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Forest ecosystems, disturbance, and climatic change in Washington State, USA

Jeremy S. Litten · Elaine E. Oneil · Donald McKenzie ·
Jeffrey A. Hicke · James A. Lutz ·
Robert A. Norheim · Marketa M. Elsner

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Abstract Climatic change is likely to affect Pacific Northwest (PNW) forests in several important ways. In this paper, we address the role of climate it. four forest ecosystem processes and project the effects of future climatic change on these processes across Washington State. First, we relate Douglas-fir growth to climatic limitation and suggest that where Douglas-fir is currently water-limited, growth is likely to decline due to increased summer water deficit. Second, we use existing analyses of climatic controls on tree species biogeography to demonstrate that by the mid twenty-first century, climate will be less suitable for key species in some areas of Washington. Third, we examine the relationships between climate and the area burned by fire and project climatically driven regional and sub-regional increases in

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J. S. Littell (✉) · R. A. Norheim · M. M. Elsner
JISAO/CSES Climate Impacts Group, University of Washington, Box 355672,
Seattle, WA 98195-5672, USA
e-mail: jlittell@u.washington.edu

E. E. Oneil
Rural Technology Initiative, School of Forest Resources, University of Washington,
Box 352100, Seattle, WA 98195-2100, USA

D. McKenzie
Pacific Wildland Fire Sciences Lab, US Forest Service, Suite 201, 400 N. 34th St.,
Seattle, WA 98103, USA

J. A. Hicke
Department of Geography, University of Idaho, P.O. Box 443021, Moscow,
ID 83844-3021, USA

J. A. Lutz · R. A. Norheim
School of Forest Resources, University of Washington, Box 352100, Seattle,
WA 98195-2100, USA

M. M. Elsner
University of WA,
Box 352700, Seattle, WA 98195-2700, USA

area burned. Fourth, we suggest that climatic change influences mountain pine beetle (MPB) outbreaks by increasing host-tree vulnerability and by shifting the region of climate suitability upward in elevation. The increased rates of disturbance by fire and mountain pine beetle are likely to be more significant agents of changes in forests in the twenty-first century than species turnover or declines in productivity, suggesting that understanding future disturbance regimes is critical for successful adaptation to climate change.

1 Introduction

Global climate change is expected to affect Earth's ecosystems in many ways (IPCC Working Group II 2007). Terrestrial ecosystems may experience widespread mortality of vegetation from the direct effects of changes in temperature and precipitation (Breshears et al. 2005; Lutz and Halpern 2006; van Mantgem and Stephenson 2007; van Mantgem et al. 2009 as well as indirectly from increased extent, intensity, and frequency of disturbance (McKenzie et al. 2004; Gedalof et al, 2005 Hicke et al. 2006; Litten 2006 Littell et al. 2009). As a result, new ecosystem types, comprising heretofore rare or non-existent combinations of species, may succeed those no longer adapted to new climates, in turn changing landscape structure and spatial pattern across a range of scales (Davis 1986). Anticipating these changes is challenging, but necessary to support long-term planning, natural resources management, and maintenance of the myriad services that ecosystems provide.

In the Pacific Northwest (PNW) region of US North America (here defined as Washington, Oregon, Idaho, and western Montana), forests, both on public and private lands, are a key natural resource. In Washington State alone, forests cover 8,926,490 ha (Fig. 1), 52% of the total area of the state. Approximately 56% (~5 million ha) of this forested land is publicly owned, administered by federal (US

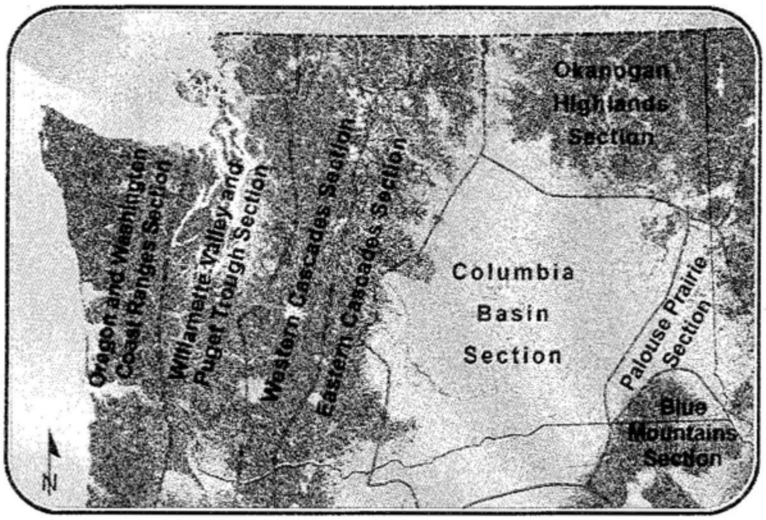

Fig. 1 Forested areas of Washington State, and Bailey's ecosections used for sub-regional fire modeling. Figure: Robert Norheim

Departments of Agriculture and Interior) and state (WA Department of Natural Resources) agencies. The remainder is managed by tribal, private, and corporate landowners. Legal mandates and owner objectives for these lands vary, but both will be affected by a changing climate,

Conifer species dominate forest ecosystems within Washington State, with hardwood species abundant only in riparian areas that experience frequent flooding or other heavily disturbed areas such as avalanche chutes or recently logged sites. Forest composition varies with both elevation and position on a broad west-east (maritime-continental) gradient across the state. At a finer scale, orographic effects on species composition are apparent on the leeward versus windward sides of both the Olympic Mountains and the Cascade Range, where complex topography produces steep gradients in the biophysical environment across relatively short distances (Williams and Lillybridge 1983 Franklin and Dyrness 1988 Henderson et al. 1989, 1992; Williams et al. 1990; Lillybridge et al. 1995).

