and Cox, 1964). Temporal dependence of observations was dealt with by coding year (*Y*) as a single random effect, which we modeled as a penalized B-spline with random coefficients (Eilers and Marx, 1996). Statistics were calculated using SAS PROC TRANSREG and SAS PROC GLIMMIX (SAS Institute, Inc, 2011). Undergrowth and surface-fire outputs were analyzed up to the level of 4-way interactions among the 5 main effects (*H*, *C*, *F*, *S*, and *Y*). Landscape responses were analyzed to the level of 4-way interactions without respect to biophysical site (*S*). To enhance clarity, graphics in this paper are plotted on a 25-year interval using distance-weighted least squares procedures (StatSoft, Inc, 2009).

3. Results

3.1. Undergrowth biomass

Simulated undergrowth (e.g., *underB*, Fig. 5) was within maximum limits imposed from our literature synthesis. The simulated maximum for shrubland was about 98% of the maximum estimated possible from literature, for herbland 60%, woodland 90%, upland mixed-conifer 81%, and riparian forest 91%. Those simulated maxima increased with soil depth and site potential (i.e., shrubland < herbland < woodland < upland forest < riparian forest).

Simulated undergrowth biomass was affected by several factors over time (Table 4, Fig. 5). Each biomass variable was sensitive to herbivory at several levels in the design ($P \leq 0.07$), but four-way interactions predominated. Each variable was affected interactively over time by climate, herbivory, and fire suppression without respect to site ($P_{Y \times C \times H \times F} < 0.01$). Climate, herbivory, fire suppression, and biophysical site interactively affected each biomass response without respect to year ($P_{C \times H \times F \times S} < 0.01$).

The effect of climate warming on total undergrowth biomass was not particularly remarkable except under the A2 (warm, dry) scenario. Under that climate the differentiation of undergrowth biomass between the two fire-suppression regimes was somewhat greater than under the other two climates, at least on forest sites ($P_{Y \times C \times H \times F} < 0.01$; Table 4, Fig. 5).

Undergrowth dynamics among herbivory regimes were qualitatively similar across biophysical sites, but differences among herbivory regimes increased quantitatively as the biophysical site potential increased (Fig. 5). Those differences increased over time to such an extent that maximal differences between herbivory regimes in riparian forest (the most productive site) were roughly an order of magnitude greater than in dry shrubland (least productive).

Multi-factor regimes involving fire suppression tended to project greater undergrowth over time than did those lacking fire suppression. Furthermore, within each fire-suppression regime, mean undergrowth loads tended to array inversely with respect to herbivory (Fig. 5). Low-demand herbivory (no herbivores, wildlife-only, cattle-only) produced relatively stable long-term undergrowth biomass, on average, regardless of the biophysical site considered. Regimes involving all three herbivore populations (wildlife + livestock, wildlife + 2*x* livestock) tended to suppress undergrowth albeit affected by fire suppression. The mid-20th century regime, which involved relatively heavy cattle grazing, projected pronounced declines in undergrowth biomass either with or without fire suppression, and it did so under all three climates. The more moderate, late-20th century regime did so consistently only in the absence of fire suppression.

Total undergrowth response more closely resembled that of its constituent shrub biomass than herb biomass. All three outputs were similarly responsive to the experimental factors at most levels in the design. However shrub and total biomasses were strongly influenced over time by herbivory ($P_{Y \times H} \leq 0.02$) and by herbivory interacting with fire suppression ($P_{Y \times H \times F} \leq 0.07$), whereas herb biomass was not responsive at those same levels in the design ($P_{Y \times H} \leq 0.84$; $P_{Y \times H \times F} \leq 0.23$).

In woodlands and forests the tree canopy's base height (hbc) can interact with surface fire behavior to affect the likelihood that a fire will migrate upward from the undergrowth stratum to become a canopy or "crown" fire (Van Wagner, 1977). While undergrowth biomass responses were each sensitive to herbivory at several levels in our design, the *hbc* response was sensitive to herbivory in interaction with other fixed factors ($P_{C \times H \times F \times S} < 0.01$) but not in a manner that was year-sensitive.

3.2. Surface fire behavior

Surface-fire responses translate herbivory's effects on the undergrowth stratum into surface-fire behavior, which in-turn may articulate a stand's grazing history to a given fire's impact on vegetation above or below the fire. Flame length, fire-line intensity, and scorch height were similarly sensitive to herbivory (Table 5). Each of those metrics responded to year, climate, herbivory, and fire suppression interactively ($P_{Y \times C \times H \times F} < 0.01$) without respect to biophysical site, and in a manner congruent with total undergrowth biomass. However, surface fires responded thermally to the experimental factors in some ways that were different from the undergrowth's. Whereas total undergrowth biomass responded to interaction among climate, herbivory, fire and site without respect to time, (see above $P_{C \times H \times F \times S} < 0.01$), fire thermal variables were not responsive to those same fixed effects together ($P_{C \times H \times F \times S} \geq 0.39$). Furthermore, surface-fire was sensitive to 3-way interactions involving those same fixed factors ($P_{C \times H \times S} \leq 0.01$, $P_{H \times F \times S} \leq 0.07$), but each of those apparent interactions was subordinate to a higher-order interaction in which the year effect was also implicated ($P_{Y \times C \times H \times S} < 0.01$ and $P_{Y \times H \times F \times S} < 0.01$, respectively), and to which the undergrowth biomass variables were not sensitive (see above $P_{Y \times C \times H \times S} = 1.00$, $P_{Y \times H \times F \times S} \leq 1.00$, respectively). Thus, time-in-simulation apparently was more important to surface-fire behavior than it was to undergrowth biomass.

Table 4
Sensitivity of undergrowth biomass and tree-canopy base height to simulated experimental effects: table entries are probabilities of greater *F* statistic for the indicated effect.

Experimental effects[a]	Response variables			
	shrubB	*herbB*	*underB*	*hbc*
H	<0.01	<0.01	<0.01	0.91
C × *H*	0.41	0.66	0.39	0.99
H × *F*	<0.01	<0.01	<0.01	0.97
C × *H* × *F*	<0.01	<0.01	<0.01	0.99
Y × *H*	0.02	0.84	<0.01	0.95
Y × *C* × *H*	0.41	0.55	0.45	0.99
Y × *H* × *F*	<0.03	0.23	<0.07	0.99
Y × *C* × *H* × *F*	<0.01	<0.01	<0.01	0.99
H × *S*	<0.02	0.01	<0.01	1
C × *H* × *S*	1	1	1	1
H × *F* × *S*	0.02	0.99	<0.07	1
C × *H* × *F* × *S*	<0.01	<0.01	<0.01	<0.01
Y × *H* × *S*	0.64	0.99	0.99	1
Y × *C* × *H* × *S*	1	1	1	1
Y × *H* × *F* × *S*	0.84	1	0.92	1

[a] C: climate; F: fire; H: herbivory; S: site; Y: year.

