Carbon dynamics of forests in Washington, USA: 21st century projections based on climate-driven changes in fire regimes

Crystal L. Raymond[1,2,3] and Donald McKenzie[2]

[1]*School of Forest Resources, University of Washington, Box 352100, Seattle, Washington 98195-2100 USA*
[2]*Pacific Wildland Fire Science Laboratory, U.S. Forest Service, 400 North 34th Street, Suite 201, Seattle, Washington 98103 USA*

Abstract. During the 21st century, climate-driven changes in fire regimes will be a key agent of change in forests of the U.S. Pacific Northwest (PNW). Understanding the response of forest carbon (C) dynamics to increases in fire will help quantify limits on the contribution of forest C storage to climate change mitigation and prioritize forest types for monitoring C storage and fire management to minimize C loss. In this study, we used projections of 21st century area burned to explore the consequences of changes in fire regimes on C dynamics in forests of Washington State. We used a novel empirical approach that takes advantage of chronosequences of C pools and fluxes and statistical properties of fire regimes to explore the effects of shifting age class distributions on C dynamics. Forests of the western Cascades are projected to be more sensitive to climate-driven increases in fire, and thus projected changes in C dynamics, than forests of the eastern Cascades. In the western Cascades, mean live biomass C is projected to decrease by 24–37%, and coarse woody debris (CWD) biomass C by 15–25% for the 2040s. Loss of live biomass C is projected to be lower for forests of the eastern Cascades and Okanogan Highlands (17–26%), and CWD biomass is projected to increase. Landscape mean net primary productivity is projected to increase in wet low-elevation forests of the western Cascades, but decrease elsewhere. These forests, and moist forests of the Okanogan Highlands, are projected to have the greatest percentage increases in consumption of live biomass. Percentage increases in consumption of CWD biomass are greater than 50% for all regions and up to four times greater than increases in consumption of live biomass. Carbon sequestration in PNW forests will be highly sensitive to increases in fire, suggesting a cautious approach to managing these forests for C sequestration to mitigate anthropogenic CO_2 emissions.

Key words: carbon; climate change; fire regime; forest; mitigation; Pacific Northwest, USA.

Introduction

Concern about mitigating global climate change has increased interest in managing forests for carbon (C). In the United States, 89% of the terrestrial C sink is in forests (SOCCR 2007) and each year forest growth and wood products offset 12–19% of the nation's CO_2 emissions (Ryan et al. 2010). Private forest owners seek economic benefits from the C stored in forests and these carbon credits are currently available as part of voluntary carbon markets in the United States (Birdsey 2006). Public agencies that manage forests need information on forest C dynamics to account for C emissions associated with natural processes and management and to support nascent policies on climate change mitigation.

Forests of the Pacific Northwest (PNW) are a large component of the U.S. forest C sink, and forests of the western PNW store the most C per unit area of any temperate forest region in the world (Smithwick et al.

2002, Hudiburg et al. 2009). These forests achieve high C stocks for three reasons: (1) the mild wet climate is favorable for growth of predominantly coniferous trees, which can photosynthesize in fall and spring when precipitation is more abundant, (2) trees are long-lived (400–800 years) and continue to assimilate biomass as they age (Harmon et al. 2004), and (3) fires were relatively infrequent during the last few centuries, allowing substantial C to accumulate in old forests. Forests of the eastern PNW store less C because colder winters and drier summers are less favorable for growth, but also because frequent fires historically limited C accumulation (Houghton et al. 2000, Hurtt et al. 2002).

Forests of the PNW, particularly the western PNW, could store more C than they currently do (Smithwick et al. 2002), but goals for C storage must reflect the natural disturbance regime to ensure long-term sustainability over large spatial scales (Galik and Jackson 2009). Although PNW forests have the highest C stocks of any region in the United States (Smith and Heath 2004), forests of the western United States were also the primary source of CO_2 emissions from fire in recent years (Wiedinmyer and Neff 2007). Interactions between fire and C storage can affect the land–atmosphere

exchange of C directly by releasing CO_2 to the atmosphere (Bowman et al. 2009) and indirectly by shifting forest age class distributions toward a greater proportion of younger forests (Kurz and Apps 1999, Euskirchen et al. 2002). Younger forests remove more C from the atmosphere annually, but have lower C stocks than older forests (Harmon et al. 1990). Based on equilibrium theory, a single stand is a sink or source at any time, but C dynamics of large landscapes are balanced with a constant disturbance regime. If the disturbance regime changes with external forcing, however, C dynamics of the landscape will no longer balance and the forest can become a source or sink until a new equilibrium is reached. Although equilibrium conditions are rarely observed (Romme 1982), the theory becomes more applicable as the temporal and spatial scale of observation increases, and can be useful for exploring landscape disturbance concepts.

Climate is an important driver of fire regimes in PNW forests. Fire regimes in the PNW vary widely, from episodic severe fires in the western maritime and subalpine forests to frequent low-severity fires in the arid east (Agee 1993). Climatic variability has shaped fire regimes in the PNW throughout the Holocene (last 10 000 years) (Gavin et al. 2007). Evidence of climatic controls on fire frequency is also apparent in more recent (last 500 years) tree-ring records (Heyerdahl et al. 2002, Hessl et al. 2004). For example, years with widespread synchronized fires in the western United States were also years in which spring and summer were warmer and drier than average (Hessl et al. 2004, Heyerdahl et al. 2008). During the 20th century, even though fire exclusion and land development influenced fire regimes, interannual variability in temperature, drought, and snowpack were correlated with annual area burned and the length of the fire season (Westerling et al. 2006, Littell et al. 2009).

Climate-driven changes in fire regimes in the 21st century are expected to be a key agent of change in some forest types of the western United States (Littell et al. 2010, Westerling et al. 2011), and this will likely affect the potential of these forests to store C. In the PNW specifically, warmer summer temperatures with little change or decreases in summer precipitation are projected to increase area burned by fire (Littell et al. 2010, Rogers et al. 2011) and fire severity (Cansler 2011). Littell et al. (2010) projected that the area burned in the PNW will double or triple by the 2080s. Two mechanisms explain these changes in fire area and severity. First, warmer temperatures increase evapotranspiration, which lowers fuel moisture. Synchronization of low fuel moisture across large areas facilitates the regional co-occurrence of separate fires (Heyerdahl et al. 2008). Second, warmer temperatures will reduce spring snowpack as more winter precipitation falls as rain rather than snow at higher elevations (Elsner et al. 2010). Earlier snowmelt may extend fire seasons in high-elevation forests by increasing the length of time that

fuels are sufficiently dry for fire spread (Westerling et al. 2006, Cansler 2011).

Research is needed to understand how climate-driven changes in fire area and severity will affect C storage in PNW forests. The response of forest C stocks to changes in fire regimes in the 21st century affects the amount of additional C that can be stored with forest management (Breshears and Allen 2002, Ryan et al. 2010) and the risk of reversal of carbon mitigation projects (Galik and Jackson 2009). Identifying forest types that are particularly vulnerable to C loss from more fire can aid in prioritizing areas for monitoring C sequestration and managing to minimize C loss from fire.

In this study, we used a novel methodology to explore the consequences of projected changes in 21st century fire regimes for C dynamics in forests of Washington (USA). We estimated historical and future C carrying capacity of forest types based on potential productivity, maximum C storage, historical fire regimes, and climate-driven projections of 21st century area burned (Littell et al. 2010). We present results for two C pools (Mg C/ha), live biomass and CWD biomass, and three C fluxes (Mg $C·ha^{-1}·yr^{-1}$), net primary productivity (NPP), live biomass consumption, and CWD biomass consumption. We focus on proportional changes in key variables under future fire regimes rather than attempting to predict their exact values. We use a forested region of Washington because its diverse thermal, hydrologic, and fire regimes provide a complex setting that portends wide variation in responses of C dynamics to changes in fire regimes. The method relies on published and publicly available data so it can be applied to any forested region for which biomass and fire history data are available.

METHODS

We used an empirical approach that takes advantage of statistical properties of fire regimes to quantify equilibrium age class distributions associated with presettlement and projected future fire regimes (Fig. 1). We quantified C pools and fluxes associated with equilibrium age class distributions using empirical models of C dynamics as a function of stand age (Raymond 2010). We calculated consumption of live and CWD biomass C based on mean annual area burned and fire severity. We used projections of 21st century area burned (Littell et al. 2010) to modify historical fire regimes and calculate proportional changes in equilibrium C pools and fluxes for different forest types and three time periods in the 21st century.

Study area

The domain of this study was the forested area of three ecosections in Washington, USA (7 500 000 ha) (Bailey 1995): Western Cascades, Eastern Cascades, and Okanogan Highlands (Fig. 2). The Western and Eastern Cascades ecosections include moderate to high elevations of the Cascade Range (CR) and have rugged
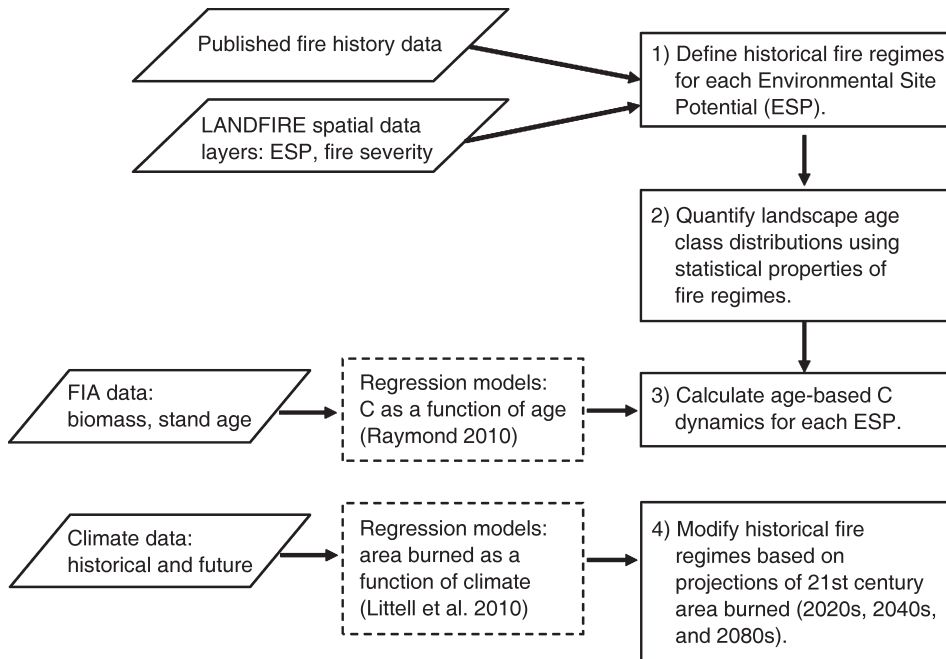
FIG. 1. Overview of the methodology used in the analysis of changes in carbon dynamics in the Pacific Northwest, USA. Parallelograms indicate sources of data. Rectangles indicate steps performed, with regression models from other studies (dashed lines) as precursors for steps 3 and 4, respectively. The historical fire regimes for each Environmental Site Potential (ESP) are modified with proportional increases in area burned (step 4), and steps 2 and 3 are recalculated for the future fire regimes of each of the three time periods (2020s, 2040s, and 2080s). FIA stands for Forest Inventory and Analysis.

mountainous terrain. The Okanogan Highlands ecosection includes western foothills of the Rocky Mountains with an elevation range of 1200 to 2400 m and more moderate slopes with broad rounded summits (Franklin and Dyrness 1988).

Climate is highly variable across the domain because of the influence of the CR. Low elevations west of the CR have a maritime climate with mild wet winters and dry summers. Climate east of the CR is transitional from maritime to continental with warmer summers and colder winters. Mean annual precipitation decreases along a west to east gradient across the Western and Eastern Cascades ecosections because of the orographic effect of the CR (Daly et al. 1994). Much of the precipitation at higher elevations falls as snow in winter. Despite high annual precipitation west of the CR, summer precipitation is low and summer droughts happen throughout the region. Soil moisture in summer is dependent on the persistence of spring snowpack. Summer precipitation increases in the far eastern portion of the Okanogan Highlands where the orographic influence of the CR weakens (Daly et al. 1994).

We used the Environmental Site Potentials (ESPs) from LANDFIRE at 90-m resolution as a spatially explicit classification of potential vegetation (*available online*).[4] ESPs are the species assemblages that can be supported on a site based on the biophysical environ-

ment in the absence of disturbance (Rollins 2009). Holsinger et al. (2006) modeled ESPs using geospatial data on biophysical gradients and field data describing vegetation composition. The biophysical gradients included topography, climate, soil, and ecophysiological parameters derived from the DAYMET weather database (Thornton et al. 1997) and the WXFIRE simulation model (Keane et al. 2002). The nomenclature for ESPs is based on Nature Serve's Ecological Systems classifications (Comer et al. 2003) and typically reflects regional climate, environmental or topographical setting, and dominant plant association. In this study, we included the 14 forested ESPs that cover the greatest area within the ecosections (Fig. 2).

Fire regimes

The historical reference period for fire regimes used in this study is the "presettlement" period commonly used in fire history studies of the PNW. The presettlement period typically ends with the onset of active fire suppression (1910–1920) and extends back to the earliest reliable fire scars (late 1500s or early 1600s). Presettlement fire regimes were a function of climate, topography, and the fire tolerance of tree species and are highly variable across the study domain. Fires burned infrequently with moderate to high severity in low-elevation forests west of the CR and forests at high elevations (see Plate 1), whereas fires burned frequently with low to moderate severity in low-elevation forests east of the CR

---

[4] http://www.landfire.gov/products_national.php

(Appendix: Table A1). Compared to forests of the eastern Cascades, fires are less frequent and more severe than in the mesic montane mixed-conifer forests of the eastern Okanogan Highlands. During the presettlement period, Native Americans also influenced fire regimes by frequently burning dry forests east of the CR (Agee 1993). Less is known about the influence of Native American burning on fire regimes west of the CR, but some evidence suggests they burned the lowest elevation dry Douglas-fir forests (Agee 1993). The North Pacific hypermaritime Sitka spruce forest covers only 10 000 ha in the study area and burns rarely (Fahnestock and Agee 1983), but fires do burn extensively and with high severity (Agee 1993). We did not include this ESP in the analysis because 10 000 ha is insufficient area for representing equilibrium conditions of this high-severity, episodic fire regime (Frelich 2002).