Research from many ecosystems around the world at many scales has documented climatic controls on vegetation (Davis and Botkin 1985; Overpeck et al. 1990; Guisan and Zimmermann 2000). Climatic limiting factors operate mechanistically through the interface between organisms and their environment, Plant growth is reduced when one or more resources (e.g., light, temperature, water, nutrients) are limiting. At broad scales, forests of western North America can be partitioned into two climatically mediated classes of limitation: energy-limited versus water-limited domains (Stephenson 1990, 1998; Milne et al. 2002; Running et al, 2004; Littell and Peterson 2005; Littell et al. 20080. Energy-limiting factors are chiefly light (e.g., in productive forests where competition reduces light to most individuals or climates where cloud cover limits light) and temperature (e.g., high-latitude or high-elevation forests). Tree growth in energy-limited ecosystems appears to be responding positively to increasing temperatures over the past 100 years (McKenzie et al. 2001).

In contrast, productivity in water-limited systems is expected to decline with increasing temperatures, as increasing water balance deficit (the condition in which potential summer atmospheric and plant demands exceed available soil moisture) constrains photosynthesis across more of the West. CO_2 fertilization may increase water-use efficiency in plants enough to partially offset future water demands (Neilson et al. 2005. Boisvenue and Running 2006; Lenihan et al. 2008). but it remains to be seen if such effects will be transient. There is evidence that water limitation could negate CO_2 fertilization benefits (Sacks et al. 2007), and summer water availability for plants will likely decrease in Washington forests if snowpack declines or summers are warmer, both of which are projected (Elsner et al. 2010; Mote and Salathe 2010).

Limiting factors can of course shift within a species range (Peterson and Peterson 2001), or between seasons, as water demands abate and energy needs increase (Stephenson 1990, 1998; Lutz 2008). For example, in high-elevation or high-latitude arid forests (e.g., eastern slopes of the Sierra Nevada, Rocky Mountain Front Range, interior boreal spruce), short growing seasons limit energy inputs, but water limitation (high vapor pressure deficit (VPD) or potential evapotranspiration, or low soil moisture) still occurs in summer. Similarly, climatic variability can alter temperature or precipitation such that limiting factors are exacerbated or mitigated for years or decades at a time. Limiting factors can therefore also be transient, particularly for populations at the transition between energy and water limitation.

The effects of climatic change may be particularly strong in mountains, because increasing temperatures reduce the depth and duration of snowpacks (Cayan 1996; Mote et al. 2005; Knowles et al. 2006), which are key limiting factors for tree growth at high elevation (Peterson and Peterson 2001; Nakawatase and Peterson 2006; Case and Peterson 2007). Population changes at upper treeline (e.g., Lloyd and Graumlich 1997) and lower treeline (e.g., Allen and Breshears 1998) are also linked to climatic variability, with the edge between forested ecosystems and other vegetation types (e.g., grassland, shrubland, or alpine meadows) clearly changing with decadal and centennial climate variability. Climatic influences are difficult to assess in mountainous areas, however, because complex topography produces steep gradients in the biophysical environment, and climate-monitoring stations are sparsely distributed, particularly at the highest elevations (Thornton et al. 2000; Daly et al. 2008).

Two important climatically mediated disturbances in forests of the Pacific Northwest are wildfire and outbreaks of the mountain pine beetle (MPB-*Dendroctonus ponderosae).* Wildfire has been linked to climatic variability via studies of Holocene charcoal sediments, fire-scar and stand-age reconstructions of fire history, and statistical models using twentieth century instrumental records (Hessl et al. 2004; McKenzie et al. 2004 and references therein; Littell et al. 2009). Of particular concern are increases in fire area in a warming climate and the effects of extreme wildfire events on ecosystems (Gillett et al. 2004; Gedalof et al. 2005; Lutz 2008; Littell et al. 2009). For example, in 2006, the Tripod Complex Fire in north-central Washington burned over 80,000 ha, much of it higher severity than expected from historical fires. Over a dozen other species of insects (defoliators and bark beetles among them) are thought to be climatically sensitive, but the climate relationships with outbreaks of these species are poorly understood. For example, some defoliators may respond positively to increased precipitation, and negatively to drought, particularly in arid ecosystems (e.g., western spruce budworm *[Choristoneura occidentalis]*, which affects ponderosa pine-Swetnam and Lynch 1993). We focus specifically on mountain pine beetle because the relationship between its life cycle and temperature is well quantified, as is the vulnerability of its host species with respect to climate.

Mountain pine beetle infestations have historically occurred frequently and extensively throughout the Pacific Northwest (Wellner 1978; Logan and Powell 2001). Climate change, in particular warming and drought, affects bark beetle life stage development rates, winter mortality, and host tree susceptibility (Logan and Powell 2001). Carroll et al. 2004; Oneil 2006). Across the western US, stand structural conditions make host species susceptible to beetle attack (Hicke and Jenkins 2008). and future climate change is predicted to increase climate suitability at higher elevations (Hicke et al. 2006).

Planning for the impacts of climate change on forests requires better understanding of the role of climate in forest ecosystem processes. In this paper, we examine four key processes in forest ecosystems that we expect to change significantly across Washington State in a warming climate:

- Douglas-fir productivity and water limitation. Douglas-fir is one of the most widespread tree species in Washington, the most important by far economically, and possibly one of the more climate-sensitive species regionally. How will future changes in climate alter Douglas-fir productivity in different parts of its range?

Can we further identify the geographic domain of future water limitation in Washington forests?

- Conifer species ranges. Management priorities for forest ecosystems in Washington depend on species composition. How will climate change affect species distributions, particularly in sensitive areas where species are near the edges of their climatic tolerances?
- Fire area burned. The area burned by fire is predicted to increase across western North America as a result of climate change, but what are the expectations for Washington State and their consequences?
- Mountain pine beetle outbreaks. In the last decade, MPB outbreaks have increased in the West and appear to be correlated with higher temperatures and drought. What are the specific consequences within Washington State?