To illustrate, Fig. 6 compares surface-fire flame lengths for the first 100 years of simulation on dry herbland and upland mixed-conifer sites. Results are congruent with those for biomass in several respects: (1) multi-factor disturbance regimes involving fire-suppression predict greater flame lengths over time; (2) flame lengths tend to array inversely with respect to herbivore demand under both fire-suppression regimes, with low-demand herbivory (no herbivores, wildlife-only, cattle-only) tending to predict longer flame lengths than high-demand herbivory (wildlife + cattle, wildlife + 2*x* cattle); and (3) differences in flame length among herbivory regimes increase with site potential. Differences in mean predicted flame lengths were generally ≤30 cm across scenarios.

Soil heating and smoke emissions from surface fires accorded generally with thermal behavior, but with some exceptions. Fire-line intensity, flame length, and scorch height were each sensitive to herbivory in all three interactions involving year (for each response: $P_{Y \times C \times H \times F} < 0.01$, $P_{Y \times C \times H \times S} < 0.01$, $P_{Y \times H \times F \times S} < 0.01$), but soil heat was sensitive to only the first two of those ($P_{Y \times C \times H \times F} = 0.05$, $P_{Y \times C \times H \times S} < 0.01$, $P_{Y \times H \times F \times S} = 0.26$). Sensitivity of the four emission responses accorded with that of soil heat (for each response: $P_{Y \times C \times H \times F} < 0.03$, $P_{Y \times C \times H \times S} \leq 0.03$, $P_{Y \times H \times F \times S} \leq 0.66$).

3.3. Responses at landscape scale

These outputs represent extents to which stand undergrowth and surface fire "scaled-up" to influence the entire landscape's respiration, production, carbon, and fire over time. At this scale each response was calculated across all stands, biophysical sites,

Table 5
Thermal and emission responses of surface fire to simulated experimental effects are analyzed for upland sites only; surface-fires on riparian site were excluded due to insufficient sample size. Table entries are probabilities of greater *F* statistic for the indicated effect.

Experimental effects[a]	Surface-fire responses							
	Thermal				Smoke emissions			
	int	flame	scorch	soilH	CO_2	CO	CH_4	$PM_{2.5}$
H	<0.01	<0.01	<0.01	0.92	<0.01	<0.01	<0.01	<0.01
$C \times H$	<0.01	<0.01	<0.01	0.58	<0.01	<0.01	<0.02	<0.01
$H \times F$	<0.01	<0.01	<0.01	<0.03	0.1	0.13	0.04	0.16
$C \times H \times F$	<0.01	<0.01	<0.01	0.34	<0.01	<0.01	<0.01	<0.01
$Y \times H$	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.21	<0.01
$Y \times C \times H$	<0.01	<0.01	<0.01	0.04	<0.01	<0.01	0.18	<0.01
$Y \times H \times F$	<0.01	<0.01	<0.01	0.16	<0.01	0.05	<0.02	0.07
$Y \times C \times H \times F$	<0.01	<0.01	<0.01	0.05	<0.01	<0.03	<0.01	0.01
$H \times S$	<0.01	<0.01	<0.05	<0.01	0.02	0.04	<0.02	<0.01
$C \times H \times S$	<0.01	<0.01	0.01	<0.01	0.2	0.08	0.11	0.03
$H \times F \times S$	<0.01	<0.01	<0.07	0.17	0.05	0.13	0.12	0.11
$C \times H \times F \times S$	0.44	0.39	0.4	0.4	0.45	0.24	0.19	0.45
$Y \times H \times S$	<0.01	<0.01	<0.01	<0.01	0.1	<0.24	0.09	0.08
$Y \times C \times H \times S$	<0.01	<0.01	<0.01	<0.01	<0.01	0.01	0.03	<0.01
$Y \times H \times F \times S$	<0.01	<0.01	<0.01	0.26	0.21	0.36	0.19	0.66

[a] C = Climate; F = Fire; H = Herbivory; S = Site; Y=Year.