We classified the fire regime of each ESP as stand-replacing, nonlethal, or a mix of the two types. Following the methods of Agee (2003) (Table 1), we defined stand-replacing fire regimes as having a negative exponential age class distribution, no maximum stand age, and replacement-severity fire (i.e., 100% of live biomass is killed by fire resetting stand age to zero). We defined nonlethal fire regimes as having a uniform age class distribution, a maximum age of 400 years, and a mix of low- and moderate-severity fires. Low- and moderate-severity fires kill a fraction of live biomass and consume a fraction of live and CWD biomass, but do not reset stand age to zero. Fire regimes of ESPs that display properties of both types were represented by dividing the area of the ESP into proportions of each fire regime type (Agee 2003) (Table 1).

Landscape age class distributions and fire frequency

We calculated equilibrium age class distributions for ESPs with stand-replacing fire regimes using a negative exponential model (Van Wagner 1978). The negative exponential model assumes a constant hazard of burning with stand age. Thus, it is most appropriate in forests where fires are stand replacing and fire return intervals are more a function of climate than fuel accumulation (Johnson and Gutsell 1994). Using the negative exponential model we calculated the proportion of the ESP area $A(t)$ in each 1-year age class (t) for presettlement fire regimes as

$$A(t) = p_h e^{-p_h t} \qquad (1)$$

where p_h is the probability of fire in a stand in any year for the historical fire regime. The mean age of all stands is $1/p_h$, or C_h, the fire cycle for the historical fire regime (the mean fire return interval of the ESP). One-third of the stands in the ESP are older than the fire cycle and two-thirds are younger. We obtained values for C_h, and thus p_h, for each ESP (or portion of an ESP) from values of fire cycles, or alternative area-based metrics of fire return intervals (composite fire interval [CFI] or natural fire rotations [NFR]), reported in fire history studies

(Appendix: Table A1; see Raymond [2010] for a list of references for fire history studies). We selected a long and short fire cycle to represent the range of observed fire cycles within ESPs (Appendix: Table A1).

We calculated equilibrium age class distributions of ESPs with nonlethal fire regimes using a uniform distribution, i.e., equal proportions of the ESP in 1-year age classes. We assumed all stands reach a maximum age of 400 years, at which time they are killed by fine-scale (<1 ha) disturbances such as insects, pathogens, or wind (Agee 2003). Thus, fire does not directly affect the age class distribution of ESPs with nonlethal fire regimes, but nonlethal fires do affect the C dynamics of these forests during the 400-year life of the stand.

We simulated the effects of fire on C dynamics in nonlethal fire regimes by calculating the change in C pools and fluxes of a single stand (1 ha) subject to frequent low- and moderate-severity fires over the 400-yr life of the stand. We calculated equilibrium conditions as the mean of 1000 400-yr replicates for each ESP. The nonlethal fire regimes of ESPs varied with respect to fire frequency and the proportion of fires that burn with moderate or low severity (Appendix: Table A2). We defined fire frequency parameters of these ESPs using point estimates of fire frequency reported in fire history studies (Appendix: Table A2). We used point estimates whenever possible because we simulated 400 years of fires in one hectare. Point estimates of fire frequency are calculated from fire return intervals recorded by one or a few fire-scarred trees and indicate the time between fires at a single point (~1 ha; Agee 1993). Point estimates can be either mean fire intervals (MFI) or Weibull median probability intervals (WMPI). Under the assumption of a Weibull distribution of fire-free intervals, the latter may give a more robust measure of central tendency (Grissino-Mayer 1999).

For each 400-yr simulation, we generated fire return intervals stochastically from a two-parameter Weibull distribution (Johnson and Gutsell 1994). The Weibull distribution is appropriate for low-severity fire regimes because it allows for changes in the hazard of burning with time since fire (Grissino-Mayer 1999). The Weibull pdf is

$$f(t) = ct^{c-1}/b^c e^{-(t/b)^c} \qquad (2)$$

where $f(t)$ is the frequency of having a fire return interval of t years, b is a scale parameter, and c is a shape parameter. At $c = 1$, the Weibull reduces to a negative exponential. Values of $c > 1$ indicate an increase in the hazard of burning with age (Johnson and Gutsell 1994), and the shape of the Weibull density becomes unimodal instead of monotone decreasing. For each ESP, we assigned the shape parameter c stochastically from a range of values (1.6–2.6) reported by McKenzie et al. (2006) in a detailed study of low-severity fire in the Eastern Cascades and Okanogan Highlands. We assigned Weibull median probability fire intervals (WMPIs) from existing fire history studies across the
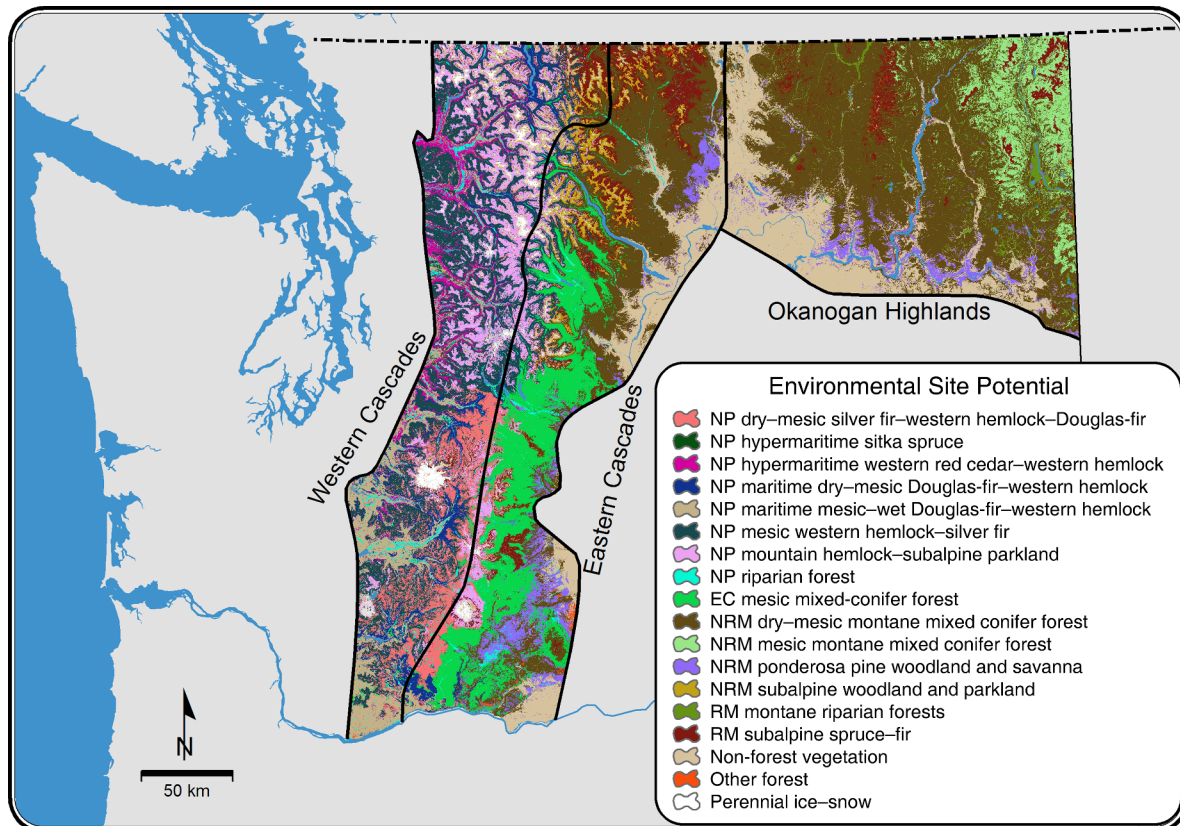
Fig. 2. Study area: three forested ecosections in Washington, USA (Eastern Cascades, Western Cascades, and Okanogan Highlands). Environmental Site Potentials are a classification of the vegetation that could be supported on a site based on the biophysical environment and in the absence of disturbance. NP is North Pacific, EC is Eastern Cascades, NRM is Northern Rocky Mountain, and RM is Rocky Mountain.

region, and used a convenient property of the Weibull distribution to calculate the scale parameter b:

$$b = \text{WMPI}/\ln(2)^{1/c}. \qquad (3)$$

We then generated a 400-yr time series of fire return intervals by selecting random numbers from a Weibull distribution until the sum of the intervals (rounded to the nearest integer) exceeded 400. All calculations and simulations used the R 2.13.0 software package (R Development Core Team 2008).

Fire severity

We defined fire-severity for each ESP using data developed by LANDFIRE, consisting of three spatial layers (30-m resolution), as the percentages (five-percent classes) of fires in a cell that burn with low-, moderate-, or high-severity fire. The fire-severity classes are defined as: low, <25% mortality; moderate, 25–75% mortality; and high, >75% mortality (Hann et al. 2004). We cross-tabulated the three fire-severity rasters with the ESP raster to calculate the area of each ESP that had each combination of low, moderate, and high severity. We multiplied the number of cells with each severity

combination by the percentages of each severity class and summed the cells within each severity class.

We used these aggregated fire-severity data to classify the fire regime of each ESP as stand-replacing, nonlethal, or a mix (Table 1). An ESP had a stand-replacing fire regime if >70% of the cells typically experienced high-severity fire, and a nonlethal fire regime if >70% of the cells typically experienced low- or moderate-severity fire. We classified all other ESPs as mixed fire regimes and divided the area of the ESP into stand-replacing and nonlethal, modeling a stand-replacing fire regime in the proportion of the area that typically burned with high severity, and a nonlethal fire regime in the area that typically burned with low or moderate severity. One exception to these classification rules was necessary for the NP mesic western hemlock–silver fir forest. The fire-severity data suggested that this ESP had a much higher ratio of moderate- to high-severity fires than would be expected given the fire intolerance of species typically found therein (Agee 2003). This ESP typically burns infrequently and with stand-replacing fires in the study area (Fahnestock and Agee 1983, Henderson et al. 1989), so we assigned it a high-severity fire regime.

TABLE 1. Area and proportion of fire-regime types for environmental site potentials (ESP) of three ecosections in Washington, USA.

Environmental site potential	Western Cascades Area (ha)	Stand-replacing	Non-lethal	Eastern Cascades Area (ha)	Stand-replacing	Non-lethal	Okanogan Highlands Area (ha)	Stand-replacing	Non-lethal
NP hypermaritime sitka spruce	10 412								
NP hypermaritime western red cedar–western hemlock	143 748	1.0		2 082†					
NP maritime mesic–wet Douglas-fir–western hemlock	271 275	1.0		12 220	1.0				
NP maritime dry–mesic Douglas-fir–western hemlock	182 300	0.25	0.75	31 277	0.25	0.75			
NP mountain hemlock–subalpine parkland	341 538	1.0		119 776	1.0				
NP mesic western hemlock–silver fir	635 276	1.0		97 547	1.0				
NP riparian forest	70 041	1.0		50 256	0.6	0.4			
NP dry–mesic silver fir–western hemlock–Douglas-fir	238 244	0.5	0.5	54 187	0.5	0.5			
EC mesic mixed-conifer forest	17 750	1.0		584 336	0.3	0.7			
NRM dry–mesic montane mixed conifer forest	25 853		1.0	741 860		1.0	1 406 904		1.0
NRM subalpine woodland and parkland	33 076	1.0		106 079	0.4	0.6			
NRM mesic montane mixed conifer forest							273 475	0.5	0.5
NRM ponderosa pine woodland and savanna	24†			162 198		1.0	105 494		1.0
RM subalpine spruce–fir	67 675	1.0		213 176	1.0		96 779	1.0	
RM montane riparian forests				432†			113 159	1.0	

Notes: "Stand-replacing" is the proportion of the area modeled with a stand-replacing fire regime, and "nonlethal" is the proportion of the area modeled with a nonlethal fire regime. NP is North Pacific, EC is Eastern Cascades, NRM is Northern Rocky Mountain, and RM is Rocky Mountain.

† The area of these ESPs was modeled with the same ESP of the neighboring ecosections because the area was too small to model separately, given area requirements of equilibrium assumptions.

We also used the fire-severity data layers to determine the probability of moderate- vs. low-severity fires in nonlethal fire regimes. For each ESP, the probability of low (PLS) or moderate severity (PMS) fires was based simply on the proportion of the ESP area that predominately (>50%) burns with each severity class. These proportions were set equal to parameters p and $1 - p$ in a binomial distribution, and compared to a uniform random number generated for each fire that burns during the 400-yr simulation to select either moderate or low severity (Appendix: Table A2).

Age-based carbon dynamics

We calculated live biomass (Mg C/ha) and net primary productivity (NPP; Mg C·ha^{-1}·yr^{-1}) for each age in the age class distribution for stand-replacing fire regimes using ESP-specific empirical models of live biomass C and NPP as a function of stand age. Empirical models were fit to chronosequences of forest inventory data from the study area, aggregated by ESP (Raymond 2010). The accumulation of live biomass as a function of stand age was modeled with a Chapman-Richards function (Richards 1959, Janisch and Harmon 2002):

$$L_{age} = L_{max}(1 - e^{-k_L age})^{c_L} \tag{4}$$

where L_{age} is live biomass for any age, L_{max} is the maximum asymptotic live biomass reached in late succession, k_L is an empirically derived rate constant, and c_L controls the position of the curve between zero and the asymptote (Appendix: Table A3). NPP as a function of stand age was modeled with a peak function (Janisch and Harmon 2002, Pregitzer and Euskirchen 2004, Hudiburg et al. 2009):

$$NPP_{age} = NPP_{max} \times \exp\left\{-0.5\lceil \ln(age/AGE_{max})/k_N\rceil^2\right\} \tag{5}$$

where NPP_{age} is the NPP for any age, NPP_{max} is the maximum NPP reached in early succession, k_N is the rate at which the stand reaches NPP_{max}, and AGE_{max} is the age at which NPP begins to decline from the

maximum. We multiplied L_{age} and NPP_{age} for each age by the area of the ESP in that one-year age class and divided by the total area of the ESP to calculate mean live biomass and NPP for the ESP.