To answer these questions, we use historical climate data, statistical and process-based ecological models, and climate (regional and global) and hydrologic simulation models to quantify the magnitude and direction of climatic influences on each forest ecosystem process. We then examine the relative importance of each of these processes for the structure, composition, and extent of Washington State forests under different scenarios for climatic change (Mote and Salathe 2010). We address both the magnitudes of effects and the temporal scales at which they operate. These four processes are by no means the only ones that will be affected by climate change; there is much that is left untreated by our emphasis on these four areas, and in most cases much more that could be said about the four we chose to emphasize. This assessment should be regarded as a first step, not an all-encompassing review.

2 Methods

We use both composite climate model output and scenarios based on individual climate models, statistically downscaled to 1/16th degree resolution (Salathe et al. 2007; Mote and Salathe 2010), Elsner et al. 2010), for future projections.

2.1 Climate, Douglas-fir growth, and changes in the area of water-limited forest

We explored the role of climate in the productivity of Washington State forests in two ways. First, we assessed potential changes in Douglas-fir growth for the period 1916-2003 (the period of time for which both tree cores and climate data exist) using growth increment measurements from 117 unmanaged stands in the Pacific Northwest (Littell et al. 2008). The sampled stands come from a wide range of local environments and represent a gradient of climatic conditions from maritime (e.g., western Olympics and western Cascades) to continental (e.g., eastern Cascades, north Idaho Panhandle, western Northern Rockies). We developed stand-level basal area increment (BAI) time series from 5 to 15 (mean = 10) canopy-dominant or co-dominant trees in each stand. Raw tree-ring series were measured to 0.02 mm (Littell et al. 2008) and converted to BAI following Nakawatase and Peterson (2006). We used pairwise Pearson correlations to assess the relationship between annual mean BAI and regional time series of summer climate and hydrological variables previously linked to Douglas-fir growth. These were maximum temperature (Tmax), potential evapotranspiration (PET), actual evapotranspiration (AET), and water balance deficit (PET-AET), taken from 1916-2003 driving data and output variables from the variable infiltration capacity (VIC) hydrologic model (Elsner et al. 2010).

Second, we evaluated the forested area in Washington that is currently energy-limited or marginally water-limited but likely to become severely water-limited during the mid twenty-first century. We defined severely water-limited forests as those forests where summer (JJA) PET exceeds annual precipitation, a conservative estimate, but frequently met in ponderosa-pine woodland or other arid low-elevation forests. This distinction of severe water limitation was made to emphasize areas most likely to be impacted by changes in water deficit, but species-specific physiological constraints can engage before such limits are reached. We defined energy-limited forests as those where annual precipitation exceeds summer evapotranspiration. We used hydrologic simulations of current (1916-2006) and future (2020s, 2040s, and 2080s) annual PPT (precipitation) and summer PET (Elsner et al. 2010) to map spatial patterns of water limitation for the current period and the three future decades.

2.2 Climate and changes in species biogeography

We assessed the potential for climate to alter important PNW tree species distributions by using spatially explicit projections from recently published analyses of climate and species habitat for western North America (Rehfeldt et al. 2006). We focused on the potential for climatic stress on regeneration and mortality in Douglas-fir, a species that is widespread and economically important, and the potential for stress in three pine species (lodgepole pine, *Pinus contorta;* ponderosa pine, *Pinus ponderosa;* and whitebark pine, *Pinus albicaulis),* all potential host species of mountain pine beetle. Range changes in other species are also important, but a full assessment is beyond the scope of this project.

Rehfeldt et al. (2006) used random forests, a machine-learning procedure that combines binary recursive partitioning with resampling (Breiman 2001), to predict climate-suitable habitat of tree species from fine-scale contemporary climate variables and locations of tree species from national forest inventories. They then projected these predictive models onto future climate scenarios (a medium emissions scenario for both HadCM3 and CGCM2, see Rehfeldt et al. 2006). We combined Rehfeldt et al. (2006) grid maps of potential future habitat for Douglas-fir to identify areas where climate in the 2060s is likely to exceed Rehfeldt et al. (2006) estimates of the tolerances of this species. We used a similar approach to assess areas of change in pine species richness for the 2060s. Following Rehfeldt et al. (2006), we assumed that areas where >75% of their individual classification trees identified suitable climate represented conditions where the species was likely to occur (high suitability). We assumed that areas with <75% but >50% agreement were potential reas of future occurrence but where climatic variability might put the species at some risk (moderate suitability), and we assumed that areas with <50% agreement were unlikely to have sustained climatic conditions appropriate for species persistence and regeneration after disturbance (low suitability).

2.3 Climate and area burned by fire

We developed statistical models that relate area burned to climate at two different spatial and temporal scales. From 1916-1969, fire data from federally protected lands were aggregated at the state level (see Littell et al. 2009) and therefore prohibit analysis for sub-regional vegetation types or at fine spatial scales. From 1970-1979, reporting of fire data is inconsistent across federal agencies. After 1980, analysis is possible at finer scales using online data from the National Fire Center and Aviation Management (NFCAM 2007), and agency reporting was consistently carried out at the agency unit (e.g., a USFS National Forest district, USDOI National Park, USDOI Bureau of Indian Affairs reservation, or USBLM district). There is therefore a tradeoff between the ability to incorporate more climatic variability inherent in the longer state-based dataset and the ability to assess climate-fire relationships by vegetation type in the shorter agency-unit-based dataset.