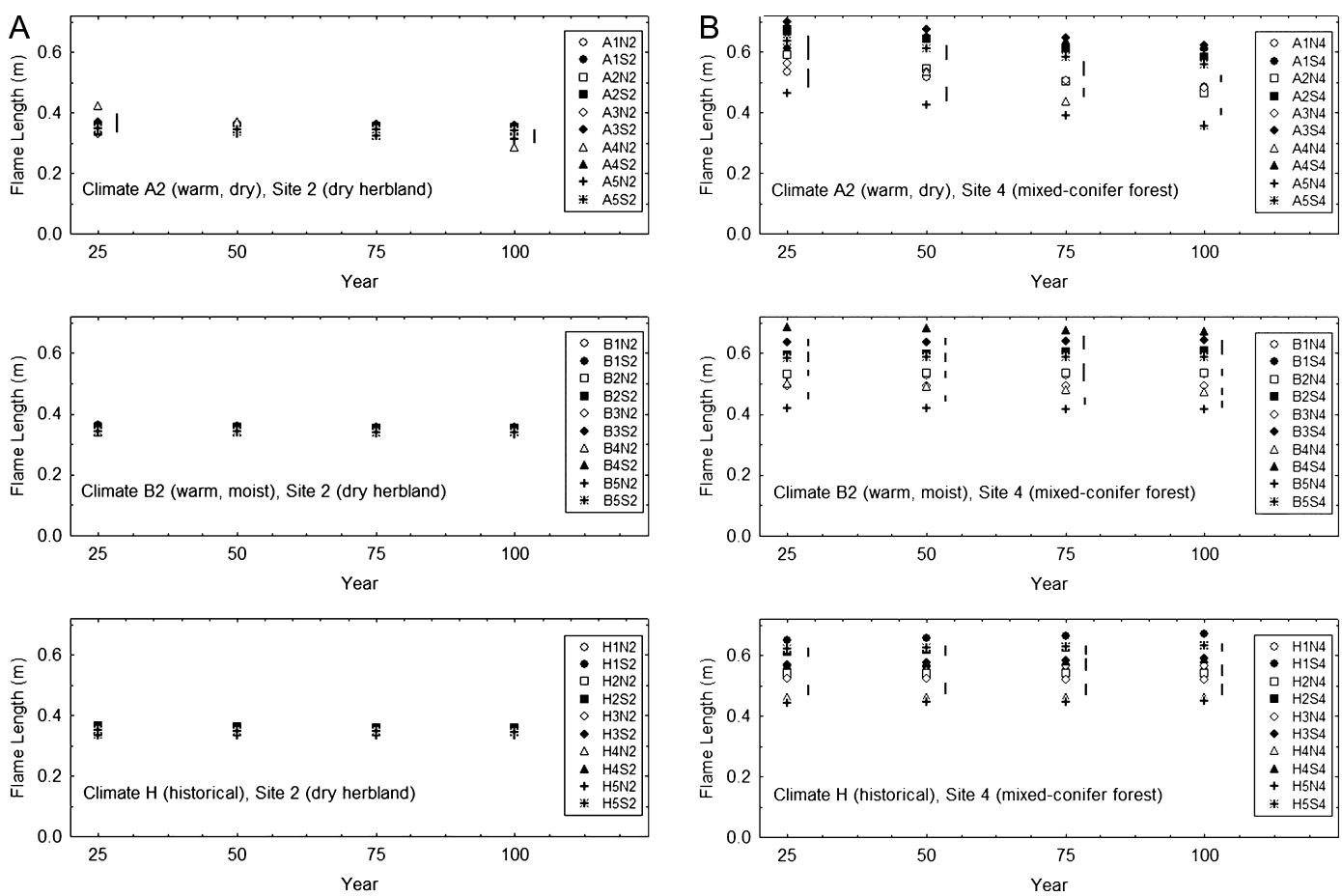

Fig. 6. Least-squares predictions for surface-fire flame length (m) are paneled for: (a) dry herbland, and (b) upland mixed-conifer forest. Outputs are graphed in each panel by climate scenario in descending order: A2, B2, and H. Predictions are plotted on a 25-year sample interval for the 1st 100 years of simulation only. Graph legends code predictions according to climate (An= A2, B = B2, H: historical), grazing regime (1, 2, 3, 4, or 5), fire suppression (S: suppression, N: none), and biophysical site (1, 2, 3, 4, or 5). For example, "H5N4" codes the mean flame length predicted under the historical climate (H), with relatively heavy multi-species grazing (grazing regime 5), without fire suppression (N), in upland mixed-conifer stands (site 4). Vertical bars separate predicted means that were statistically different ($P = 0.05$). Flame lengths were higher in forests and woodlands, higher with fire suppression than without it, and arrayed inverse to herbivory regime. Herbivory had no effect in the hot dry shrubland. Its effect was intermediate in woodland, and not testable in riparian forest because the number of simulated fires was insufficient for analysis there.

Table 6
Landscape-scale responses to experimental effects: Table entries are probabilities of a greater *F* statistic.

Experimental effects[a]	Landscape-scale responses										
	mr	*hr*	*gr*	*gpp*	*npp*	*nep*	*totC*	*abC*	*bgC*	*fria*	*area*
H	0.59	0.74	0.85	0.87	0.71	0.8	0.93	0.94	0.83	0.09	0.45
$C \times H$	0.98	0.99	0.99	0.89	0.79	0.89	0.99	0.99	0.96	0.71	0.87
$H \times F$	0.54	0.88	0.58	0.71	0.68	0.91	0.57	0.62	0.49	0.02	0.14
$C \times H \times F$	0.86	0.83	0.99	0.9	0.89	0.77	0.85	0.88	0.85	0.82	0.88
$Y \times H$	0.64	0.68	0.83	0.88	0.75	0.74	0.89	0.89	0.79	0.14	0.8
$Y \times C \times H$	0.99	0.99	0.99	0.99	0.8	0.83	0.99	0.98	0.99	0.89	0.58
$Y \times H \times F$	0.73	0.95	0.57	0.94	0.78	0.9	0.69	0.73	0.71	0.67	0.07
$Y \times C \times H \times F$	0.84	0.84	0.99	0.96	0.9	0.73	0.82	0.86	0.84	0.93	0.55

[a] C: climate; F: fire; H: herbivory; S: site; Y: year.

and fires, thus integrating tree dynamics and crown fires as well as undergrowth dynamics and surface fires.

Increasing the grazing regime generally lengthened the landscape's fire return interval average (*fria*), but herbivory's influence was modest compared to that of the climate and fire suppression. The *fria* was sensitive to herbivory only at three levels in our design (Table 6). The main effect of herbivory: (1) was marginally significant ($P_H = 0.09$); (2) marginally increased over time ($P_{Y \times H} = 0.14$); and (3) increased the return interval more in the absence of fire suppression than with it ($P_{HxF} = 0.02$). Neither 3-way nor 4-way interactions were statistically significant ($P_{Y \times H \times F} = 0.67$; $P_{Y \times C \times H \times F} = 0.93$). Fire-suppression and the climate each influenced the return interval more strongly than did herbivory ($P_F < 0.0001$, $P_C < 0.02$, $P_{C \times F} = 0.12$), but fire suppression lengthened the return interval, while the A2 climate shortened it (Fig. 7).

Other responses to herbivory at landscape scale were not compelling. Herbivory regimes and fire suppression regimes interactively influenced the size of individual fires over time ($P_{Y \times H \times F} = 0.07$) but without a clear pattern (Fig. 8). Over time, climate and fire-suppression each had a stronger influence on fire area than did herbivory ($P_{Y \times C} < 0.01$; $P_{Y \times F} < 0.01$; $P_{Y \times H} = 0.80$). Respiration (maintenance, heterotrophic, growth), primary production (gross, net, net ecosystem) and carbon (total, above-ground, below-ground) were each insensitive to differences among the simulated herbivory regimes (Table 6), as illustrated for net primary production (Fig. 9).

4. Discussion

Perhaps the most important challenge facing applied ecologists is to develop the capability to predict how various ecosystems will respond to combinations of multiple disturbance agents. This will require integration of sometimes disparate modeling approaches. As discussed by Weisberg et al. (2006), herbivory models have typically taken one of two approaches: focus on herbivore dynamics or focus on vegetation dynamics, with the latter approach emphasizing either herbivory's effects on plant production (biomass-based models) or it effects on tree regeneration (forest GAP models). FireBGCv2/GrazeBGC combines biomass and GAP emphases in one model. Those authors also made compelling arguments for integrating the herbivore- and vegetation-focused approaches, particularly when the making of long-term predictions requires understanding how feedbacks will operate between plant and animal populations over time. The most notable advancement toward that particular level of integration remains SAVANNA, which has been widely applied in western North America, and particularly in Rocky Mountain ecosystems that are similar in many respects to ours (Coughenour and Singer, 1996; Coughenour, 2002; Weisberg et al., 2002; Weisberg and Coughenour, 2003). FireBGCv2/GrazeBGC provides similar integration to a point; it does enable feedbacks that contribute to spatially–explicit regulation of vegetation biomass, fire behavior, and thus herbivory over time, but as yet the system does not contain a mechanism for feedback regulation of herbivore populations.