We calculated live biomass C and NPP differently for nonlethal fire regimes because fire does not directly affect stand age, but fire does affect NPP and reduce live biomass. Live biomass and NPP are a function of stand age (Eqs. 4 and 5) until a fire occurs, at which time L_{age} is reduced by fractions for mortality (i.e., transfer to dead biomass) and consumption that are a function of the fire's severity. The mortality fraction is drawn from a uniform distribution, with a range of 0.1–0.24 for low-severity fires and 0.25–0.74 for moderate-severity fires (Hann et al. 2004). After reducing live biomass by mortality and consumption, a new "age" of the stand is calculated by back-solving Eq. 4 for age from postfire live biomass (Nonaka et al. 2007). The new stand age is used to calculate the live biomass (Eq. 4) and NPP (Eq. 5) for the year after the fire and is incremented by one until the next fire. NPP increases or decreases when a fire occurs depending on the shape of the NPP function and the stand age at the time of the fire. We simulated 1000 replicates of the 400-yr time series of live biomass and NPP for each ESP. Based on the assumption of a uniform age class distribution, mean live biomass and NPP of the ESP are the means of the 1000 replicates, divided by 400.

We calculated the accumulation of CWD biomass (Mg C/ha) from chronic mortality of live biomass (i.e., gap dynamics) between fires using empirical models of CWD biomass as a function of stand age (Raymond 2010). Several ESPs did not have significant empirical models, in which cases we used ecosection-scale models (Raymond 2010). Furthermore, patterns of CWD biomass accumulation with age differed among ecosections. For the Eastern Cascades and Okanogan Highlands, ecosection-scale models (and some ESPs in these ecosection) fit a U-shaped pattern (Janisch and Harmon 2002):

$$D_{\text{age}} = D_0(e^{-k_{D1}\text{age}}) + D_{\max}(1-e^{-k_{D2}\text{age}})^{c_D} \qquad (6)$$

where D_{age} is dead biomass at any age, D_0 is the initial legacy biomass, k_{D1} is an empirically derived rate constant for the decomposition of legacy biomass, $D_{\max}$ is the asymptotic maximum biomass reached in late succession, k_{D2} is an empirically derived rate constant for the accumulation of new biomass, and c_D is a shape parameter. For the Western Cascades ecosection, the CWD biomass data were better fit with a linear model (Raymond 2010). Therefore, we used a linear model for the accumulation of CWD biomass from chronic mortality in ESPs of the Western Cascades and assumed the maximum CWD biomass for ages >800 years was the fitted value for the oldest age in the original data used to build the model (800 years). CWD biomass from chronic mortality is not subtracted from live biomass for

each age because Eq. 4 accounts for biomass lost from chronic mortality.

We also calculated CWD biomass from fire-caused mortality and added this to Eq. 6. The two fire regimes required different methods for calculating fire-caused CWD biomass. For stand-replacing fire regimes, we calculated fire-caused CWD biomass as the legacy from the stand-initiating fire and used this value for D_0 in Eq. 6. We calculated D_0 as the mean of live and CWD biomass per hectare that burns annually reduced by the amount consumed. Based on the exponential model, mean annual area burned is assumed to be an equal proportion of the area in each age class because each age class has the same probability of burning. Therefore, we calculated the mean D_0 (Mg C/ha) as the area (hectare) of each age class that burns annually multiplied by L_{age} and D_{age} of the age class divided by the total annual area burned. D_0 decomposes with time since stand-initiating fire based on ESP or ecosection-specific decomposition rates in Eq. 6.

For nonlethal fire regimes, all live biomass is assumed to be killed in year 400 by fine-scale disturbances other than fire. Therefore, we calculated legacy CWD biomass (D_0 in Eq. 6) for each ESP as the sum of mean L_{400} and mean D_{400} reduced by a fraction that is fine woody debris (FWD). Mean L_{400} and mean D_{400} are the means of L_{400} and D_{400} from 100 preliminary simulations of the 400-yr time series for each ESP. When a fire burns during the 400-yr time series, the fraction of L_{age} that is killed is reduced by the fraction consumed and the age-dependent fraction that is FWD (Appendix: Table A3) and is added to D_0. D_{age} the year after the fire, and each year until another fire occurs, is calculated with Eq. 6.

Consumption factors

We calculated the amount of live and CWD biomass consumed by fire following Campbell et al. (2007). Using data in Campbell et al. (2007), we calculated consumption factors by severity class that could be applied to total live and CWD biomass by mass-weighting individual component consumption factors. Consumption factors were 0.11, 0.08, and 0.01 for live biomass, and 0.18, 0.07, and 0.03 for CWD biomass, respectively, for high-, moderate-, and low-severity fires. Live biomass consumption factors do not apply to coarse roots, but Eq. 4 includes accumulation of coarse roots (Raymond 2010), so we reduced L_{age} by an age-dependent fraction of coarse roots before calculating consumption (Appendix: Table A3).

Projections of changes in 21st century fire regimes

We estimated changes in fire regimes for the 21st century using projections of future area burned from empirical models of area burned as a function of climatic variables (Littell et al. 2010). Littell et al. (2010) fit statistical models of area burned in the late 20th century as functions of summer temperature, precipitation, and hydrological variables (potential evaporation, actual

TABLE 2. Proportional increases in mean annual area burned for the 21st century by time period and SRES emission scenarios (Littell et al. 2010).

| | Proportion of 1980–2006 area burned | | | | | |
| | 2020s | | 2040s | | 2080s | |
Ecosection	B1	A1B	B1	A1B	B1	A1B
Western Cascades	1.6	1.8	2.4	3.5	4.6	11.9
Eastern Cascades	1.3	1.1	1.5	1.4	1.9	2.0
Okanogan Highlands	1.2	0.4	1.5	1.7	2.0	3.1

Notes: Proportional increases are proportions of the 1980–2006 mean annual area burned for each ecosection. B1 and A1B are SRES emission scenarios from the Intergovernmental Panel on Climate Change, Fourth Assessment Report. B1 is a low-emissions scenario, and A1B is a middle-of-the-road scenario.

evaporation, and water-balance deficit) at the scale of ecosections. They used these models to project mean area burned based on climatic variables averaged for three time periods: 2020s (2010–2039), 2040s (2030–2059), and 2080s (2070–2099). Models explained 50–65% of variability in area burned. Littell et al. (2010) used down-scaled projections of 21st century temperature and precipitation from Mote and Salathé (2010), who used output on future climate from the ensemble of 20 GCMs (general circulation models) archived for the IPCC AR4 (Intergovernmental Panel on Climate Change Fourth Assessment Report). The hydrological variables used in the statistical fire models were output from the variable infiltration capacity (VIC) hydrologic model (Elsner et al. 2010), for which simulations were also driven by down-scaled climate projections from the 20-model ensemble average (Mote and Salathé 2010). Climatic variables and area burned were projected for two SRES emissions scenarios (Special Report on Emissions Scenarios), A1B (moderate) and B1 (low), which are similar until the 2020s, but thereafter A1B produces higher climate forcing (Mote and Salathé 2010).

We estimated changes in fire regimes for each ESP using the ecosection-scale projections of 21st century area burned. We downscaled ecosection-scale projections to ESPs by applying proportional increases in mean annual area burned (Table 2) to the presettlement mean annual area burned for each ESP as follows. For stand-replacing fire regimes, a property of the negative exponential model is that the probability of a stand burning in any year (p) is equal to the proportion of the landscape that burns annually (Johnson and Gutsell 1994). Thus, for the historical period, we calculated annual area burned, AAB_h, for each ESP as

$$AAB_h = p_h \times A \qquad (7)$$

where p_h is the historical annual probability of a stand burning and A is the area of the ESP. For each time period and emissions scenario, we calculated the future annual area burned, AAB_f, as

$$AAB_f = AAB_h \times PI \qquad (8)$$

where PI is the proportional increase in area burned (Table 2). We calculated the future probability that a

stand burns (p_f) as

$$p_f = AAB_f / A. \qquad (9)$$

We used this value of p_f in Eq. 1 to calculate the equilibrium age class distribution for each ESP, time period, and emissions scenario. For nonlethal fire regimes, we calculated AAB_h for the historical period based on the following property of the Weibull distribution:

$$AAB_h = \left(\frac{1}{b\Gamma\left(\frac{1}{c} + 1\right)} \right) \times A \qquad (10)$$

where b is the scale parameter, c is the shape parameter, and Γ is the gamma function. We calculated AAB_f from AAB_h using the same method as we used for stand-replacing fire regimes.

Specific projections of climate-driven changes in fire severity are not available for the PNW, and the relationship between climate and fire severity remains less certain than the relationship between climate and area burned. Therefore, we used a scenario-based approach to explore the sensitivity of changes in forest C pools and fluxes to changes in fire severity, as well as changes in area burned. Based on projections by Lutz et al. (2009) for dry coniferous forest in California, the area burned at moderate and high severity is expected to increase 20% by 2049. Fire severity and area burned cannot be expected to increase indefinitely because fuel availability will eventually limit both. To account for these opposing effects, we used three scenarios of future fire severity: no change, a 10% decrease, and a 10% increase for each time period, to test the sensitivity of changes in C pools and fluxes. Unlike changes in area burned, we assumed that changes in fire severity were consistent between emissions scenarios. We simulated changes in fire severity for only the three ESPs with the greatest probability of low-severity fire.

We calculated C dynamics for the 2020s, 2040s, and 2080s, but focus on results for the 2040s to simplify the discussion and because uncertainty increases as projections of climate change and its effects are extended further into the future. Uncertainty in emissions scenarios, potential feedbacks in the climate system,

and other changes in vegetation dynamics increase in the late 21st century so results for the 2080s should be interpreted with caution. Our methodology includes some simplifying assumptions and combines statistical models, each of which introduces uncertainty into the output calculations of C dynamics. Thus, we present results as percentage changes, rather than absolute values, between the presettlement and future time periods, and as comparisons among ecosections, ESPs, and emissions scenarios.

RESULTS

Live biomass carbon

Changes in live biomass C for ecosections reflect differences in fire regimes, projections of future area burned, and C storage potential (Fig. 3). For the 2020s, live biomass is projected to increase in the Okanogan Highlands with the A1B scenario, for which area burned decreases by about half. For the 2040s, live biomass C decreases in all ecosections. On average, 1.5 times the area burned caused a 20% reduction in live biomass C. The Western Cascades has the largest projected decrease (Fig. 3). Decreases in live biomass C are similar for the Eastern Cascades and Okanogan Highlands with the B1 scenario, but are greater in the Okanogan Highlands with the A1B scenario (Fig. 3).

For the 2040s, live biomass C decreases by 7–56% for ESPs in the Western Cascades (Fig. 3). Both the smallest and largest decreases in live biomass C are in ESPs in this ecosection. Live biomass decreases by 7–25% for ESPs in the Eastern Cascades and 11–39% for ESPs in the Okanogan Highlands (Fig. 3). Among ESPs, percentage decreases in live biomass show a bimodal response with respect to biomass accumulation rates and presettlement fire return intervals (FRI). The largest decreases are projected for two types of ESPs: (1) ESPs with the short FRIs and intermediate ages at which stands accumulate 90% of asymptotic maximum biomass and (2) ESPs with both long FRIs and late ages at which stands accumulate 90% of asymptotic maximum biomass (Fig. 4A).

Net primary productivity

Projected changes in mean landscape net primary productivity (NPP) (Mg C·ha^{-1}·yr^{-1}) vary by ecosection, reflecting large differences among ecosections in historical landscape NPP and projections of future area burned. For the 2040s, mean landscape NPP is projected to increase in the Western Cascades but decrease in the Eastern Cascades and Okanogan Highlands. NPP increases in the Okanogan Highlands for the A1B scenario in the 2020s reflecting the decrease in area burned projected for this scenario.

Projected changes in NPP are highly variable among ESPs within ecosections, particularly for the Western Cascades. For the 2040s, NPP is projected to change by −25% to 42% for the B1 scenario and −34% to 56% for the A1B scenario among ESPs in the Western Cascades

(Fig. 5). Variability among ESPs is smaller in the Eastern Cascades and Okanogan Highlands, in which NPP is projected to change by <10% for the 2040s. Decreases >25% are not projected until the 2080s (Fig. 5). Increases in NPP are projected for ESPs with long FRIs (>600 years) and young ages (<150 years) at which NPP reaches a maximum (Fig. 4B). In ESPs in the Western Cascades, NPP continues to increase with more area burned later in the 21st century, but this trend begins to reverse in the 2080s with the high area burned for A1B scenario. NPP is not projected to increase in the mountain hemlock–subalpine parkland ESP for any emissions scenario or time period despite its long FRI. NPP peaks at a much older age in this ESP compared to other ESPs with similar FRIs, so even a substantial leftward shift in the age class distribution does not increase NPP. The greatest decreases in NPP are projected for ESPs with long FRIs and old ages at which NPP reaches a maximum (Fig. 4B). Little change in NPP is projected for ESPs with short FRIs and young ages at which NPP reaches a maximum (Fig. 4B).