For the regional analysis (first spatial scale), we used updated annual fire area burned data aggregated to the PNW region from state data for Washington, Oregon, Idaho, and Montana (Littell et al. 2009). For sub-regional analyses, we used the NFCAM annual fire area burned data for all USFS, USBLM, USDOI NPS and USDOI BIA units. We developed statistical models for the period 1916-2006 to assess the role of climatic variability on area burned in the PNW. Climate variables included were annual and seasonalized monthly means of observed minimum and maximum temperature (Tmin and Tmax) and precipitation (PPT; Mote and Salathe

We used correlation analyses to identify potentially significant climatic drivers of area burned in the PNW, and these variables were iteratively entered as predictors in stepwise multiple linear regression models using AIC to arrive at the best model (Akaike Information Criterion-Akaike 1974). Based on information theory, AIC provides a metric to optimize the tradeoff between model goodness-of-fit and parsimony (fewer parameters). The final regression maximized the variance explained by the model while retaining only multiple regression predictors significant at $a = 0.1$.

The regional models were used to develop finer-scale models at the level of Bailey's ecosections (Bailey 1995-Fig. 1) for the Pacific Northwest ecosystems in Washington: Coast Ranges/Olympic Mountains, Puget Trough/Willamette Valley, Western Cascades, Eastern Cascades, Okanogan Highlands, Palouse Prairie, Blue Mountains, and Columbia Basin. The procedure used in the regional analysis was repeated with ecosection-averaged climate variables (1980-2006, Tmin, Tmax, PPT), and three additional predictors from hydrological model output: PET, AET, and PET-AET, or deficit (Elsner et al. 2010) to estimate ecosection area-burned time series.

At both scales of inquiry, we then used future climate projections from the 2020s, 2040s, and 2080s in the regression equations to predict area burned for the region and for each ecosection in WA. For the regional climate modeling, we used the ECHAM5 and CGCM-t47 AlB projections (Mote and Salathe 2010) and for sub-regional ecosection models, we used ecosection-average composite downscaled projections, with hydrologic model forecasts for the three additional predictors (Variable Infiltration Capacity, see Elsner et al. 2010). Both methods superimpose the observed climate variability on future changes in mean values, so the extrapolated fire area burned assumes that the range of future interannual variability in climate is comparable to the twentieth century. For the future regional area burned projections, we also calculated 95% exceedence probabilities (the probability that a given year would exceed the 95% quantile in the 1916-2006 record) for the 2020s, 2040s, and 2060s.

2.4 Climate and the mountain pine beetle

We approached the problem of climate-related mountain pine beetle impacts on forests in two ways. First, we addressed the vulnerability of host lodgepole pine trees to beetle attack as a function of climate. Second, we addressed the role of climate in accelerating the beetle life cycle.

2.4.1 Host vulnerability

We used data on twentieth century mountain pine beetle (MPB) outbreaks, climate conditions, and site and stand inventories to develop generalized linear models of the likelihood of successful attack by MPB on susceptible stands of lodgepole pine in the Okanogan and Colville National Forests located in eastern Washington (Oneil 2006). Susceptible stands were those with densities, basal area, and age classes historically associated with MPB attacks (Oneil 2006). We then projected these models onto future climate space to estimate the magnitude of future MPB impacts on all locations within the current range of susceptible pine species.

We built upon the empirical predictive models of Oneil (2006), which used forest inventory data (stand density variables) from the Current Vegetation Survey (http://www.fs.fed.us/r6/survey/), and locations of MPB attacks from the USDA Forest Service Aerial Detection Surveys (www.fs.fed.us/r6/nr/fid/as/index.shtml). and. climate variables from DAYMET (Thornton et al. 2000), in an analysis in eastern Washington. This analysis indicated that three measures of vapor pressure deficit (VPD), the difference between the amount of water vapor in the atmosphere at saturation vapor pressure and the amount of water vapor that could occur at average daylight temperature, were the best predictors of the number of MPB attacks from 2000 to 2003. These VPD measures were average summer VPD, maximum VPD during the year, and length of time VPD exceeded various thresholds.

We rebuilt models with VPD variables as predictors, and also revisited the best predictors of MPB attacks prior to 2000 from Oneil (2006). We explored generalized linear models (GLMs) of the Poisson family (Venables and Ripley 2002), to estimate counts of the total number of years in which an attack occurred over the periods from 2000-2003. We tested a variety of predictors that included site, stand, and climate variables, and their interaction terms, and retained the models with the minimum AIC (Akaike 1974), We then used these models to estimate MPB attack in future climate space. As we lacked detailed projections that could account for ongoing and future mortality of susceptible stands, we assumed that in the future these would still be present within the current range of pine species. All models were developed with the R statistical software (www.r-project.org).

Projections of future climate (Mote and Salathe 2010) for the host-vulnerability analysis provided daily data to compute composite delta values (change in temperature, Tdelta, and change in precipitation, Pdelta) for each time period and emission scenario. These were added to a historic time series (1980-2003) of daily weather data generated using the DAYMET model (www.daymet.org) (Thornton and Running Thornton et al. 1997). We used these composites to generate plot-specific estimates of climate conditions for the six scenarios: 2020s, 2040s, and 2080s for AIB and Bl emissions scenarios. We increased the historical Tmax and Tmin values equally by Tdelta, and averaged the resulting future Tmax and Tmin to obtain a daily average temperature. From these, we calculated daily dewpoint temperature (Tdew), daily VPD, and daily potential evapotranspiration (PETday). For PETday, we used the methods of Lutz (2008) which correct for slope, aspect, and elevation. We also calculated the number of days VPD exceeded two different thresholds for each plot. We used methods from Kimball et al. (1997) to adjust VPD estimates for arid and semi-arid regions where minimum daily temperature may not be sufficiently low to reach the dewpoint temperature.

We projected GLMs of host vulnerability onto the future-scenario composite data sets across our model domain (lodgepole and ponderosa pine forests of eastern Washington). Predicted future values from the climate composites were examined to see where we could be extrapolating too far outside the ranges of the predictor variables used to build the models. For example, predicted values of total attacks much above 4 (the period of record was 4 years) would be an indicator that projections were too far outside the domain in which models were built.