Ecologists concerned with predicting relationships between climate, vegetation, and fire have been faced with challenges similar to those faced by herbivore ecologists. In fire science those challenges have motivated the advancement of LFSMs, in which vegetation-focused models concerned with production, regeneration, and succession are variously integrated with models for fire ignition, behavior, and effect. FireBGCv2 is one of those, which uses

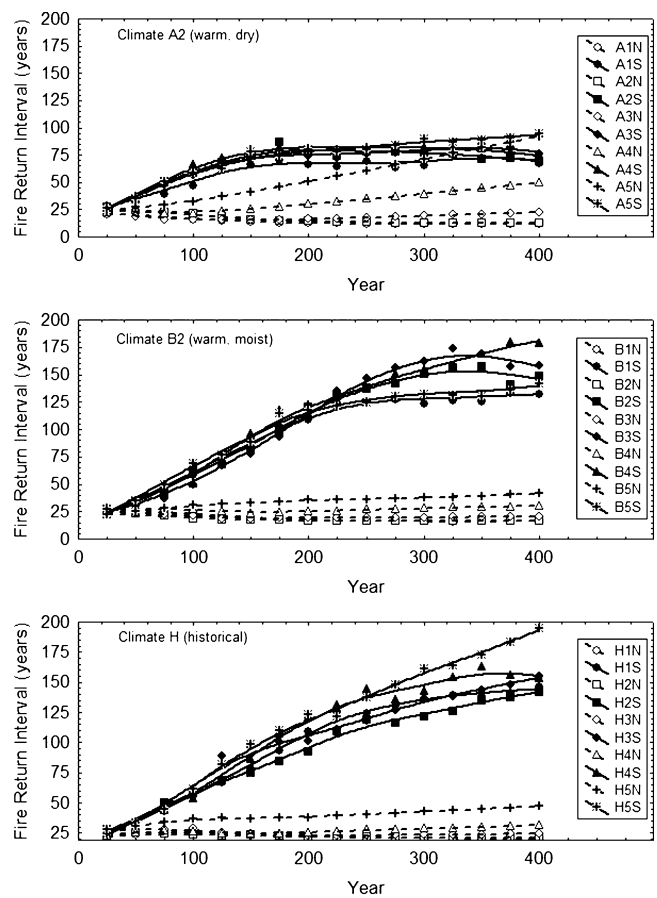

Fig. 7. The MMC's fire-return interval average (*fria*) is predicted from replicated simulation of different scenarios. Each graph represents a different climate scenario (A = A2, B = B2, H: historical), within which grazing regimes (1, 2, 3, 4, or 5) and fire-suppression scenarios (S = 90% suppression, N: none) are crossed. For example, "H5N" codes the mean return interval under the historical climate (H), with relatively heavy multi-species grazing (grazing regime 5) and without fire suppression (N). The influence of herbivory was insignificant compared to that of fire suppression, except in the warm and dry climate.

both mechanistic biogeochemical and process-based GAP concepts to predict spatially–explicit biomass, fuels, and fire, and which has been widely applied to a variety of fire- and climate-related problems (for examples see http://www.firelab.org/project/firebgcv2-simulation-platform-and-projects).

Herbivory models and LFSMs are not mutually-exclusive, and from each discipline has come some notable attempts to integrate one with the other (e.g., Coughenour and Singer, 1996; Jeltsch et al., 1997; Bachelet et al., 2000; Butler et al., 2007; Joly et al., 2012; Pachzelt et al., 2013; Rupp et al., 2006). However reviews in each discipline illustrate that comprehensive integration has not been a prominent focus in either one (Keane et al., 2004; Weisberg et al., 2006). Weisberg et al. (2006) identified five challenges to integrating herbivore- and vegetation-focused models: (1) interaction between multiple plant and animal species; (2) cultural features and land use change, (3) interaction among herbivores and other disturbances; (4) non-herbivore effects at landscape scale such as plant propagule dispersal; and (5) multi-scale processes and interactions. FireBGCv2/GrazeBGC attempts to address those challenges by integrating spatially–explicit herbivory as a modifier of time- and spatially–explicit plant growth and biomass accrual, which then can interact with climate and weather, fire and with the other disturbance agents that drive vegetation dynamics in individual stands of vegetation and thus across landscape mosaics. The system's chief quality is its inter-disciplinary construction, which forces herbivory into common temporal and spatial contexts with plant growth and other disturbance agents. Some of the system's other benefits include: (1) seamless modification of plant biomasses from stand to landscape scales; (2) spatially–explicit interaction between herbivore populations; (3) articulation of episodic disturbance to prior plant growth and herbivory; (4) spatially–explicit feedbacks to future herbivory from episodic disturbance and succession; and (5) a capability to infer succession and potential stable-state transitions from changes in stand-scale biomass composition over time. Its diversity-matrix architecture is flexible and enables its vegetation outputs to be used as inputs to post-process habitat analyses for animal species. Nevertheless, its integration of herbivory remains imperfect because it still lacks mechanisms for negative feedbacks to herbivore population dynamics.