Coarse woody debris biomass carbon

Increases in area burned in the 21st century are projected to reduce CWD biomass (Mg C/ha) in the Western Cascades, but have little effect on or slightly increase CWD in the Eastern Cascades and Okanogan Highlands (Fig. 6). CWD increases in the Okanogan Highlands with decreases in area burned projected for the 2020s A1B scenario. For the 2040s, ecosection mean CWD is projected to decrease in the Western Cascades by 15–21%, but to remain unchanged in the Eastern Cascades and increase slightly in the Okanogan Highlands (Fig. 6).

At the ESP scale, CWD is projected to decrease in most ESPs for most time periods and emissions scenarios, with the notable exception of a few ESPs in which CWD biomass increases (Fig. 6). For the 2040s, ESPs in the Western Cascades have the greatest range of projected changes in CWD, −42% to 32% for the B1 scenario and −55% to 45% for the A1B scenario. The range of projected changes is much smaller for ESPs in the Eastern Cascades (−9% to 13%) and Okanogan Highlands (−10% to 12%). The largest percentage decreases in CWD are projected for high-elevation ESPs with replacement-severity fire regimes and moderate FRIs. Increases in CWD biomass are projected for ESPs with nonlethal and mixed fire regimes. Of these ESPs, dry–mesic Douglas-fir–western hemlock is projected to have the largest percentage increase in CWD. This ESP has the highest biomass accumulation potential of ESPs with nonlethal or mixed fire regimes (Fig. 6). A large percentage increase in CWD is also projected for dry–mesic montane mixed conifer, which has lower potential to accumulate biomass but a higher proportion of low-severity fire. Projected increases in CWD decline for the A1B scenario in the 2080s and some ESPs that show increases for the 2020s and 2040s show decreases with the higher area burned projected for the 2080s.
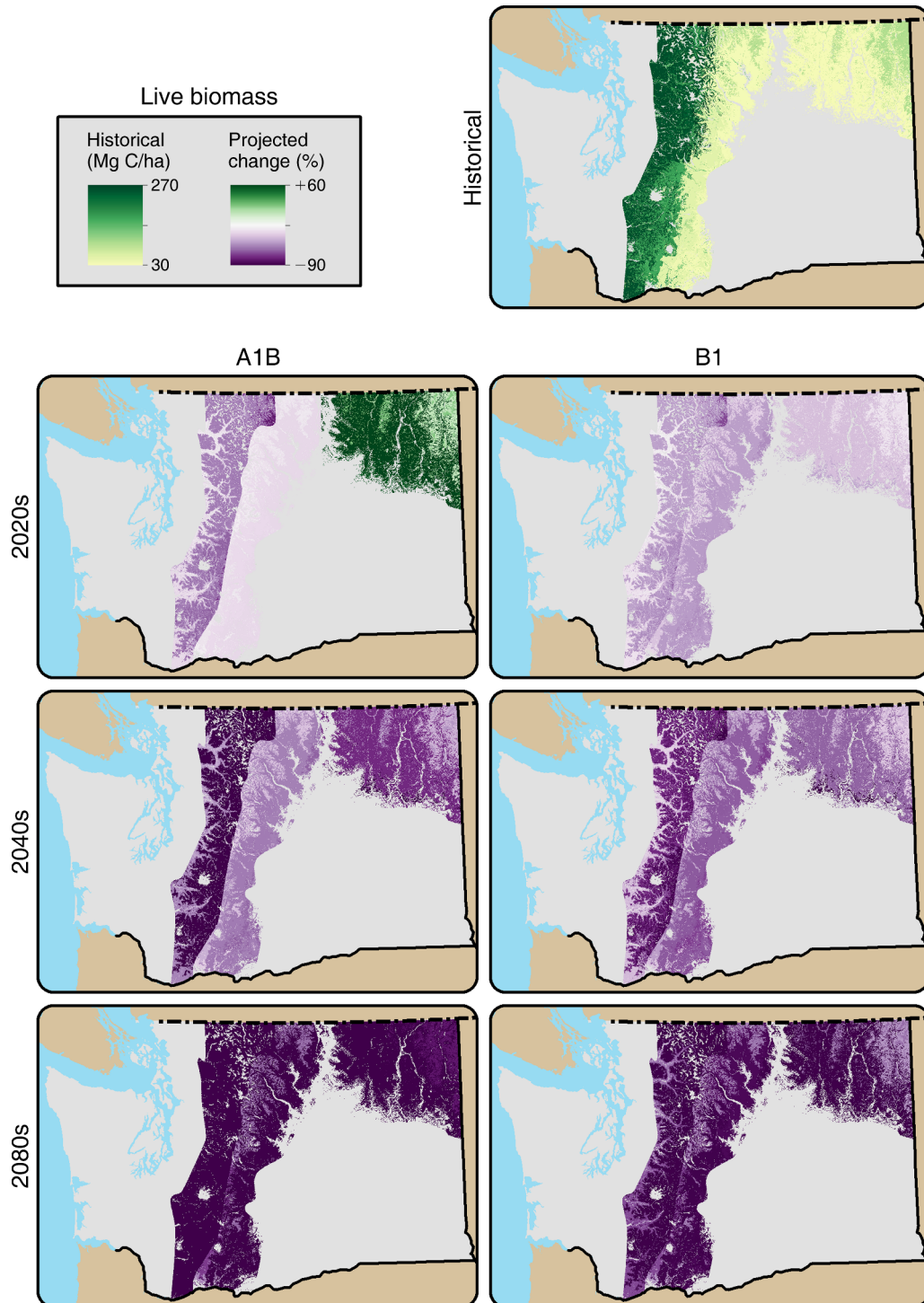
FIG. 3. Projected percentage changes in live biomass carbon for two SRES emissions scenarios (Special Report on Emissions Scenarios: A1B is a middle-of-the-road scenario; B1 is a low-emissions scenario) and three time periods (2020s, 2040s, 2080s) in relation to historical values (top right). Projected values are mean equilibrium conditions for each time period.

Live biomass consumption

Mean annual consumption of live biomass (Mg C·ha^{-1}·yr^{-1}) is projected to increase relative to preset-tlement conditions for all emissions scenarios and time periods that are projected to have increases in area burned (Fig. 7). Percentage increases are four to eight times greater in the Western Cascades compared to the
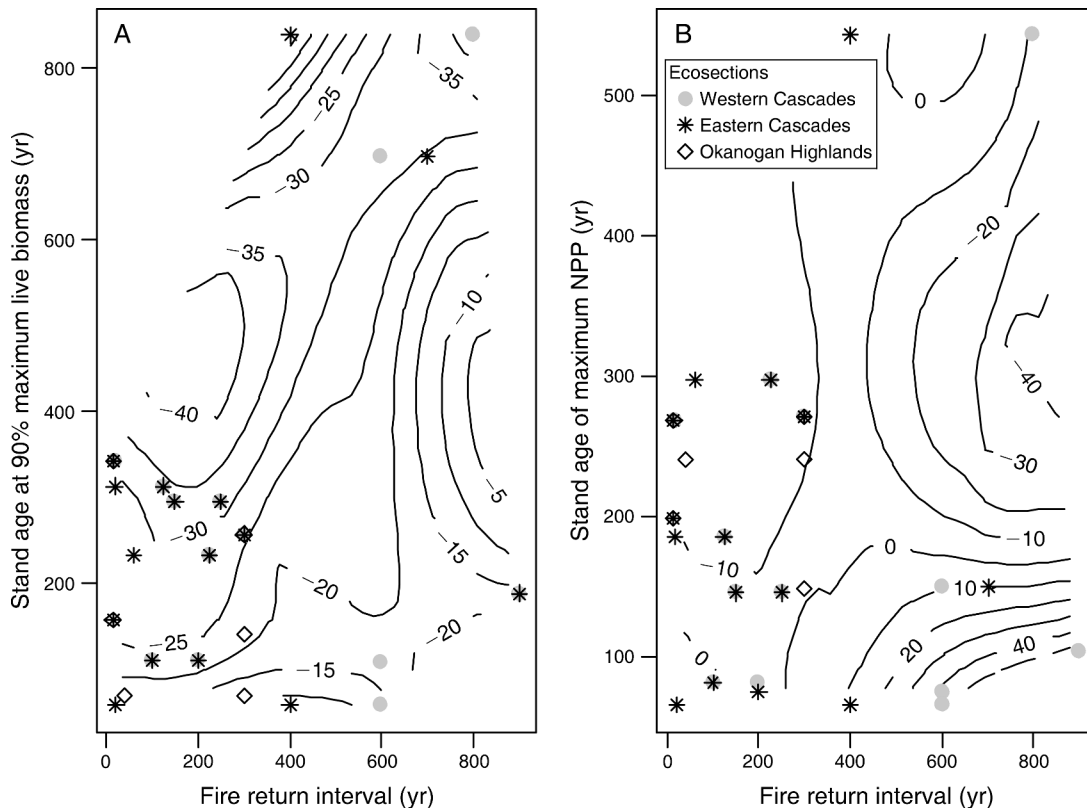
Fig. 4.   Percentage changes in mean (A) live biomass C and (B) NPP within each ESP, plotted as smoothed response surfaces (contours) interpolated linearly, in the 2-D (two-dimensional) space of predictors, between their values at ESPs. Symbols locate the mean values for ESPs within an ecosection of presettlement fire return intervals (x-axes) and stand ages associated with key values of the respective response variables (y-axes). Calculations are for the 2040s under the A1B emissions scenario.

Eastern Cascades and Okanogan Highlands (Fig. 7). Consumption of live biomass decreases in the Okanogan Highlands for the A1B scenario in the 2020s, reflecting the decrease in area burned projected for this scenario. For the 2040s, projected increases are <30% for the Eastern Cascades and Okanogan Highlands, but the Okanogan Highlands has a substantial increase in consumption in the 2080s (Fig. 7).

Projected increases in the consumption of live biomass are highly variable among ESPs in the Western Cascades but less variable among EPSs in the Eastern Cascades and Okanogan Highlands (Fig. 7). For ESPs in the Western Cascades, projected increases in consumption of live biomass range from 33% to 130% for the B1 scenario and from 44% to 218% for the A1B scenario in the 2040s. For ESPs of the Eastern Cascades, consumption of live biomass is projected to increase by only 10–43% for the B1 scenario and 9–36% for the A1B scenario in the 2040s. For ESPs of the Okanogan Highlands, consumption of live biomass is projected to increase by only 3–41% for the B1 scenario and 2–57% for A1B scenario in the 2040s. ESPs with long FRIs are projected to have the largest increases in consumption of live biomass with the exception of ESPs that have long FRIs but also have both high maximum live biomass and slow

rates of accumulation (e.g., mountain hemlock–subalpine parkland and mesic western hemlock–silver fir). ESPs with nonlethal fire regimes and short presettlement FRIs (<20 years) are projected to have the smallest percentage increases in consumption of live biomass because these ESPs also have relatively low potential to accumulate live biomass.

Coarse woody debris biomass consumption

Mean annual consumption of CWD ($Mg\ C\cdot ha^{-1}\cdot yr^{-1}$) is also projected to increase relative to presettlement conditions for all emissions scenarios and time periods that are projected to have increases in area burned (Fig. 8). For the 2040s, increases in CWD consumption are projected to be >50% for all ecosections and emissions scenarios (Fig. 8) and up to four times greater than increases in live biomass consumption. For the 2080s, projected increases in consumption of CWD are similar for the Western Cascades and Okanogan Highlands but are lower for the Eastern Cascades because of generally lower fire severity, increases in area burned, and potential accumulation of CWD (Fig. 8).

For ESPs in the Western Cascades, consumption of CWD is projected to increase by 44–271% for the B1 scenario and by 63%–550% for the A1B scenario in the
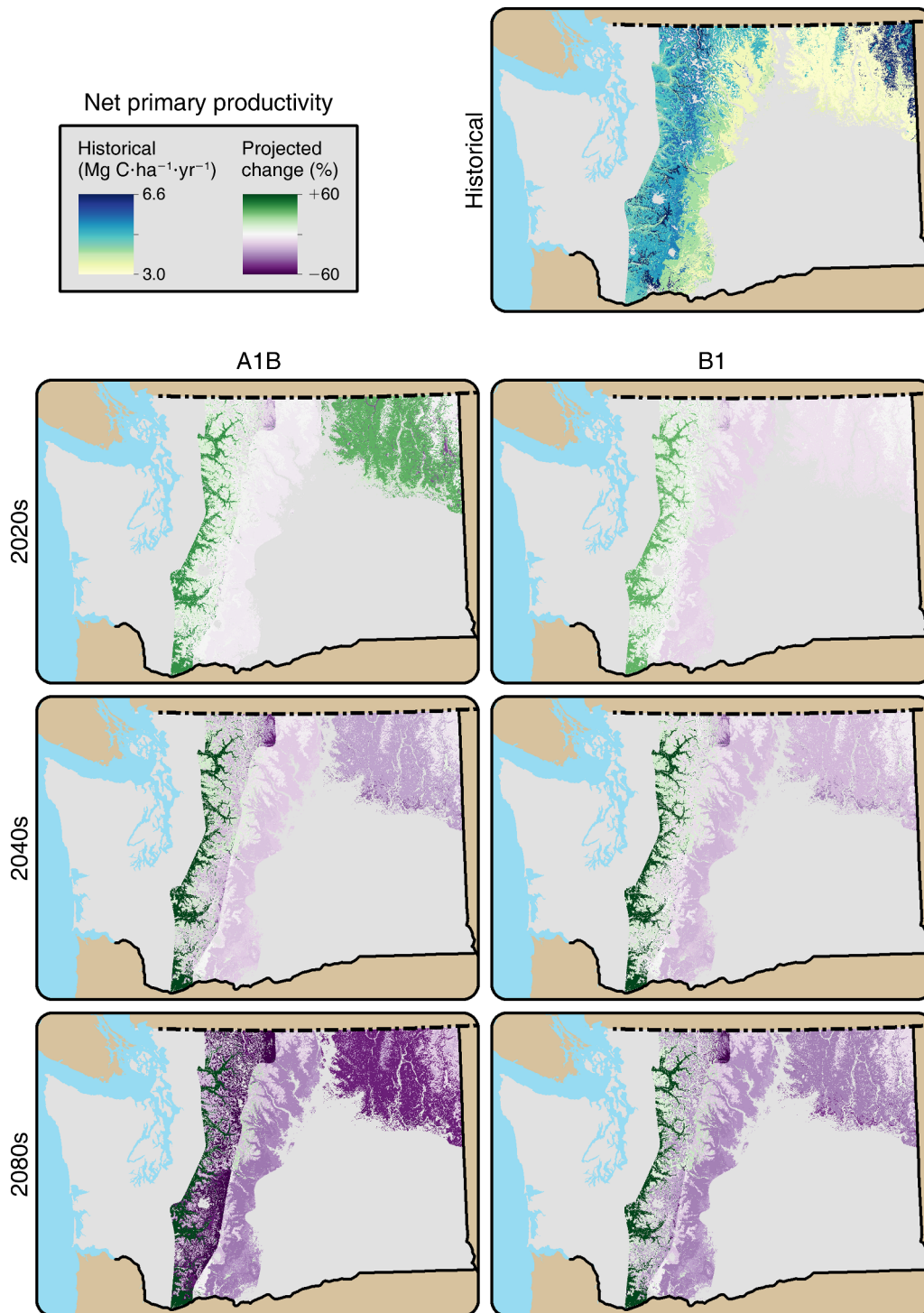
FIG. 5. Projected percentage changes in net primary productivity for two SRES emissions scenarios (A1B and B1) and three time periods (2020s, 2040s, 2080s). All values are mean equilibrium conditions for each time period.