2.4.2 Adaptive seasonality: temperature effects on the life cycle of the mountain pine beetle

We evaluated the effects of changes in year-round (all seasons, hourly data) temperatures on the climatic suitability for mountain pine beetle outbreaks. The mountain pine beetle's life cycle is primarily controlled by temperature (Logan and Bentz 1999; Powell and Logan 2005). We simulated the development of life stages of the mountain pine beetle as a function of temperature with a model built using laboratory measurements (Bentz et al. 1991. Loga and Amman 1986; Logan et al. 1995; Logan and Powell 2005). The model computes a developmental index in each life stage by combining the annual course of hourly temperatures with the life-stage development rate, thereby calculating the time spent in each life stage.

"Adaptive seasonality" refers to beetle life cycle timing that is conducive to rapid reproduction, synchronized mass attacks on trees, and high survival rates in winter, This condition is predicted by the model when temperatures influence life-stage development rates such that: (1) the simulated population completes a life cycle in one year (instead of two); (2) the population is synchronized for mass attacks on host trees by a life cycle exactly one year long; and (3) adult emergence from brood trees occurs at a suitable time of year (late summer) such that the most cold-resistant life stages coincide with winter. The model was originally evaluated in a region in central Idaho that experienced a rapid increase in mountain pine beetle populations in the late 1990s (Logan and Powell 2004). Long-term changes at coarse spatial resolution were analyzed with this model across the western USA by Ricke et al. (2006).

In this study, we used historical (1970-1999) temperatures to predict current adaptive seasonality. We also estimated future (2070-2099) temperature suitability for two future climate scenarios (ECHAM5 and HADCM, AlB SRES scenario). Hourly temperatures were estimated from daily minimum and maximum temperatures by simulating a sawtooth pattern of hourly temperatures sensu Hicke et al. (2006).

3 Results

3.1 Douglas-fir growth and changes in the area of water-limited forest

Douglas-fir growth in the PNW was highly variable in space and time during the twentieth century (Littell et al. 2008), and this variability was generally associated with water limitation (e.g., positively correlated with summer precipitation and actual evapotranspiration but negatively correlated with summer maximum temperature and potential evapotranspiration). The strength of the correlation between water deficit and tree growth depends on the location of the stand along a gradient of mean summer water deficit-the most water-limited stands had the greatest sensitivity. The mean BAI time series has a significant increasing trend or about 13 mm^2/year/tree (Mann-Kendall tau $= 0.634$, $P < 0.001$; Fig. 2), but we could not attribute this growth trend to any single climatic factor, although there are weak but significant positive correlations with minimum temperature. The historical interannual variability about the trend in BAI (Fig. 2) is not sufficiently explained by climatic variables to warrant statistical modeling of projected future productivity but it is best correlated ($r =$ 0.42) with year prior July-August water balance deficit averaged over the sampled watersheds.

The area of WA forest that is severely water-limited will likely increase (relative to 1970-1999) by 32% in the 2020s and an additional 12% increase in both the 2040s and the 2080s (all values relative to twentieth century water-limited forests, Fig. 3). These changes are projected to occur on the east side of the Cascade Mountains and west side of the Rocky Mountains in the northern part of the state.

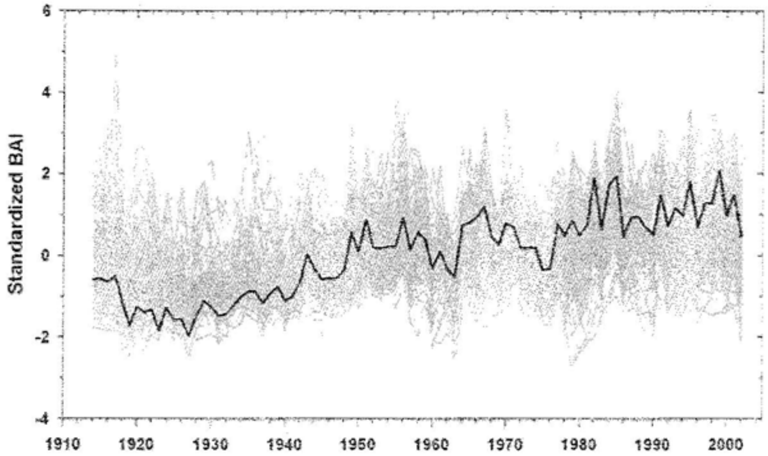

Fig. 2 Douglas-fir network basal area increment (BAI) time series 1914–2002. Gray traces represent individual plot-level time series; black line is the mean of all series. Standardization is the observed value minus the mean and divided by the standard deviation for each BAI series. Positive standardized BAI is higher-than-normal growth, negative standardized BAI is lower than normal growth. A positive trend and an increase in variability both occurred during this time period