Our principal interest was in understanding extents to which FireBGCv2's predictions would change by adding spatially–explicit herbivory. We addressed the problem with an experiment in grass-tree mosaic that is typical of much of the interior northwestern United States. Here stand-level modification by herbivores of forest undergrowth and succession (Alldredge et al., 2001; Kelly et al., 2005; Monfore 1983; Riggs et al., 2000), fire behavior in forests (Zimmermann and Neuenschwander, 1983, 1984), tree growth (Weigand et al., 1993), and nutrient processes (Riggs et al., 2000; Stewart et al., 2006) have empirical basis generally consistent with research in boreal forests (e.g., Pastor et al., 1993; Pastor and Cohen, 1997). Those observations have bolstered logical arguments that large herbivores and domestic livestock in particular were prominent drivers of succession and fire across western landscapes in the 20th century (Belsky and Blumenthal, 1997; Hyerdahl et al., 2001; Langston, 1995). Less clear

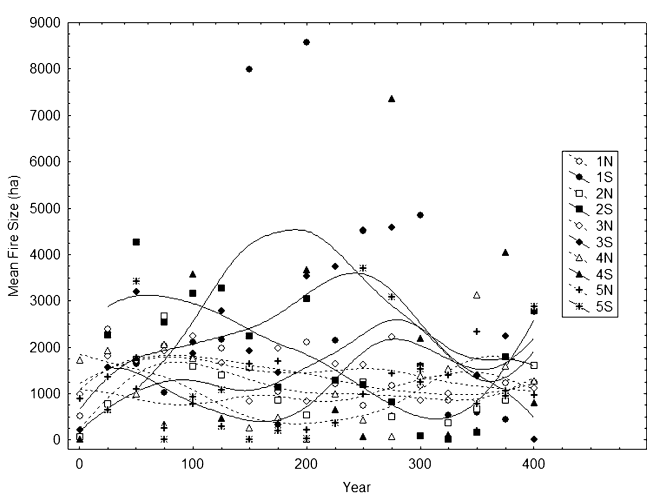

Fig. 8. Simulation results for the average area burned by individual fires are plotted on a 25-year sample interval. Each data point is the mean of individual fire areas during the indicated year, including all stands on all biophysical sites represented within each fire's perimeter. Grazing regimes (1,2,3,4, or 5) and fire-suppression regimes (S: suppression, N: none) are crossed with one another over time. For example, "1N" codes the mean fire size given no ungulate herbivory (grazing regime 1) and given no fire suppression (N). Means were calculated from 10 replicate, 400-yearr simulations of each multi-factor regime. The hypothesized herbivory effect was only marginally significant in an interaction with fire suppression over time ($P_{YxHxF} = 0.07$). Climate and fire-suppression (not shown) each had a stronger unilateral influence on fire size over time than did herbivory ($P_{YxC} < 0.01$; $P_{YxF} < 0.01$; $P_{YxH} = 0.80$), and there were no other significant interactions involving herbivory ($P_{YxCxH} = 0.58$; $P_{YxCxHxF} = 0.55$).

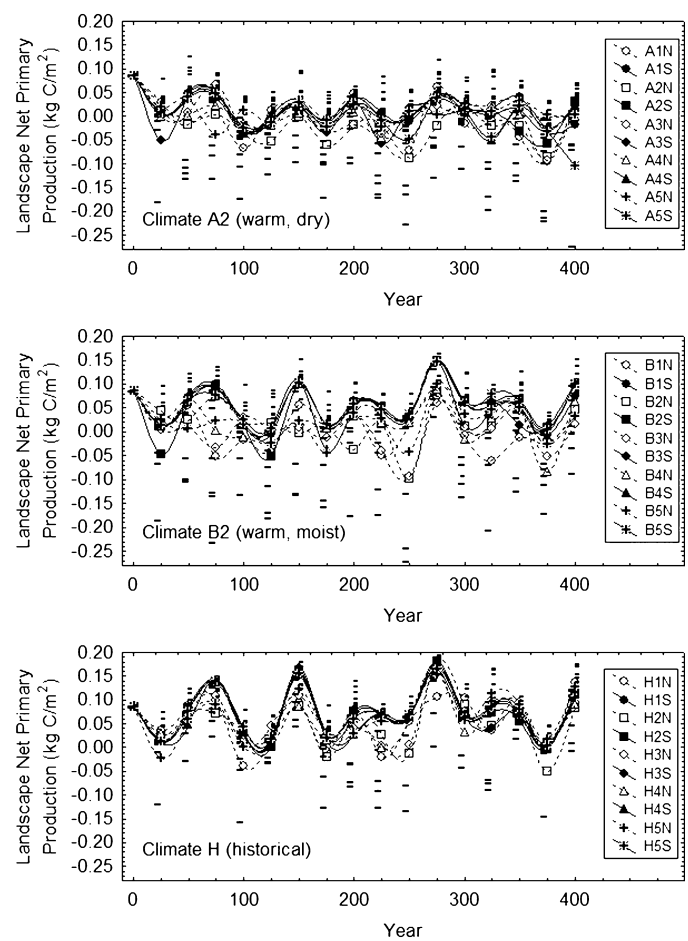

Fig. 9. Results for landscape net primary production (*npp*) are plotted on a 25-year interval. Each graph represents a different climate (A = A2, B = B2, H: historical), within which grazing regimes (1, 2, 3, 4, or 5) and fire-suppression (S or N) are crossed with one another. For example, "H5N" codes the mean *npp* under the historical climate (H), with sustained heavy multi-species grazing (grazing regime 5) and without fire suppression (N). Means were calculated from 10 replicate, 400-year simulations of each multi-factor regime. To illustrate the range of response variability, upper and lower confidence limits (95% families) are shown with small and large horizontal bars, respectively. Climate and fire-suppression effectiveness were the dominant influences on landscape *npp*. Modeled herbivory did not significantly affect the platform's respiration, productivity, or carbon outputs at this spatial scale (see Table 6).

is the future importance of shifting herbivore composition (wild versus domestic herbivores) or that of aggregate herbivory to landscape dynamics, as compared to that of other agents – most notably fire suppression and climate change – which cannot be known with certainty. In our experiment herbivory affected vegetation in ways that were: (1) qualitatively similar across biophysical sites but quantitatively site-specific in magnitude; (2) contingent on the effectiveness of future fire suppression and on expected future climate; (3) pronounced when herbivory involved all three herbivore populations near historical average; and (4) diminished as the spatial scale of analysis increased.

Our analysis of undergrowth biomass focused on guild aggregates (*shrubB, herbB, underB*) to capture the dynamics of undergrowth fuels. Biomass in those aggregates was suppressed by increasing herbivory, and differences in biomass accrual among herbivory regimes translated into suppressed surface fire behavior. Herbivory's effects on undergrowth biomass and on fire behavior increased with site potential.

The apparent site specificity of herbivory's effects may be viewed as a proximate result of the module's spatially–explicit allocation of herbivore demand, which responds to inter-stand variation in nutritional biomass. In this landscape, plant growth is ultimately controlled by the combination of moisture input from winter-spring precipitation and the spatially-variable ability of soils to capture and retain that moisture into the summer drought. Precipitation per se is not necessarily limiting, but moisture retention is so that relatively high plant production persists longer on forest soils than on the shallower soils of non-forest sites. The module's spatial and diet algorithms respond by shifting each herbivore population's biomass consumption toward its preferred guilds on the more-productive sites in the summer drought, thereby producing site-specific effects.