2040s. Variability in projected increases in CWD consumption is much lower for ESPs in the Eastern Cascades and Okanogan Highlands. CWD consumption increases from 39% to 91% for the B1 scenario and from 32% to 73% for the A1B scenario in ESPs of the Eastern Cascades and from 41% to 86% for the B1 scenario and from 53% to 129% for the A1B scenario in ESPs of the Okanogan Highlands. ESPs that are projected to have
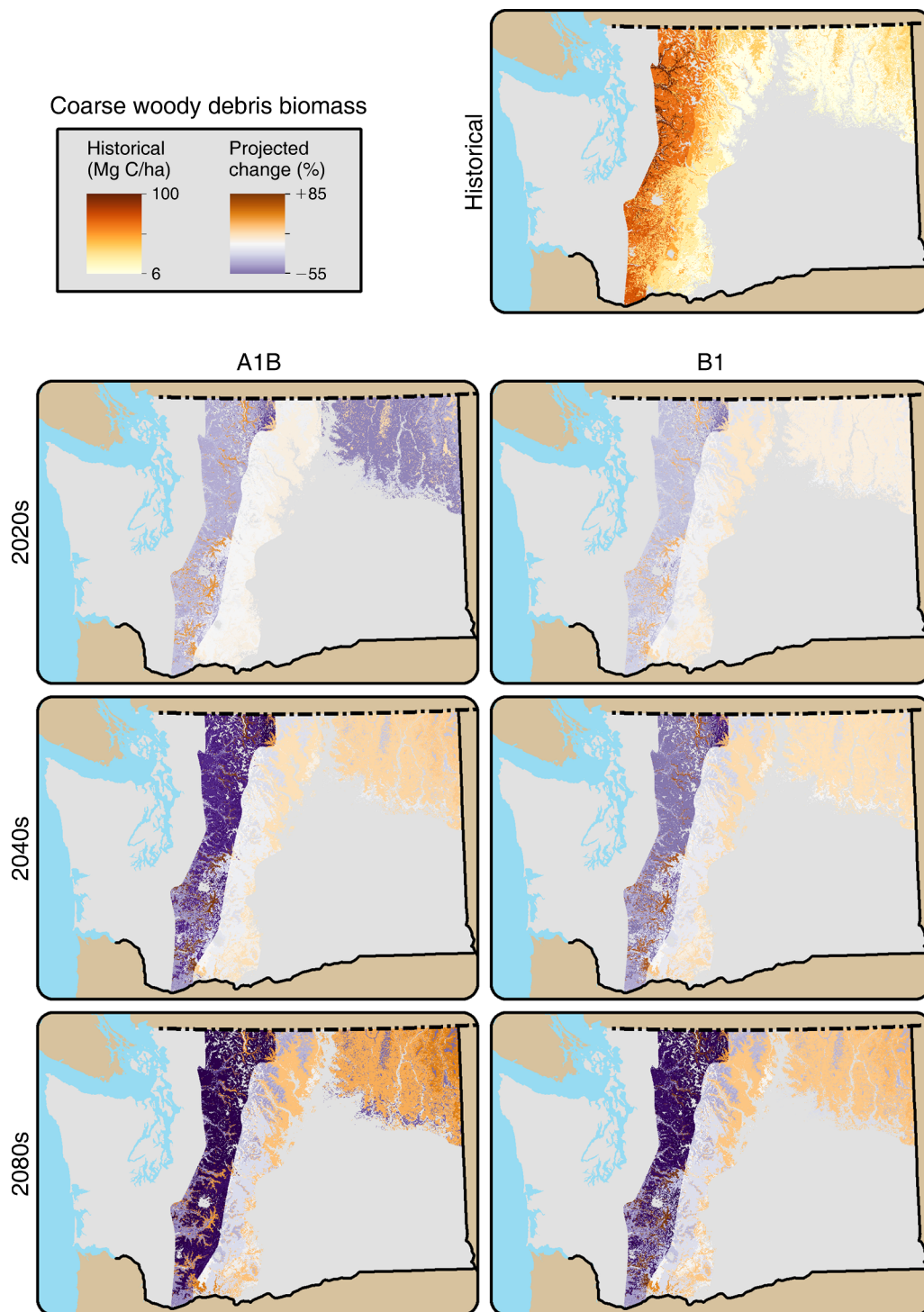
Fig. 6. Projected percentage changes in coarse woody debris biomass carbon for two SRES emissions scenarios (A1B and B1) and three time periods (2020s, 2040s, 2080s). Projected values are mean equilibrium conditions.

the largest percentage increases in CWD consumption are the same ESPs that are projected to have the largest increases in CWD biomass (dry–mesic Douglas-fir–western hemlock and dry–mesic montane mixed coni-

fer). CWD biomass increases from fire-caused mortality, part of which is consumed in subsequent fires contributing to large percentage increases in CWD consumption. The smallest increases in CWD consumption are
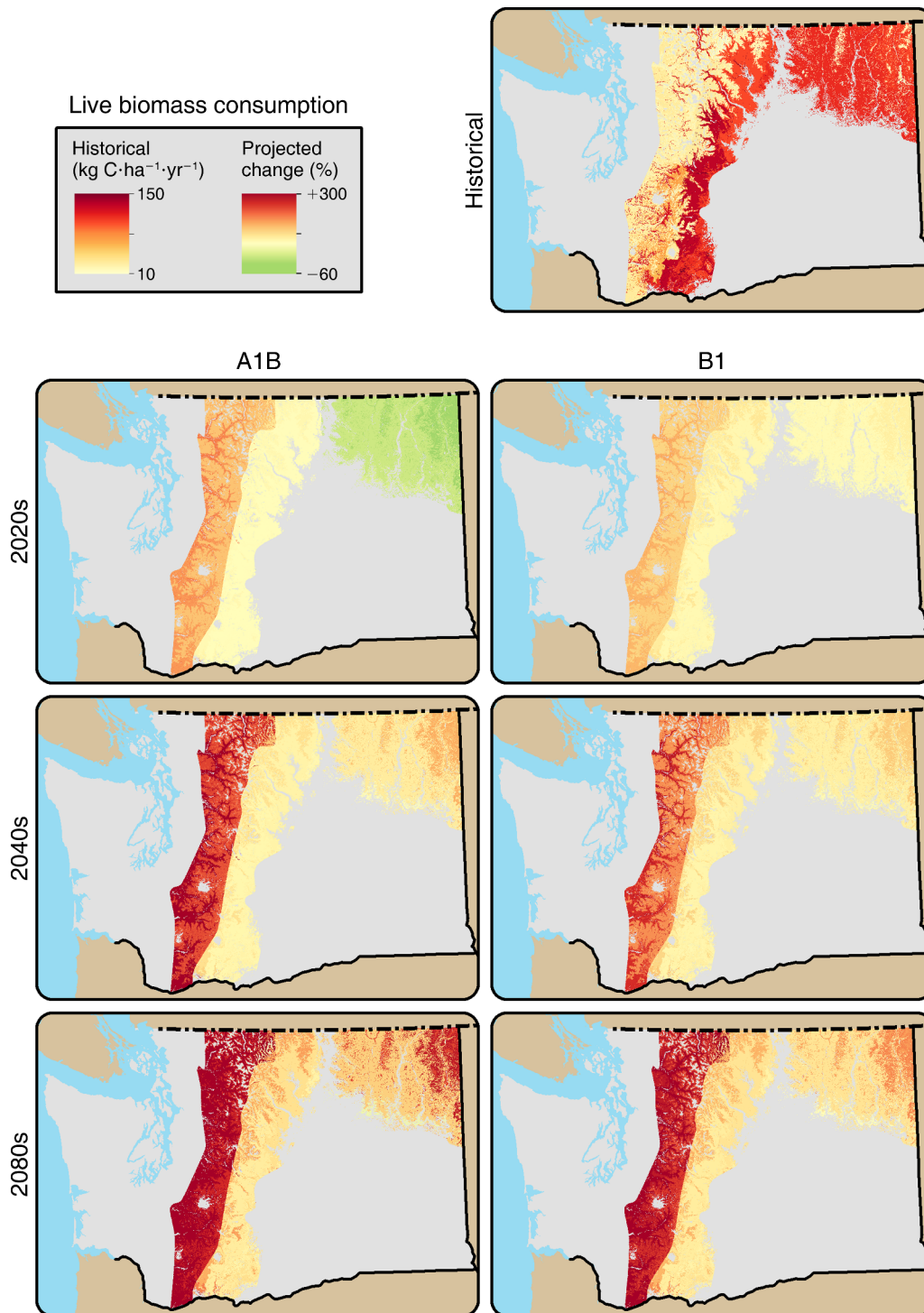
Fig. 7. Projected percentage changes in consumption of live biomass carbon for two SRES emissions scenarios (A1B and B1) and three time periods (2020s, 2040s, 2080s). Projected values are mean equilibrium conditions.

projected for high-elevation ESPs that have moderate FRIs and low biomass accumulation potential. CWD biomass is not projected to increase from fire-caused mortality in these ESPs.

Sensitivity of carbon pools and fluxes to changes in fire severity

For the 2040s, changes in fire severity have only a small effect on C pools and fluxes in ESPs with nonlethal
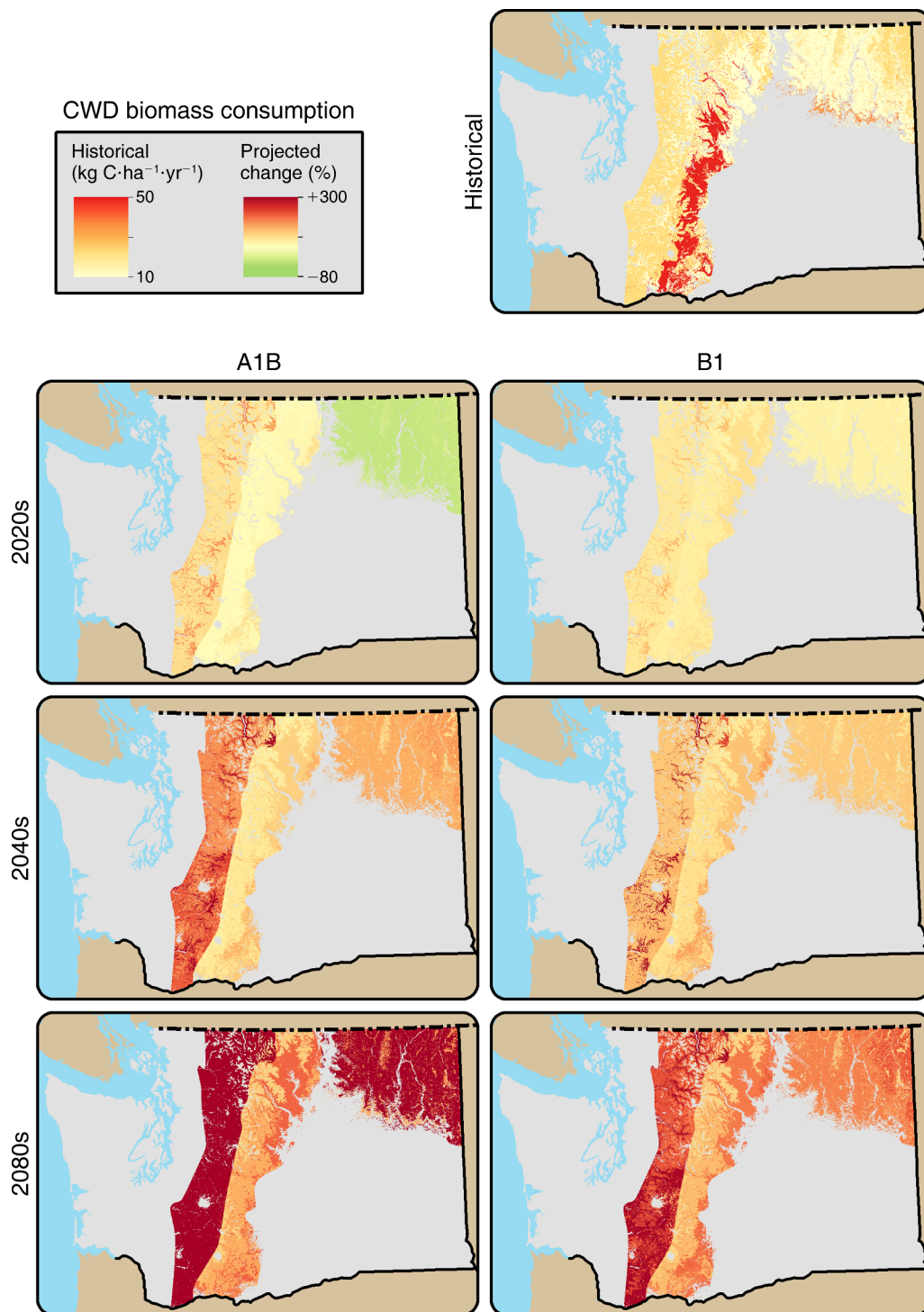
FIG. 8.   Projected percentage changes in consumption of coarse woody debris (CWD) biomass carbon for two SRES emissions scenarios (A1B and B1) and three time periods (2020s, 2040s, 2080s). Projected values are mean equilibrium conditions.

fire regimes. A 20% increase in the probability of moderate severity fire is projected to reduce live biomass C by an additional 5–10% and CWD biomass C by an additional 2–5% over increases in area burned alone. A 20% decrease in the probability of moderate severity fire

has a slightly greater effect. Projected losses of live biomass are reduced by 5–12% and CWD biomass by 2–7%. A 20% change in fire severity is projected to have little effect on equilibrium landscape NPP. A 20% decrease in fire severity offsets projected reductions in

NPP by 1–7%, whereas a 20% increase in fire severity further reduces NPP by a similar percentage. Increases or decreases in fire severity changed projections of live biomass consumption by only 3–5% but had a much bigger effect on projections of CWD consumption. A 20% decrease in fire severity is projected to offset increases in CWD consumption by 7–86% and a 20% increase in fire severity is projected to further increase CWD consumption by an additional 10–58%. ESPs with a higher probability of moderate severity fire historically are more sensitive to changes in fire severity.