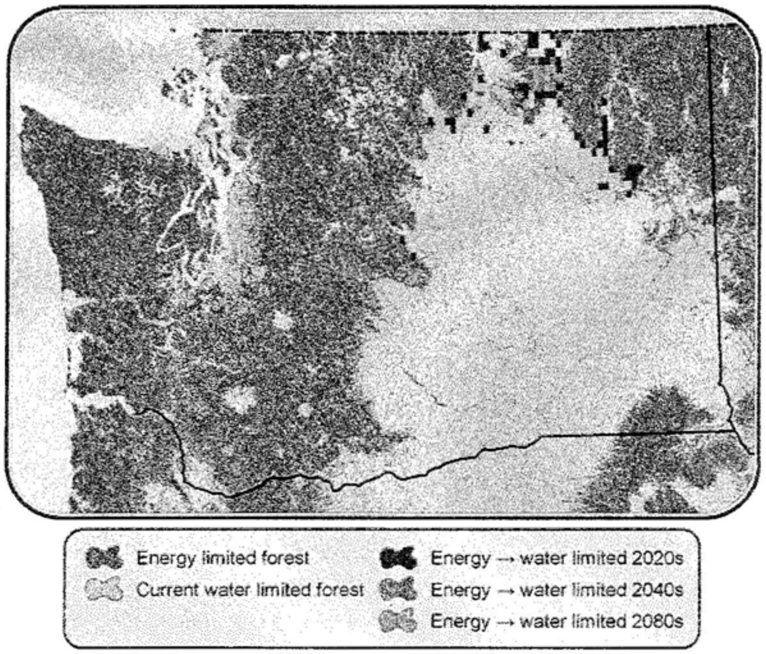

Fig. 3 Locations of energy- and severely water-limited forests in WA in the current climate as well as predicted changes to water limitation in the future. Energy-limited forests can be water-limited seasonally, but we focused on the chronic, long-term water limitation for forests where summer PET exceeds annual precipitation as the area most vulnerable to deficit related impacts. Climate projections indicate that areas within the Okanogan Highlands and the foothills of the northeastern Cascade Mountains will transition to severely water-limited forest by the 2080s. Forested area grid cells are smaller than the VIC cells (see Section 2.2) used to derive water balance variables for this map. Energy-limited forests can be either light- or thermally limited—we do not consider the former. Figure: Robert Norheim

3.2 Climate and changes in species biogeography

By the end of the 2060s, independent species range modeling based on IPCC scenarios suggests that climate will be sufficiently different from the late twentieth century to put Douglas-fir at increasing risk at the edges of its current range in Washington (Fig. 4). This is probably due to increases in temperature and decreases in growing season water availability in more arid environments (e.g., in the Columbia Basin) but could be due to other variables in less arid parts of the species' range. About 32% of the area currently classified as appropriate climate for Douglas-fir will be outside the identified climatic envelope by the 2060s, and about 55% of the area will be in the 50%-75% range of marginal climatic agreement among models. Only about 13% of the current area would be climatically suitable for Douglas-fir in >75% of the statistical species models. The decline in climatically suitable habitat for Douglas-fir is most widespread at lower elevations and particularly in the Okanogan Highlands, south Puget Sound and the southern Olympic Mountains (Fig. 4).

In pine forests, climate is likely to be a significant stressor in the Columbia Basin and eastern Cascades by the 2060s, particularly in parts of northeastern WA

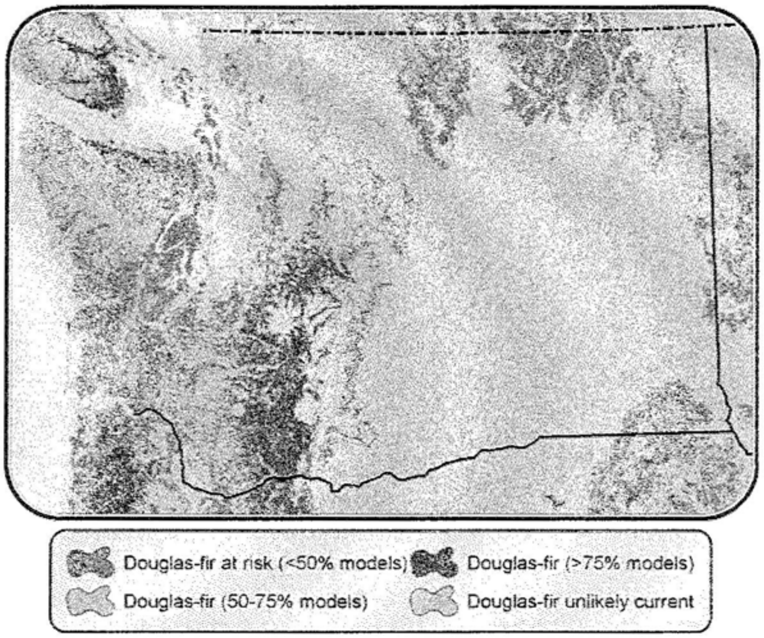

Fig. 4 Change in area of climate suitable for Douglas-fir. *Tan* indicates areas where current climate is not suitable" for Douglas-fir; *all other colors* indicate locations where current climate is suitable. *Orange* indicates area where fewer than 50% of the statistical models suggest climate appropriate for Douglas-fir presence in the 2060s and thus indicates locations where climate is likely to move from currently suitable to unsuitable. *Dark green* indicates areas where more than 75% of statistical models agree that climate is currently suitable for Douglas-fir and will remain so in the 2060s. *Light green* indicates an intermediate amount of model agreement, suggesting that these areas having current climate suitability may be at some risk due to interannual variability in climate or additional climate change beyond 2060. Data from Rehfeldt et al. (2006). Figure: Robert Norheim

(e.g., Colville National Forest, Colville Reservation), and the central Cascade Range (Fig. 5). Of the area that is climatically suitable today for at least one pine species, only 15% will remain suitable for all current pine species, whereas 85% will be outside the climatically suitable range for one or more current pine species (74% loss of climate suitable for one species, 11% loss of climate suitable for two species, <1 % loss of climate suitable for three species).