The magnitude of herbivory's suppressive effect on undergrowth biomass was influenced by the landscape's fire-suppression regime and by site potential. Multifactor regimes involving fire suppression accumulated more undergrowth biomass than those without fire suppression. Furthermore, on a given biophysical site and under a given fire-suppression regime, increasing herbivory resulted in less biomass accumulation.

Herbivory's effects on surface-fire behavior were greater under those regimes that involved both wild herbivores and domestic livestock. Our experiment was not formulated to determine the relative importance of herbivore density compared to herbivore richness as fire-suppression factors; the two factors were linked in our design. However additional herbivore populations certainly increased biomass consumption and thus also the suppression of undergrowth fuels without regard to guild specificity. In this landscape the preferences of deer and elk compliment those of domestic cattle (Cook et al., 2004,b; DelCurto et al., 2014a,b); wildlife tend to prefer shrubs and forbs more than do cattle, whereas cattle tend to strongly prefer grasses. Consequently, addition of cattle to the wildlife-only regime broadened consumption of biomass across plant guilds in addition to increasing the quantity of biomass consumed.

It has been argued that large herbivores are the major drivers of ecosystem shape and function (Danell et al., 2006). Our results may temper expectations somewhat, depending on a given landscape's structure, its fire management and herbivore populations. If a landscape is principally grassland or savanna, then herbivory probably can be managed with fire to effectively maintain a current condition by reducing undergrowth fuels and thus facilitate relatively moderate ground-fire behavior over time. However, herbivory's effectiveness is probably reduced in those landscapes where prolonged fire suppression has facilitated transition from savanna-like woodlands into closed-canopy forests (where fuels are predominately woody, not herbaceous, and where herbivore carrying capacity is low). Even in savanna woodlands relatively high levels of multi-species grazing are probably required to influence fire behavior across an entire landscape. Our results do support the notion that 19th and early 20th century livestock grazing contributed to modifying fire regimes. However our results also suggest that herbivory's influence on future fire will more-likely be a function of multi-species grazing interacting with fuel and fire management, rather than a mere function of livestock grazing alone. This conclusion may be particularly salient to managers where the balance between wild herbivores and livestock is shifting (e.g., Irwin et al., 1994).

Repeated use of particular landscape settings is a predictable result of herbivores converging on selected resources (Stubblefield et al., 2006). In our simulations, nutritionally-driven herbivory had its greatest effects on biomass and fire in stands where high nutritional biomass was facilitated by high site potential, which was itself driven by soil depth and moisture. That result accords generally with the idea that herbivore functions are mediated through grazing intensity and animal density (e.g., Singer and Schoenecker, 2003), which is somewhat different from the idea that those functions are inversely proportional to site productivity (e.g., Augustine and deCalesta, 2003). Our result may seem counter-intuitive if one assumes that less-productive vegetations (e.g., hot dry herblands or shrublands) must be intrinsically the less-resilient to grazing. Nevertheless, herbivory's spatially–explicit impact on vegetation must vary as a function of those factors that drive spatial heterogeneity in grazing intensity (e.g., Hunt, 2001; Palmer et al., 2003). The principal factor driving that heterogeneity in the MMC is the interaction between seasonal precipitation and site-specific soil depth, which drives the site productivity to which our grazing algorithms responded. Foraging dynamics in this model are congruent with expectations based on site-level differences in plant phenology (Korfhage et al., 1980; Skovlin, 1967), site-dependent nutrient mineralization and plant production (Singer and Schoenecker, 2003; Stewart et al., 2006; DelCurto et al., 2005; Persson et al., 2009), and with expectations that herbivory should be temporally and spatially transient in episodically-disturbed landscapes (Canon et al., 1987; Collins and Urness, 1983; Darambazar et al., 2013; Hobbs, 1996; Riggs et al., 1996; Skovlin et al., 1989; Van Dyke and Darragh, 2007).

Another result of our experiment was that shrub and total undergrowth biomasses were more sensitive than herb biomass to herbivory and fire over time. This particular result is largely explained by the different rates of intrinsic biomass growth among plant guilds (η) and their biomass maxima ($UBIOMASS_{\max}$), which are supplied by the platform (Eq. (3)). On average, shrubs have higher biomass maxima than herbs in this landscape, while the intrinsic rate of biomass growth for shrubs is relatively low. In our simulations, η was much lower for shrubs than for either perennial or annual herbs (1.14, 5.48 and 10.86, respectively), and thus shrubs were predisposed to relatively slow biomass accrual following fire and browsing in any stand. Also, much of the difference in total undergrowth biomass in forests in particular (see Section 2.3.1 above) is attributable to the woody biomass of shrubs that accumulates in stands over time albeit at slow rates. Relatively slow rates of biomass growth interact with high biomass maxima to cause shrub biomass (and total biomass by extension) to be more responsive than herb biomass to factors that either slow biomass growth and accumulation (herbivores) or re-start succession (fires). Therefore, good understanding of how those rates and maxima vary among guilds is crucial. Our results agree with shifts in forest successions, from shrub- to herb-dominated undergrowth states, which have been observed following episodic disturbance and herbivory (Riggs et al., 2000).

Herbivory involving wild and domestic herbivores tended to reduce undergrowth biomasses over the long-term – ultimately to near zero after 150 or more years of simulation (depending on the scenario; Fig. 5). This particular result is largely attributable to the module's current lack of nutritionally-mediated negative feedbacks to the herbivore populations. We did vary herbivore demands within each year to reflect anthropogenic forcing (livestock rotation), seasonal migrations (of elk and deer), births and deaths (elk and deer), and body-mass dynamics (all three species); but we held each population's intra-annual dynamic constant from one year to the next. Consequently, secondary successions following fires were grazed from outset at levels contrained only by the initialized herbivore demands. Our strategy was reasonable for exploring the translation of herbivory into fire behavior, but it nevertheless ignored any likelihood that numerically dynamic herbivore populations would buffer vegetation response. Modeling nutritional feedbacks to herbivore mortality, emigration, and/or spatial management of populations following hard winters or large fires will be important in lengthy simulations (Illius, 2006).