Sensitivity to fire cycle parameterization for stand-replacing fire regimes

Given the range of published fire cycle values for each ESP, we calculated projections of C dynamics for both a long and short fire cycle (Appendix: Table A1) for all ESPs with a stand-replacing fire regime to test the sensitivity of results to the fire cycle parameter. Sensitivity generally depended on the length of the fire cycle in relation to parameters of the empirical models of C dynamics. Sensitivity of live biomass to the fire cycle parameter increased as the ratio of the fire cycle to Age_{90max} (the age at which 90% of maximum asymptotic biomass is reached) increased. For ESPs with large ratios, shifts in the age class distribution as the fire cycle decreases affect mean landscape biomass less because the mean age of the landscape remains close to the age at which the asymptote is approached. In contrast, for ESPs with a small ratio, shifts in the age class distribution greatly affect live biomass because the mean age of the landscape shifts leftward along the steep portion of the live-biomass curve.

In contrast, sensitivity of NPP to the fire cycle parameter increases as the ratio of the fire cycle to the age of maximum NPP increases. In ESPs for which this ratio is low (i.e., the fire cycle and age of maximum NPP are similar), shifts in the age class distributions greatly affect landscape NPP because stand ages shift around the steepest portions of the NPP curve. For a single emissions scenario and time period, NPP at the ESP scale changed by 3–22% with use of the shorter fire cycle.

Use of the shorter fire cycle parameter would further increase consumption of live biomass and CWD in all ESPs. In the Western Cascades, use of the shorter fire cycle parameter increases live biomass consumption by an additional 10–24% for the B1 scenario and 15–43% for the A1B scenario in the 2040s. In the Eastern Cascades and Okanogan Highlands, the difference between fire cycle parameters is only 3–14% for the B1 and A1B scenarios. In the Western Cascades, ESPs with intermediate fire cycles and large increases in the consumption of live biomass were most sensitive to the fire cycle parameter.

DISCUSSION

The results show large differences among ecosections in percentage changes of C stocks and fluxes with increases in area burned in a warmer climate, reflecting not only differences in projected area burned, but also differences in maximum potential C uptake and storage. Area burned in the Western Cascades is more sensitive to projected changes in climate than the Eastern Cascades and Okanogan Highlands. For example, Littell et al. (2010) project a two- to threefold increase in area burned by the mid-21st century. The greater relative changes and C pools and fluxes in the Western Cascades reflect this greater sensitivity of area burned to projected changes in climate. Forests of the Western Cascades also have higher rates of C uptake (NPP) and store more C in older forests. Thus shifts in age class distributions with increasing area burned affect equilibrium C dynamics more. Projections of future area burned, and thus changes in C pools and fluxes, do not consider potential feedbacks from decreases in fuel continuity or changes in vegetation types (McKenzie and Littell 2011). Nevertheless, we expect that increases in area burned are likely to have substantial consequences for C storage throughout the region and that C dynamics of forests of the Western Cascades will be most sensitive.

Live biomass carbon

Most forests of the western Cascades that have experienced little or no fire in the last few centuries accumulate substantial C stocks in live biomass, but these forests are projected to have the largest relative decreases in live biomass C with more fire in a warmer climate. When these forests burn, it is typically under extreme weather; fire spread is extensive and fire severity is high (Henderson et al. 1989, Agee 1993) so fires consume more of the live biomass. Within the Western Cascades ecosection, differences among ESPs in percentage changes in live biomass C reflect differences in potential C storage and fire regimes. Drier ESPs with intermediate fire return intervals (FRIs) (100–200 years) showed the greatest sensitivity to decreases in live biomass C with more area burned. In contrast, moist low-elevation ESPs with the longest historical FRIs were relatively less sensitive to decreases in live biomass C with increasing area burned. In these ESPs, FRIs projected for the 21st century remain long relative to the time required for the forest to accumulate large live C stocks.

Fire regimes of the Eastern Cascades and Okanogan Highlands are projected to be relatively less affected by changes in 21st century climate (Littell et al. 2010, Rogers et al. 2011). Fires during the presettlement period burned predominantly with low and moderate severity (Agee 1993, Hessburg et al. 2005). Tree species in this region have high crowns and thick bark enabling greater resistance to fire-caused mortality and regenerate well postfire. If climate change increases the proportion of area that burns with high severity, however, as well as area burned, losses of biomass will be greater than with increases in area burned alone. These results, however,

PLATE 1. Remnant fire-killed trees still standing more than 15 years after a high-severity fire in subalpine forests on the eastern slopes of the Cascade Range in Washington, USA. Fires are typically stand-replacing in fire-intolerant subalpine forests of this region, but the rugged terrain creates a mosaic of burned and unburned patches. Photo credit: Victor Mesny.

depend on the use of presettlement fire regimes as the historical reference condition. Changes in land use and fire exclusion have increased tree density and biomass, shifting tree species composition toward a greater proportion of fire intolerant species (Peterson et al. 2005). Therefore, increases in area burned may be accompanied by an increase in fire severity that is driven by a legacy of management effects on forest structure and composition. This would further increase losses of live biomass C.

Coarse woody debris biomass carbon

The large variation in projected changes in CWD by ecosection and ESP can be attributed to the different processes that control inputs to and outputs from the CWD pool. In this study, an important process that controls differences in landscape mean CWD is the relative change in age class distributions. In ESPs with replacement-severity fire regimes, CWD biomass decreases with increases in area burned because the fire cycle shortens, thus reducing the proportion of the landscape in older age classes. Older age classes have larger accumulations of CWD because of chronic mortality and slow decomposition (Spies et al. 1988, Harmon and Hua 1991). In ESPs with nonlethal fire regimes, however, CWD biomass depends more on the difference between inputs from fire-caused mortality and

losses from decomposition and consumption. High-elevation forests have low CWD input from chronic mortality and fire because these forests have less accumulation of live biomass (Raymond 2010). Therefore, in high-elevation forests increases in CWD consumption are projected to dominate the effects of more fire, and CWD biomass is projected to decrease. In contrast, in low-elevation ESPs with short FRIs, inputs from fire-caused mortality exceed losses from consumption so CWD biomass is projected to increase. Increases in CWD biomass decline late in the 21st century because fire-caused mortality, a fraction of live biomass, decreases as live biomass decreases.

These projected increases and decreases in CWD biomass C in our study differ from the Rogers et al. study (2011), which projected widespread increases in dead biomass C with increases throughout the 21st century. The difference is likely because we modeled equilibrium age class distributions, and changes in age class distributions greatly affect losses of CWD in forests of the Western Cascades. Another reason for the difference could be that we modeled changes in only CWD. More frequent fire will likely increase FWD because of fire-caused mortality, but this FWD is subject to greater consumption in subsequent fires (Rogers et al. 2011).

Net primary productivity

NPP is projected to increase in the Western Cascades and decrease in the Eastern Cascades and Okonogan Highlands with changes in 21st century fire regimes. Increases in NPP in some ESPs of the Western Cascades are the result of more frequent fires shifting equilibrium age class distribution toward younger stands, which remove more C from the atmosphere annually than older stands (Harmon et al. 1990). Regionally, this increase in annual C uptake may be offset by increases in C emissions from fire and decreases in NPP in forests of eastern Washington. Estimates of net ecosystem productivity (NEP) would be a better metric of the forest's status as a C sink or source, but NEP requires decomposition rates, and could not be calculated across our domain from the existing data.

Projected changes in NPP do not include direct effects of changes in climate and atmospheric chemistry on NPP, which are likely to have a different geographic pattern from effects of shifting age class distributions. Changes in NPP in forests of the PNW will be driven by complex interactions between disturbance regimes, direct effects of changes in temperature and precipitation, and possible fertilization from elevated atmospheric CO_2 and nitrogen (Schimel et al. 2000, Boisvenue and Running 2006). NPP in energy-limited forests at high elevations may increase with warmer temperatures because of longer growing seasons (Graumlich et al. 1989, Hicke et al. 2002). In contrast, warmer temperatures with no change or decreases in summer precipitation may reduce NPP in water-limited forests by accentuating moisture stress (Littell et al. 2008). In water-limited forests, higher concentrations of atmospheric CO_2 may offset moisture stress by increasing water use efficiency (Soule and Knapp 2006), but this effect may be short term (Oren et al. 2001) and not large enough to overcome moisture limitations (Sacks et al. 2007). NPP in nitrogen-limited forests may also increase with nitrogen deposition (Magnani et al. 2007). Simulation experiments with multiple factors suggest that the balance of these factors is expected to increase C uptake in forests of the western United States by 5%, but this response is sensitive to CO_2 fertilization and precipitation (Lenihan et al. 2008).

Biomass consumption

PNW forests may become a greater source of CO_2 emissions from fire during the 21st century, as fires become more frequent. Western Cascades forests have substantial biomass and typically burn with high severity, so a large fraction of live and CWD biomass is consumed by fire. In moist forests of the Western Cascades and eastern Okanogan Highlands, increases in consumption of live and CWD biomass are expected because these forests have higher C densities in CWD and live biomass (Smithwick et al. 2002). In contrast, modest increases are expected in dry forests of the Eastern Cascades and eastern Okanogan Highlands, for

three reasons: (1) lower-severity fires typical of these forests consume less biomass; (2) these forests accumulate less biomass (Smithwick et al. 2002); and (3) decomposition is faster (Harmon et al. 1986).

The differences between these regions are not as extreme for projected changes in consumption of CWD as consumption of live biomass. Greater area burned decreases CWD in forests of the Western Cascades but increases CWD in dry forests of the Eastern Cascades and Okanogan Highlands, so dry forests have a greater potential stock of CWD biomass to be consumed. Forests with mixed-severity fire regimes are most sensitive to increases in consumption of CWD for two reasons: (1) more frequent fire, and thus more fire-caused mortality, than high-severity fire regimes, and (2) greater consumption of CWD than low-severity fire regimes.

Limitations and assumptions

These projections represent plausible scenarios of future C dynamics in this forested region of Washington, but the utility of the results lies in the relative differences between ecosections, ESPs, time periods, and emissions scenarios, rather than the absolute values of projected results in C pools and fluxes. Given the limitations and uncertainties associated with the statistical models used (fire–climate models, age-based C models, and age class distributions) and other necessary assumptions, our results should be considered exploratory.

We did not quantify changes in consumption of dead biomass pools other than CWD. The forest inventory and analysis data (Waddell and Hiserote 2005) that we used to fit empirical models of C accumulation included only live and CWD biomass, not FWD, litter, and soil C (Raymond 2010). Including these pools would certainly affect results for consumption of dead biomass C. Increases in fire-caused mortality would increase FWD, but a large portion of this biomass would be consumed by subsequent fires.

We assumed that equilibrium age class distributions in forests with stand-replacing fire regimes fit a negative exponential model. We applied the negative exponential model to large forested areas (Table 1) with stand-replacing fire regimes, the domain for which the model was intended to be used (Van Wagner 1978). Research in the PNW suggests that the model may fit poorly when applied at the scale of individual watersheds (Hemstrom and Franklin 1982), but adequately when applied to age class distributions at the regional scale (Fahnestock and Agee 1983). We also assumed that age class distributions are in equilibrium with the disturbance regime of each time period. Although no forest stand is in equilibrium, the assumption is appropriate for large forested landscapes (Bormann and Likens 1979, Shugart and West 1981, Frelich 2002). Frelich's criterion for equilibrium is met under two conditions: (1) the size of disturbances must be small relative to the size of the

study area and (2) disturbances must occur at relatively constant rates over time. Age class reconstructions suggest that very large fires have burned in the western Cascades in the past (Henderson et al. 1989, Agee 1993), but despite the potential for a rare large fire that burns substantial area, the equilibrium assumption can be used in this study because we calculated equilibrium conditions for large forested regions. Frelich's second criterion is more problematic. A changing climate implies changing, rather than constant, fire regimes over time. Forests with long fire return intervals are unlikely to reach equilibrium within 20 to 30 years, so the results of this study are best interpreted as equilibrium conditions for each of three time periods, rather than a progression of changes through the 21st century. A useful interpretation is to consider results for each time period as the conditions that would be expected if future area burned were to stabilize at the area burned represented by the time period.