3.3 Climate and area burned by fire

Regional fire models suggest that summer precipitation and temperature historically played a large role in the area burned by fire. About half the variance in annual regional area burned can be explained either by July and August temperature and precipitation or July and August water-balance deficit. The best model includes June-August total precipitation (negative relationship with fire), July-August average temperature (positive), and January precipitation (negative-total November to March precipitation performs similarly). Future area burned projected from the best statistical model suggests a doubling or tripling by the 2080s (Fig. 6). The future median regional area burned, averaged over both GCMs, is projected to increase

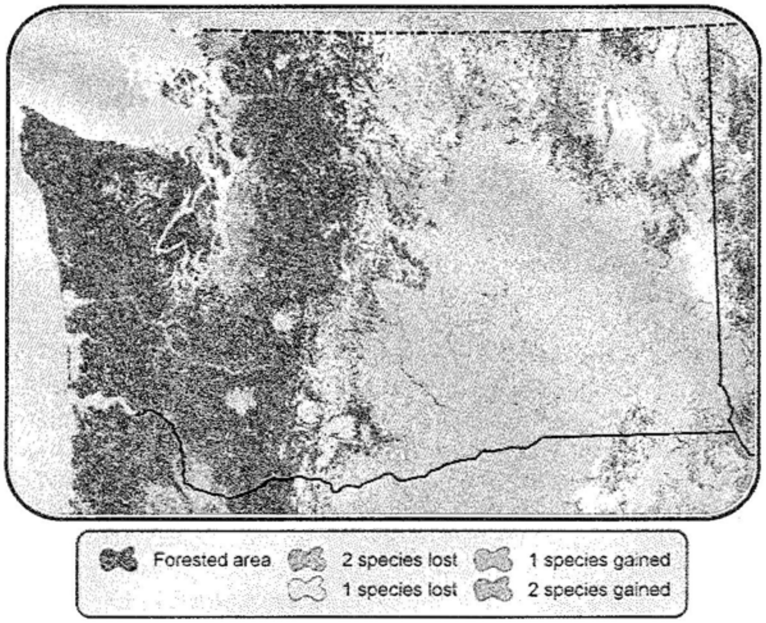

Fig. 5 Change in climate suitability for multiple pine species, from the present to the 2060s. Decreases indicate places where climate will be no longer suitable for some species, whereas increases indicate places where climate is currently unsuitable for some species and but may be in the 2060s. Areas in the Columbia Basin with gains projected by statistical models frequently already have patchy cover of ponderosa pine, whereas areas with gains at higher elevations in the Okanogan Highlands likely represent upward migration of suitable climate for one or more pine species. Data from Rehfeldt et al. (2006). Figure: Robert Norheim

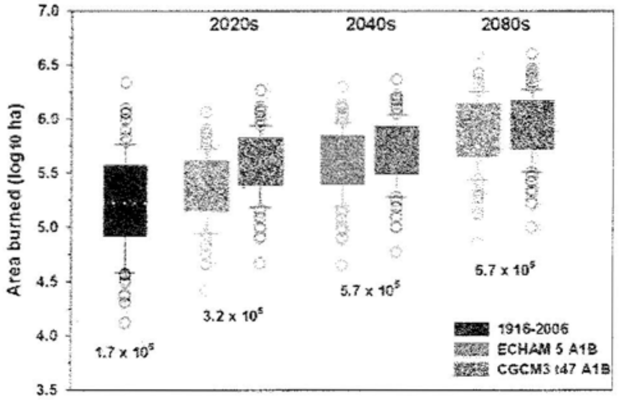

Fig. 6 Annual area burned for the last 90 years and predicted for the 2020s, 2040s, and 2080s for two GCMs with moderate warming (Echam5 and CGCM_t47). The white dashed line inside each box indicates the mean area burned, the solid areas the second and third quartiles, and the whisker caps the tenth and ninetieth percentiles. The values below the plots indicate the mean area burned (ha) for the indicated time period and are averaged across both GCMs for the future projections

from about 0.2 million ha (0.5 M ac) to 0.3 million hectares (0.8 M ac) in the 2020s, 0.5 million ha (1.1 M ac) in the 2040s, and 0.8 million ha (2.0 M ac) in the 2080s. The probability of exceeding the 95% quantile area burned for the period 1916-2006 increases from 0.05 to 0.48 by the 2080s (Table 1).

At the ecosection level, the strongest historical models occur in drier forest types and shrubland ecosystems (>55% variance explained by climate), whereas west of the Cascade Range, the relationship between fire and climate is weaker and adequate statistical models are difficult or impossible to construct due to the low annual area burned. Models including potential evapotranspiration or deficit frequently performed better than those using only temperature, precipitation, and their interactions. Projections of future fire in the wetter ecosections therefore have greater uncertainty than those in drier ecosections, because of the lesser explanatory power of their associated models. Other methods with a more mechanistic treatment of fire, weather, and climate, at finer spatial scales, will be required to fully understand the future role of fire in these ecosystems.

Statistical models of area burned were adequate for six out of the eight ecosections in Washington for the period 1980-2006, but in the Coast Ranges/Olympic Mountains and Puget Trough/Willamette Valley ecosections annual area burned and its variability were too low. In the other six ecosections, regression models explained between 50% and 65% of the variability in area burned. The most important explanatory variable in five of the six models was either potential evapotranspiration or water balance deficit (PET-AET), and two models had July-August T max terms. Lagged precipitation terms and deficit terms (wetter antecedent climate) were important in the Columbia Basin, Palouse Prairie, and Okanogan Highlands. These six models project increases in mean area burned between 0 and 600% depending on the ecosystem in question, the sensitivity of the fire model, the emissions scenario, and the time frame of the projection (Fig. 7). By the 2040s, the area burned in non-forested ecosystems (Columbia Basin and Palouse Prairie) is expected to increase on average by a factor of 2.2. In forested ecosystems (Western and Eastern Cascades, Okanogan Highlands, Blue Mountains) the mean area burned is expected to increase by a factor of 3.8 compared to 1980-2006. Notably, the future increase in area burned is accompanied by an increase in variability in some of the more arid systems- Palouse Prairie and Columbia Basin. The largest proportional increases are in the Western Cascades and Blue Mountains, although the Western Cascades model was the weakest statistically acceptable model, and the area burned is still small despite

Table 1 Modern and projected future exceedence probabilities for PNW regional area burned