We also explored the extent to which the platform translated site- and stand-level effects of herbivory into effects on landscape metabolism and fire. Most research concerning effects of herbivores on plant production has been conducted at relatively fine scales (plant, stand), but it is impossible to project effects observed at those scales to a landscape as a whole without simulation modeling. In theory, stand-level effects could translate into significant effects at the landscape scale if herbivory's modifications of vegetation are of sufficient magnitude and sufficiently widespread. Notwithstanding that logic, only the fire-return interval was sensitive to herbivory regimes in our experiment. Mean fire size was not clearly influenced by herbivores, while landscape respiration, primary production, and carbon were insensitive (Table 6).

The apparent insensitivity of landscape metabolism to herbivores may be largely attributable to the stochastic variability produced by fire and weather on this platform. However it may also be attributable in some part to the lack of any detailed nitrogen cycling in its mechanistic GAP simulations. Without an articulate cycling routine it is not possible to simulate accelerated nitrogen returns through herbivore digestive tracts. In our analysis of stand attributes, the *hbc* response was not sensitive to herbivory but in theory it could have been so, assuming that tree growth is principally nitrogen-limited and assuming sufficiently accelerated nitrogen return from forage plants to trees through herbivores. Even so, those returns would have to be reconciled with returns to undergrowth plants and with nitrogen fluxes due to fire and other factors (Keane et al., 2011:47; Tanentzap and Coomes, 2012).

We used the platform's mechanistic GAP option, which does not have a detailed nutrient cycling routine. The BGC option (which we did not use) does simulate returns from decomposition of organic matter, and it does so in a manner that can be adapted to address facilitation by herbivores (e.g., as reviewed by Hobbs, 1996, 2006). Nevertheless, implementing herbivore-mediated returns to a landscape in any meaningful way requires knowledge of where those returns will be distributed spatially (Schoenecker et al., 2004) – among stands and among guilds or species within stands. We did not have that detailed knowledge for our landscape, and so we used mechanistic GAP rather than the platform's BGC simulations.

Our results are nonetheless intriguing in light of some previous field research in our own study area. Stewart et al. (2006) found that modification of net above-ground primary production (NAPP) by elk and deer was insignificant in field plots that they had placed on shallow soils typical of our dry herbland and woodland sites. While on deeper soils typical of our upland forest site, they found that elk and deer herbivory apparently explained up to 27% of the variation in NAPP for undergrowth plants in aggregate. Our module's logic produces temporal-spatial transience in herbivory in the same landscape, from dry sites to forest sites as spring and summer progress. This transience could help explain the findings of Stewart et al. (2006) on shallow soils. Furthermore, highly variable results on forest soils might be explained by spatial variation in conifer canopy density, species compositions, and resulting fine-scale variation in grazing intensity that are accounted for in the modeling system as well. In any event, the estimates of "NAPP" by Stewart et al. (2006) represented only undergrowth (shrubs, graminoids, forbs) whereas our simulated "*npp*" included 16 undergrowth guilds and trees as well. Thus the two studies are not strictly comparable.

Our simulations allocated herbivory among stands with a purely nutritional approach. Adapted from Senft (1987), our approach allocates biomass consumption according to the landscape's mosaic of nutritionally-relevant plant growth, and it does so without limiting the minimum amount of that growth to which herbivores can respond. Other options certainly exist, some perhaps allowing greater flexibility to nutritional constraint (see Hobbs and Swift, 1985), greater sensitivity to the density of acceptable biomass and foraging efficiency (Hobbs et al., 2003; Spalinger and Hobbs, 1992; Wickstrom et al., 1984), less sensitivity to total nutritional biomass (e.g., Wilmshurst et al., 1994), greater attention to nutrient balance among plant guilds (e.g., Hanley et al., 2012), or greater specificity to plant secondary chemistry (e.g., McArthur et al., 1993). Here we simply note that a variety of approaches can be implemented in the FireBGCv2/GrazeBGC system by modifying its plant models and/or the conditioning of nutritional biomass.

Non-nutritional factors can also influence where herbivores forage (e.g., topography, snow cover, barriers including fences, distance to water, disturbance by humans, sheltering cover from weather, etc.). We used resource selection functions to show how GrazeBGC can be used to implement multiple drivers, but other types of models might also be used. SAVANNA, for example, has used a habitat suitability approach, and there is no serious obstacle to using that approach on this platform. The salient point is that models containing both nutritional and non-nutritional drivers may provide useful insights beyond those attainable from a purely nutritional approach. Stubblefield et al. (2006), for example, found that elk responded spatially to forage biomass in meadows and to meadow shape. Our nutritional algorithm could capture the importance of nutritional biomass in meadows, but it could not capture that of meadow shape.

Regardless of the particular algorithm one uses to drive herbivory spatially in an LFSM, the foraging distribution it predicts should not be confounded by other activities, and explicit attention should be given to underlying assumptions (Keating, 2004). RSPF predictions across landscapes, for example, generally assume that resource availabilities (those which underlie the RSPF's coefficients) remain relevant across a heterogeneous landscape (Boyce and McDonald, 1999; Ciarniello et al., 2007). But that assumption will be weak if the herbivore's selection strategy is sensitive to spatial variation in resource availability (Osko et al., 2004). Such considerations may be particularly important in LFSMs because the spatially-explicit disturbance and vegetation dynamics produced by these models can substantially vary resource availabilities over time as well as over space, and to very different extents among the disturbance regimes that are being modeled.

We allocated herbivory spatially as an aggregate behavior of each herbivore population. Aggregate behavior models project

the average behavior of animals in a population, but they do so without explicit respect to the cognitive processes of individuals that underlie their aggregate behavior. For comparison, individual-based models do try to account for individual cognition (e.g., Beecham et al., 2002; Oom et al., 2002, 2004, 2008; Avgar et al., 2013). But the parameterization of individual models can be rather abstract, including for example an animal's "determinism" to eat certain things, or its "foraging extent bias" to constrain foraging spatially based on individual knowledge (e.g., Oom et al., 2008). Our algorithm produced deterministic foraging and it assumed perfect knowledge of each zonal mosaic by each population's individuals in aggregate. The "perfect knowledge" assumption may not be realistic for individual animals or even for entire populations. When herbivore densities are very low, for example, our algorithm could produce unrealistically low grazing intensities spread variously across the entire landscape, and this could require defining a minimum population size for simulation or perhaps the addition of an individual-based clustering algorithm to limit foraging extent. At high herbivore densities our algorithm forces all grazing to remain within the landscape, when perhaps some displacement out of it might be a more reasonable expectation.