Results of this study partially depend on the use of presettlement fire regimes as the historical reference. Current age class distributions in Washington are different from what would be expected with presettlement fire regimes because of harvesting, land development, and fire exclusion (Wimberly et al. 2000). In the Western Cascades, a greater proportion of the forested area is in younger age classes so current rates of C uptake are higher as forests grow following a more frequent harvest regime (Houghton and Hackler 2000, Hurtt et al. 2002, Ryan et al. 2010). In the Eastern Cascades and Okanogan Highlands, forests currently have higher biomass density than would be expected with presettlement fire regimes because fire exclusion increased fire return intervals and shifted age class distributions to more area of old forest (Hessburg et al. 2000). Because we are estimating proportional changes, however, we are still able to use the proportional changes in area burned between the current and future periods (Littell et al. 2010), without biases, to represent climate-driven changes.

We used projections of area burned based on statistical models of 20th century area burned as a function of climate. The models explain 50–65% of the variability in area burned (Littell et al. 2010), thus factors other than climate (e.g., fuel amount and continuity) affected area burned in the 20th century and will continue to affect area burned in the future. These statistical fire–climate models do not include feedbacks between increasing area burned and reductions in fuel or changes in vegetation types, both of which could lead to novel fire regimes (McKenzie and Littell 2011). The largest proportional increases in area burned were projected for the Western Cascades ecosection and thus we observed the greatest relative changes in C pools and fluxes in this ecosection. The fire–climate model for this ecosection had the weakest statistical relationship suggesting that this ecosection has the most complex interactions between fire, climate, and

fuels (McKenzie and Littell 2011). Results of other studies reinforce the plausibility of the projected increases in area burned. Fire history evidence suggests that large fires have burned in this region in the past 500 years (Henderson et al. 1989). Similar projections of greater than 10-fold increases in area burned have been made for the western Cascades with a mechanistic fire model (Rogers et al. 2011) and for the infrequent, high-severity fire regimes of the Greater Yellowstone Ecosystem with a statistical model (Westerling et al. 2011). Results for the Western Cascades in the 2080s in particular should be interpreted with caution, however, because of the limitations of statistical models for future projections into a climate space outside that in which they were developed.

Process-based approaches may appear to treat more thoroughly the interactions between climate and other controls on fire regimes, such as fuel amount and continuity and topography. For example, dynamic general vegetation models (DGVMs) that include fire modules simulate the interactions between fire and the direct effects of climate on productivity, decomposition, and vegetation distributions (e.g., Lenihan et al. 2008). DGVMs require many parameters whose selection is partially subjective, yet the results can be highly sensitive to the values of those parameters (Lenihan et al. 2008). DGVMs also have simplified representations of vegetation types and differences in fire regimes do not account for species-specific tolerances to fire. Furthermore, many of the processes simulated in process-based models ultimately rely on empirical relationships. Given that both types of models have strengths and weaknesses, we can ask complex questions regarding climate change effects on ecosystems with both empirical and process-based approaches, to identify consistent results, which increase confidence, and inconsistent results, which suggest future research needs.

Increases in rates of other disturbances may amplify changes in C pools and fluxes caused by fire, further reducing live biomass C and increasing CWD biomass C. Fire is the primary disturbance in this region, but other natural and anthropogenic disturbances affect C storage potential, including windstorms, insect outbreaks (Kurz et al. 2008), pathogens, drought-induced mortality (Breshears et al. 2005, van Mantgem et al. 2009), and land-use change. In a warmer climate, water-limited forests in this region are expected to be more vulnerable to insect outbreaks (Logan et al. 2003, Hicke et al. 2006) and drought (van Mantgem and Stephenson 2007). Future C dynamics in forests of the PNW will also depend on rates of land development and harvesting (Plantinga and Birdsey 1993, Turner et al. 1995, Harmon and Marks 2002), although our study area is predominantly U.S. federal land, so these are expected to be low. All these disturbances interact with fire, increasing or decreasing area burned by altering fuel availability and continuity (Breshears and Allen 2002, Bigler et al. 2005, McKenzie et al. 2009).

Implications for forest management

Projected increases in forest C loss with more extensive and severe fires in the 21st century will challenge management on private and public lands in the PNW. Carbon credits are currently sold in voluntary markets in the United States (Birdsey 2006). Recipients are required to demonstrate "permanence" (forests must be expected to store the additional C for a specified amount of time). Some risk associated with C loss to natural disturbances is typically accounted for in carbon offsets, usually as a buffer added to the amount of the credit (Galik and Jackson 2009). Our study suggests that the historical range of variability for the frequency and severity of fires is not a useful guide for setting these credits and buffers. Climate-driven increases in area burned and severity and associated C loss suggest the need to increase buffers for carbon offsets. Buffers may need to be increased more in the Western Cascades than the Eastern Cascades and Okanogan Highlands because fire regimes are more sensitive to changes in climate and shifts in age class distributions affect biomass pools more.

Forest management may be able to reduce projected C loss by suppressing fire, preventing human ignitions, and adapting to climate change. We did not consider the effects of fire suppression on projected area burned, fire severity, or C pools and fluxes. Fire suppression can change C fluxes and pools by reducing area burned and fire severity in some forest types, but the effects are likely to be short term. Simulation experiments suggest that fire suppression can increase C stocks in forests of the western United States, but only in dry fire-adapted forests where fire intensity is low and fire suppression is more likely to be effective (Rogers et al. 2011). Rogers et al. (2011) found that fire suppression affected C stocks in forests of the western PNW less because fires typically burn under conditions that render fire suppression ineffective. Fire suppression will certainly continue, to protect the urban interface, air quality, and wildlife habitat, but will not prevent C loss from increases in area burned, because it is the few fires that cannot be suppressed that burn most of the area (Strauss et al. 1989).

Prescribed burning (Narayan et al. 2007, Wiedinmyer and Hurteau 2010) and silvicultural fuel treatments (e.g., North et al. 2009) may be useful for reducing C emissions from wildfire. Prescribed burning and silvicultural treatments are commonly used to reduce fuels, fire hazard, and fire severity, but the benefits of these treatments for C storage are uncertain. Fuel treatments remove C from the system and must be implemented more often than wildfires occur in order to maintain lower fire hazard (Mitchell et al. 2009, Ryan et al. 2010). The balance between averted C emissions through fuel treatments and C loss from wildfire depends on the fire regime (Narayan et al. 2007, Mitchell et al. 2009), the potential to treat fuels across large areas (Amiro et al.

2001), and the end use of biomass removed (Finkral and Evans 2008).

Managing smoke emissions will be more challenging under a warmer climate if live and CWD biomass consumption increase as projected. Emissions from fires have consequences for public health and impairment of scenic views in national parks and wilderness areas. The western Cascades, which has been relatively less affected by smoke emissions in the last century, will be at greater risk in the 21st century because of the greater sensitivity of these forests to increased fire with changes in climate.

Management that facilitates forest adaptation to climate change (Joyce et al. 2009) may also reduce C loss from increases in fire. More C is lost from the system if fires are followed by delays in forest regeneration (Keyser et al. 2008), substantially reduced forest density (Kashian et al. 2006), or vegetation conversions to grasslands or shrublands (Savage and Mast 2005). The greater likelihood of fire in the 21st century increases the need for post-disturbance management even in forests of the western Cascades in which historical fires were infrequent. Post-disturbance management will more effectively reduce C loss from wildfire by recognizing that climate at the time of the disturbance differs from the climate under which the forest established.

CONCLUSION

The complexity of the modeling effort and its associated uncertainties limit us to preliminary inferences about how climate-driven changes in fire regimes will affect C dynamics through the 21st century. Although results themselves were complex and varied, and not always intuitive, one principal message of this work is that contrasting outcomes among ecosections and ESPs yield to sound ecological reasoning, consistent with both field studies and other modeling efforts. For example, the Western Cascades appear to be the most sensitive to the changes in fire regimes currently expected. This reflects their relative complacency to fire historically compared to the drier ecosections in which fire has been a dominant ecosystem process, but a complacency that is expected to change as they become more vulnerable in a hotter drier climate. A key need for future studies like this one is an understanding of the sensitivities associated with the components of an integrated model, whether it is empirical like ours or process-based. Complementary efforts along both of these lines should be compared actively to improve both the quantification of the many uncertainties and the robustness of future projections.

LITERATURE CITED

Agee, J. K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C., USA.

Agee, J. K. 2003. Historical range of variability in eastern Cascades forests, Washington, USA. Landscape Ecology 18:725–740.

Amiro, B. D., B. J. Stocks, M. E. Alexander, M. D. Flannigan, and B. M. Wotton. 2001. Fire, climate change, carbon and fuel management in the Canadian boreal forest. International Journal of Wildland Fire 10:405–413.

Bailey, R. G. 1995. Description of the ecoregions of the United States. Second edition. USDA Forest Service Miscellaneous Publication Number 1391 (revised), Washington, D.C., USA.

Bigler, C., D. Kulakowski, and T. T. Veblen. 2005. Multiple disturbance interactions and drought influence fire severity in Rocky Mountain subalpine forests. Ecology 86:3018–3029.

Birdsey, R. A. 2006. Carbon accounting rules and guidelines for the United States forest sector. Journal of Environmental Quality 35:1518–1524.

Boisvenue, C., and S. W. Running. 2006. Impacts of climate change on natural forest productivity—evidence since the middle of the 20th century. Global Change Biology 12:862–882.

Bormann, F. H., and G. E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York, New York, USA.

Bowman, D., et al. 2009. Fire in the Earth system. Science 324:481–484.

Breshears, D. D., and C. D. Allen. 2002. The importance of rapid, disturbance-induced losses in carbon management and sequestration. Global Ecology and Biogeography 11:1–5.

Breshears, D. D., et al. 2005. Regional vegetation die-off in response to global-change-type drought. Proceedings of the National Academy of Sciences USA 102:15144–15148.

Campbell, J., D. Donato, D. Azuma, and B. Law. 2007. Pyrogenic carbon emissions from a large wildfire in Oregon, United States. Journal of Geophysical Research 112:1–11.

Cansler, C. A. 2011. Drivers of burn severity in the northern Cascade Range, Washington, USA. Thesis. University of Washington, Seattle, Washington, USA.

Comer, P., D. Faber-Langendoen, R. Evans, S. Gawler, C. Josse, G. Kittel, S. Menard, M. Pyne, M. Reid, K. Schulz, K. Snow, and J. Teague. 2003. Ecological systems of the United States: a working classification of U.S. terrestrial systems. NatureServe, Arlington, Virginia, USA.

Daly, C., R. P. Neilson, and D. L. Phillips. 1994. A statistical topographic model for mapping climatological precipitation over mountainous terrain. Journal of Applied Meteorology 33:140–158.

Elsner, M. M., L. Cuo, N. Voison, J. S. Deems. A. F. Hamlet, J. A. Vano, K. E. B. Mickelson, S.-Y. Lee, and D. P. Lettenmaier. 2010. Implications of 21st century climate change for the hydrology of Washington State. Climatic Change 102:225–260.

Euskirchen, E. S., J. Chen, H. Li, E. J. Gustafson, and T. R. Crow. 2002. Modeling landscape net ecosystem productivity (LandNEP) under alternate management regimes. Ecological Modelling 154:75–91.

Fahnestock, G. R., and J. K. Agee. 1983. Biomass consumption and smoke production by prehistoric and modern forest fires in western Washington. Journal of Forestry 81:653–657.

Finkral, A. J., and A. M. Evans. 2008. Effects of a thinning treatment on carbon stocks in a northern Arizona ponderosa pine forest. Forest Ecology and Management 255:2743–2750.

Franklin, J. F., and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oregon, USA.

Frelich, L. E. 2002. Forest dynamics and disturbance regimes. Cambridge University Press, Cambridge, UK.

Galik, C. S., and R. B. Jackson. 2009. Risks to forest carbon offset projects in a changing climate. Forest Ecology and Management 257:2209–2216.

Gavin, D. G., D. J. Hallett, F. S. Hu, K. P. Lertzman, S. J. Prichard, K. J. Brown, J. A. Lynch, P. Bartlein, and D. L. Peterson. 2007. Forest fire and climate change in western North America: insights from sediment charcoal records. Frontiers in Ecology and the Environment 5:499–506.

Graumlich, L. J., L. B. Brubaker, and C. C. Grier. 1989. Long-term trends in forest net primary productivity: Cascade Mountains, Washington. Ecology 70:405–410.

Grissino-Mayer, H. D. 1999. Modeling fire interval data from the American Southwest with the Weibull distribution. International Journal of Wildland Fire 9:37–50.

Hann, W., A. Shlisky, D. Havlina, K. Schon, S. Barrett, T. DeMeo, K. Pohl, J. Menakis, D. Hamilton, J. Jones, M. Levesque, and C. Frame. 2004. Interagency fire regime condition class guidebook version 1.3. www.frcc.gov

Harmon, M. E., K. Bible, M. G. Ryan, D. C. Shaw, H. Chen, J. Klopatek, and X. Li. 2004. Production, respiration, and overall carbon balance in an old-growth *Pseudotsuga–Tsuga* forest ecosystem. Ecosystems 7:498–512.

Harmon, M. E., W. K. Ferrell, and J. F. Franklin. 1990. Effects on carbon storage of conversion of old-growth forests to young forests. Science 247:699–702.

Harmon, M. E., et al. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15:133–302.

Harmon, M. E., and C. Hua. 1991. Coarse woody debris dynamics in two old-growth ecosystems. Comparing a deciduous forest in China and a conifer forest in Oregon. BioScience 41:604–610.

Harmon, M. E., and B. Marks. 2002. Effects of silvicultural practices on carbon stores in Douglas-fir–western hemlock forests in the Pacific Northwest, USA: results from a simulation model. Canadian Journal of Forest Research 32:863–877.

Hemstrom, M. A., and J. F. Franklin. 1982. Fire and other disturbances of the forests in Mount Rainier National Park. Quaternary Research 18:32–51.