Herbivore responses to spatial changes in their foraging substrates are likely to be slowed or retarded as spatial extent increases relative to herbivore numbers. Furthermore, the learning time required to become familiar with resources should be somewhat greater in disturbance-affected landscapes than in static ones. Learning time may lag herbivory's spatially–explicit influences on vegetation (see McNulty et al., 1997; Porter et al., 1991 in Augustine and deCalesta, 2002) and thereby produce temporary spatial refuges where some plants are grazed to lesser extents. We did not impose such lags, but they probably are important drivers of plant establishment particularly when herbivore densities are low relative to spatially-shifting plant production.

Finally, our simulations omitted several factors that could have modified results. Most of the MMC is forest (Fig. 3). Forest-management sequences can have strong implications for overstory-undergrowth dynamics, soil disturbance and seed beds, and for the composition and density of undergrowth biomass in secondary succession (Riggs et al., 2000, 2004; Young et al., 1967). Insect infestations and plant diseases also affect plant composition, fuels, and fire behavior (Hicke et al., 2012). FireBGCv2's other modules implement spatially–explicit timber harvest scenarios and some tree pathogens (Keane et al., 2011), but we did not implement those. Predator avoidance by herbivores has been proffered as a significant driver of spatially–explicit vegetation dynamics (Ripple and Beschta, 2004, 2007), but we lacked equations to implement it as such. Herbivores also influence plants in ways that extend beyond simple biomass consumption (Hester et al., 2006) including depression of seed production (e.g., Kay and Chadde, 1992; Kay, 1995; Chadde and Kay, 1991) and modification of seedling demography (Liang and Seagle, 2002). We did not model those effects. Fire modifies seed beds, seed banks and vegetative propagates through first-order effects (Stephan et al., 2010), and we did not model those explicitly. Any of those concepts could have produced somewhat different results from ours. Those differences would certainly be of interest heuristically, perhaps important to the veracity of conclusions, and thus are important avenues for simulation-based research.

5. Conclusions and management implications

Climate change increases our need to understand how vegetation mosaics will respond to other disturbance agents over time. The challenge is inter-disciplinary. It is important not only for understanding vegetation dynamics for their own sake, but also for understanding limits to herbivore production (Cook et al., 2004, 2013) and the sustainability of landscape-management systems (DelCurto, 2005; Vavra et al., 2005; Weisberg et al., 2002). Managers and policy analysts will increasingly require integrated models that sensitize their understanding of landscape disturbance and succession to large herbivores as well as to episodic agents.

Furthermore, resource management's credibility increasingly depends on integrating multiple disciplines in ways that can be understood by policy makers and the public as well as by practitioners and scientists (Hanley, 1994; Weisberg et al., 2006). Spatially–explicit interactions between multi-species grazing, episodic disturbance, and climate certainly must matter to those who must think strategically. LFSMs offer integrative capability that can provide strategic insights to how landscapes work, which cannot be gleaned using non-integrative approaches alone.

We conclude, as others have, that herbivory should be considered a potentially crucial component of any modeling that is aimed at predicting succession or fire. This is particularly true if there is uncertainty regarding future herbivore-management policies or uncertainty regarding their possible interactions with other disturbance agents. The system we have presented offers useful integration provided there is sufficient data and expertise to run it. It continues to develop, and its use is certainly not beyond the capabilities of public resource-management agencies, large private-sector companies, or independent research groups, particularly if they all collaborate.

Regional literature from the western U.S. has historically focused on livestock as the dominant large-herbivore disturbance agent, and it has done so without a great deal of regard to wildlife populations outside of parks and other reserves. Our results nevertheless illustrate the functional significance of multi-species regimes in which herbivory by wildlife is as important as that by livestock to our expectations for landscape vegetation dynamics. That result alone should help justify improved strategic integration of wild herbivores with livestock in land management, and hopefully in ways that will reconcile their aggregate herbivory with other disturbance agents. If vegetation mosaics are to be managed successfully for resilience in the face of a variable climate, then managers must be able to foresee how optional herbivore strategies will interactively affect landscapes a priori, not merely react to prevailing regimes post hoc. Such efforts will benefit from further development of integrated landscape fire succession models.

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Appendix A.

Index to FireBGCv2/GrazeBGC variables.

Variable	Equation	Definition
A	(32)	A seasonal vector of herbivore preferences for plant guilds
α	(24)	A plant guild's individual coefficient in a preference vector
A	(8)	A spatial area
AU	(12)	A female herbivore and her calf
AUM	(8)	One AU stocked on pasture for 30 days
B	(16)	A stand's biomass of preferred undergrowth
$\underline{B}$	(23)	A stand's biomass of nutritionally relevant undergrowth
b	(24)	A plant guild's biomass that is relevant to herbivory
β	(27)	Probability coefficient for a prediction factor (RSPF)
CYG	(26)	A plant guild's biomass grown in the current year
c	(30)	daily increment for cropping a guild's biomass
DE	(25)	Digestible energy in a plant guild's biomass
DMD	(26)	Dry-matter digestibility of a plant guild's CYG
d_{in}	(12)	Julian day a dominant herbivore population enters a zone
d_{out}	(12)	Julian day a dominant herbivore population leaves a zone
F	(5)	An herbivore population's forage biomass demand (kg)
f	(17)	Forage biomass demand that is allocated to a stand
$\hat{G}$	(16)	Proportion of grazing time or effort allocated spatially
g	(4)	A plant guild's daily growth increment
λ	(34)	Speed of a plant guild's growth response to utilization
N_i	(12)	Number of days for an herbivore population in-zone
N_k	(18)	Number of herbivore populations in a zone
$NETGROWTH$	(31)	The amount of CYG remaining after consumption
η	(3)	A multiplier for a plant-guild's annual biomass accrual
p	(5)	Proportion of a biomass demand allocated to a zone
RCP	(16)	Relative community preference
r	(9)	Rate of herbivore zonal displacement
$rSHADE$	(3)	Factor that adjusts a plant guild's growth for light deficit
$rWATER$	(3)	Factor that adjusts a plant guild's growth for water stress
RNQ	(22)	Relative nutritional quality of plant species or guilds
RP	(22)	Relative preference for a plant species or guild
$UBIOMASS$	(3)	A plant guild's annual peak standing biomass
$UCROPPED$	(30)	A guild's biomass that is consumed by herbivores
$UGROWTH$	(3)	A guild's biomass production, annually equivalent to CYG
u	(34)	Utilization of a plant guild's growth biomass
w^*	(27)	Probability that a stand will be foraged (RSPF)
X	(27)	A stand of vegetation that is available for foraging (RSPF)
x	(27)	A predictor variable (RSPF)
z	(8)	A density-dependent AUM equivalent

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