Henderson, J. A., D. H. Peter, R. D. Lesher, and D. C. Shaw. 1989. Forested plant associations of the Olympic National Forest. USDA Forest Service, Pacific Northwest Region R6-ECOL-TP 001-88.

Hessburg, P. F., J. K. Agee, and J. F. Franklin. 2005. Dry forests and wildland fires of the inland Northwest USA: contrasting the landscape ecology of the pre-settlement and modem eras. Forest Ecology and Management 211:117–139.

Hessburg, P. F., B. G. Smith, R. B. Salter, R. D. Ottmar, and E. Alvarado. 2000. Recent changes (1930s–1990s) in spatial patterns of interior northwest forests, USA. Forest Ecology and Management 136:53–83.

Hessl, A. E., D. McKenzie, and R. Schellhaas. 2004. Drought and Pacific Decadal Oscillation linked to fire occurrence in the inland Pacific Northwest. Ecological Applications 14:425–442.

Heyerdahl, E. K., L. B. Brubaker, and J. K. Agee. 2002. Annual and decadal climate forcing of historical fire regimes in the interior Pacific Northwest, USA. Holocene 12:597–604.

Heyerdahl, E. K., D. McKenzie, L. D. Daniels, A. E. Hessl, J. S. Littell, and N. J. Mantua. 2008. Climate drivers of regionally synchronous fires in the inland Northwest (1651–1900). International Journal of Wildland Fire 17:40–49.

Hicke, J. A., G. P. Asner, J. T. Randerson, C. Tucker, S. Los, R. Birdsey, J. C. Jenkins, C. Field, and E. Holland. 2002.

Satellite-derived increases in net primary productivity across North America, 1982–1998. Geophysical Research Letters 29:1029/2001GL013578.

Hicke, J. A., J. A. Logan, J. Powell, and D. S. Ojima. 2006. Changing temperatures influence suitability for modeled mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in the western United States. Journal of Geophysical Research Biogeosciences 111:1–12.

Holsinger, L., R. E. Keane, R. A. Parsons, and E. Karau. 2006. Development of biophysical gradient layers for the LANDFIRE prototype project. Pages 99–122 in M. G. Rollins and C. K. Frame, editors. The LANDFIRE prototype project: nationally consistent and locally relevant geospatial data for wildland fire management. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Houghton, R. A., and J. L. Hackler. 2000. Changes in terrestrial carbon storage in the United States. 1: The roles of agriculture and forestry. Global Ecology and Biogeography 9:125–144.

Houghton, R. A., J. L. Hackler, and K. T. Lawrence. 2000. Changes in terrestrial carbon storage in the United States. 2: The role of fire and fire management. Global Ecology and Biogeography 9:145–170.

Hudiburg, T., B. Law, D. P. Turner, J. Campbell, D. Donato, and M. Duane. 2009. Carbon dynamics of Oregon and Northern California forests and potential land-based carbon storage. Ecological Applications 19:163–180.

Hurtt, G. C., S. W. Pacala, P. R. Moorcroft, J. Caspersen, E. Shevliakova, R. A. Houghton, and B. Moore. 2002. Projecting the future of the U.S. carbon sink. Proceedings of the National Academy of Sciences USA 99:1389–1394.

Janisch, J. E., and M. E. Harmon. 2002. Successional changes in live and dead wood carbon stores: implications for net ecosystem productivity. Tree Physiology 22:77–89.

Johnson, E. A., and S. L. Gutsell. 1994. Fire frequency models, methods, and interpretations. Advances in Ecological Research 25:239–287.

Joyce, L. A., G. M. Blate, S. G. McNulty, C. I. Millar, S. Moser, R. P. Neilson, and D. L. Peterson. 2009. Managing for multiple resources under climate change: national forests. Environmental Management 44:1022–1032.

Kashian, D. M., W. H. Romme, D. B. Tinker, M. G. Turner, and M. G. Ryan. 2006. Carbon storage on landscapes with stand-replacing fires. BioScience 56:598–606.

Keane, R. E., M. G. Rollins, C. H. McNicoll, and R. A. Parsons. 2002. Integrating ecosystem sampling, gradient modeling, remote sensing, and ecosystem simulation to create spatially explicit landscape inventories. USDA Forest Service General Technical Report RMRS-92. Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Keyser, T. L., L. B. Lentile, F. W. Smith, and W. D. Shepperd. 2008. Changes in forest structure after a large, mixed-severity wildfire in ponderosa pine forests of the Black Hills, South Dakota, USA. Forest Science 54:328–338.

Kurz, W. A., and M. J. Apps. 1999. A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. Ecological Applications 9:526–547.

Kurz, W. A., C. C. Dymond, G. Stinson, G. J. Rampley, E. T. Neilson, A. L. Carroll, T. Ebata, and L. Safranyik. 2008. Mountain pine beetle and forest carbon feedback to climate change. Nature 452:987–990.

Lenihan, J. M., D. Bachelet, R. P. Neilson, and R. Drapek. 2008. Simulated response of conterminous United States ecosystems to climate change at different levels of fire suppression, CO_2 emission rate, and growth response to CO_2. Global and Planetary Change 64:16–25.

Littell, J. S., D. McKenzie, D. L. Peterson, and A. L. Westerling. 2009. Climate and wildfire area burned in western U.S. ecoprovinces, 1916–2003. Ecological Applications 19:1003–1021.

Littell, J. S., E. E. Oneil, D. McKenzie, J. A. Hicke, J. A. Lutz, R. A. Norheim, and M. M. Elsner. 2010. Forest ecosystems, disturbance, and climatic change in Washington State, USA. Climatic Change 102:129–158.

Littell, J. S., D. L. Peterson, and M. Tjoelker. 2008. Douglas-fir growth in mountain ecosystems: water limits tree growth from stand to region. Ecological Monographs 78:349–368.

Logan, J. A., J. Regniere, and J. A. Powell. 2003. Assessing the impacts of global warming on forest pest dynamics. Frontiers in Ecology and the Environment 1:130–137.

Lutz, J. A., J. W. van Wagtendonk, A. E. Thode, J. D. Miller, and J. F. Franklin. 2009. Climate, lightning ignitions, and fire severity in Yosemite National Park, California, USA. International Journal of Wildland Fire 18:765–774.

Magnani, F., et al. 2007. The human footprint in the carbon cycle of temperate and boreal forests. Nature 447:848–850.

McKenzie, D., A. E. Hessl, and L. K. B. Kellogg. 2006. Using neutral models to identify constraints on low-severity fire regimes. Landscape Ecology 21:139–152.

McKenzie, D., and J. S. Littell. 2011. Climate change and wilderness fire regimes. International Journal of Wilderness 17:22–27,31.

McKenzie, D., D. L. Peterson, and J. J. Littell. 2009. Global warming and stress complexes in forests of western North America. Pages 317–337 in A. Bytnerowicz, M. Arbaugh, A. Riebau, and C. Anderson, editors. Wildland fires and air pollution. Elsevier, Amsterdam, The Netherlands.

Mitchell, S. R., M. E. Harmon, and K. E. B. O'Connell. 2009. Forest fuel reduction alters fire severity and long-term carbon storage in three Pacific Northwest ecosystems. Ecological Applications 19:643–655.

Mote, P. W., and E. P. Salathé. 2010. Future climate in the Pacific Northwest. Climatic Change 102:29–50.

Narayan, C., P. M. Fernandes, J. van Brusselen, and A. Schuck. 2007. Potential for CO_2 emissions mitigation in Europe through prescribed burning in the context of the Kyoto Protocol. Forest Ecology and Management 251:164–173.

Nonaka, E., T. A. Spies, M. C. Wimberly, and J. L. Ohmann. 2007. Historical range of variability in live and dead wood biomass: a regional-scale simulation study. Canadian Journal of Forest Research 37:2349–2364.

North, M., M. Hurteau, and J. Innes. 2009. Fire suppression and fuels treatment effects on mixed-conifer carbon stocks and emissions. Ecological Applications 19:1385–1396.

Oren, R., D. S. Ellsworth, K. H. Johnsen, N. Phillips, B. E. Ewers, C. Maier, K. V. R. Schafer, H. McCarthy, G. Hendrey, S. G. McNulty, and G. G. Katul. 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO_2-enriched atmosphere. Nature 411:469–472.

Peterson, D. L., M. C. Johnson, J. K. Agee, T. B. Jain, D. McKenzie, and E. D. Reinhardt. 2005. Forest structure and fire hazard in dry forests of the western United States. USDA Forest Service General Technical Report PNW-628. Pacific Northwest Research Station, Portland, Oregon, USA.

Plantinga, A. J., and R. A. Birdsey. 1993. Carbon fluxes resulting from United States private timberland management. Climatic Change 23:37–53.

Pregitzer, K. S., and E. S. Euskirchen. 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. Global Change Biology 10:2052–2077.

R Development Core Team. 2008. R: language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raymond, C. L. 2010. Carbon dynamics of forests in Washington, U.S. and the effects of climate-driven changes in fire regimes on carbon storage potential. Dissertation. University of Washington, Seattle, Washington, USA.

Richards, T. J. 1959. A flexible growth function for empirical use. Journal of Experimental Botany 10:290–300.

Rogers, B. M., R. P. Neilson, R. Drapek, J. M. Lenihan, J. R. Wells, D. Bachelet, and B. E. Law. 2011. Impacts of climate change on fire regimes and carbon stocks of the U.S. Pacific Northwest. Journal of Geophysical Research Biogeosciences 116:1–13.

Rollins, M. G. 2009. LANDFIRE: a nationally consistent vegetation, wildland fire, and fuel assessment. International Journal of Wildland Fire 18:235–249.

Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs 52:199–221.

Ryan, M. G., M. E. Harmon, R. A. Birdsey, C. P. Giardina, L. S. Heath, R. A. Houghton, R. B. Jackson, D. C. McKinley, J. F. Morrison, B. C. Murray, D. E. Pataki, and K. E. Skog. 2010. A synthesis of the science on forests and carbon for U.S. forests. Issues in Ecology 13:1–17.

Sacks, W. J., D. S. Schimel, and R. K. Monson. 2007. Coupling between carbon cycling and climate in a high-elevation, subalpine forest: a model-data fusion analysis. Oecologia 151:54–68.

Savage, M., and J. N. Mast. 2005. How resilient are southwestern ponderosa pine forests after crown fires? Canadian Journal of Forest Research 35:967–977.

Schimel, D., et al. 2000. Contribution of increasing CO_2 and climate to carbon storage by ecosystems in the United States. Science 287:2004–2006.

Shugart, H. H., and D. C. West. 1981. Long-term dynamics of forest ecosystems. American Scientist 69:647–652.

Smith, J. E., and L. S. Heath. 2004. Carbon stocks and projections on public forestlands in the United States, 1952–2040. Environmental Management 33:433–442.

Smithwick, E. A. H., M. E. Harmon, S. M. Remillard, S. A. Acker, and J. F. Franklin. 2002. Potential upper bounds of carbon stores in forests of the Pacific Northwest. Ecological Applications 12:1303–1317.

SOCCR. 2007. The first state of the carbon cycle report (SOCCR): the North American carbon budget and implications for the global carbon cycle. A report by the U.S. Climate Change Science Program and the Subcommittee on Global Change Research. National Oceanic and Atmospheric Administration, National Climatic Data Center, Asheville, North Carolina, USA.

Soule, P. T., and P. A. Knapp. 2006. Radial growth rate increases in naturally occurring ponderosa pine trees: a late-20th century CO_2 fertilization effect? New Phytologist 171:379–390.

Spies, T. A., J. F. Franklin, and T. B. Thomas. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology 69:1689–1702.

Strauss, D., L. Bednar, and R. Mees. 1989. Do one percent of forest fires cause ninety-nine percent of the damage? Forest Science 35:319–328.

Thornton, P. E., S. W. Running, and M. A. White. 1997. Generating surfaces of daily meteorological variables over large regions of complex terrain. Journal of Hydrology 190:214–251.

Turner, D. P., G. J. Koerper, M. E. Harmon, and J. J. Lee. 1995. Carbon sequestration by forests of the United States. Current status and projections to the year 2040. Tellus Series B: Chemical and Physical Meteorology 47:232–239.

van Mantgem, P. J., and N. L. Stephenson. 2007. Apparent climatically induced increase of tree mortality rates in a temperate forest. Ecology Letters 10:909–916.

van Mantgem, P. J., N. L. Stephenson, J. C. Byrne, L. D. Daniels, J. F. Franklin, P. Z. Fule, M. E. Harmon, A. J. Larson, J. M. Smith, A. H. Taylor, and T. T. Veblen. 2009. Widespread increase of tree mortality rates in the western United States. Science 323:521–524.

Van Wagner, C. E. 1978. Age-class distribution and the forest fire cycle. Canadian Journal of Forest Research 8:220–227.

Waddell, K. L., and B. Hiserote. 2005. The PNW-FIA integrated database. Forest Inventory and Analysis Program, Pacific Northwest Research Station, Portland, Oregon, USA.

Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. Science 313:940–943.

Westerling, A. L., M. G. Turner, E. A. H. Smithwick, W. H. Romme, and M. G. Ryan. 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. Proceedings of the National Academy of Sciences USA 108:13165–13170.

Wiedinmyer, C., and M. D. Hurteau. 2010. Prescribed fire as a means of reducing forest carbon emissions in the western United States. Environmental Science and Technology 44:1926–1932.

Wiedinmyer, C., and J. C. Neff. 2007. Estimates of CO_2 from fires in the United States: implications for carbon management. Carbon Balance and Management 2:1–12.

Wimberly, M. C., T. A. Spies, C. J. Long, and C. Whitlock. 2000. Simulating historical variability in the amount of old forests in the Oregon Coast Range. Conservation Biology 14:167–180.

SUPPLEMENTAL MATERIAL

Appendix

Parameters of fire regimes and empirical models of carbon accumulation with stand age for environmental site potentials in the study area (*Ecological Archives* A022-084-A1).