Exceedence	Modern*	2020s		2040s		2080s	
		ECHAM5	CGCM3	ECHAM5	CGCM3	ECHAM5	CGCM3
95% (year)	5	1	8	10	20	43	44
95% (p)	0.05	0.01	0.09	0.11	0.22	0.47	0.48
Number of years > 1 M ac	23	23	44	47	61	74	79
Number of years > 3 M ac	2	0	2	5	8	30	34

Ninety-five percent exceedence (year) refers to the count of years in a future record equivalent to the study record that would exceed the historical 1916–2006 95% quantile area burned; Exceedence (p) refers to the probability of a year exceeding the 1916–2006 95% quantile in the future

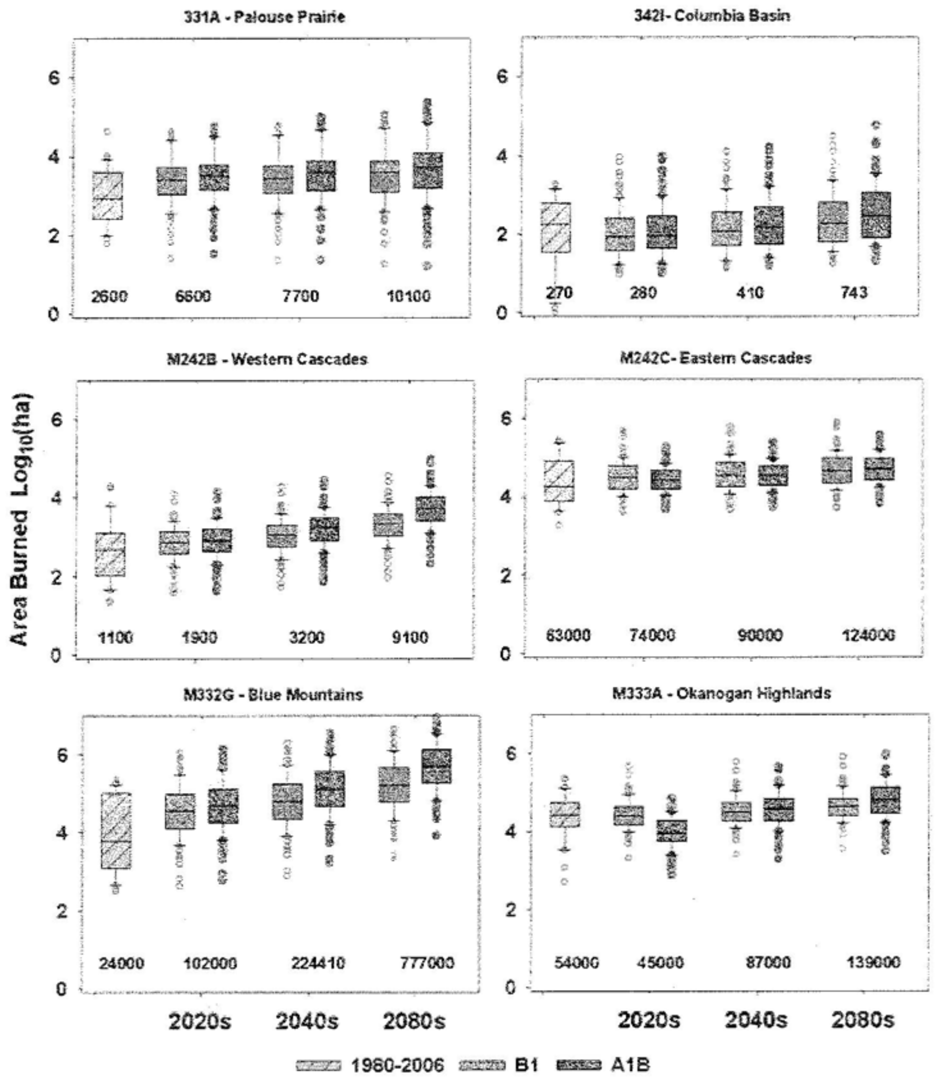

Fig. 7 Projections of future area burned in WA ecosections for , which adequate statistical fire models could be constructed. All model projections were based on delta-method composite future climate (Mote and Salathé 2010). The values below each set of box-and-whiskers plots indicate the average of A1B (*red*) and B1 (*orange*) future area burned estimates for the ecosections in hectares

the large proportional increase. The Blue Mountains model was extremely sensitive, and projected area burned increased at a rate faster than any other ecosection.

3.4 Climate and the mountain pine beetle: host vulnerability and adaptive seasonality

Our analysis of host vulnerability identified a substantial change in the future average water deficit across all sites within the current range of lodgepole pine (Table 2).

Table 2 Expected water deficit and precipitation changes for six future scenarios and historical DAYMET-based calculations in the lodgepole pine forests of Washington

Scenario	Year	Scenario climate			% Change from 1980–1999			
		Mean water deficit (mm)	Annual PPT (mm)	Summer PPT (mm)	Mean water deficit	Annual PPT	Summer PPT	# Plots with deficit > 250 mm
A1B	2020	142	1,242	34	294%	132%	29%	116
	2040	177	1,935	17	367%	206%	15%	228
	2080	209	2,831	12	432%	302%	11%	442
B1	2020	93	1,604	88	193%	171%	75%	27
	2040	114	1,756	70	236%	187%	60%	18
	2080	158	2,199	29	326%	235%	25%	116
Historical	2000–2003	96	767	60	199%	82%	51%	33
Historical	1980–1999	48	937	118	100%	100%	100%	2

Even though all future climate projections indicate an increase in annual precipitation over the pre-2000 period average (Mote and Salathe 2010), the summer water deficit increases two to three times because of reduced summer precipitation and increased temperature (see above). This is consistent with hydrologic assessments suggesting reduced snowpack, reduced summer soil moisture, and increased PET (Elsner et al. 2010). In Washington State, lodgepole pine is rarely found on sites with climatic water deficit > 250 mm (two of 1,630 plots). In both the Bl and AlB climate scenarios, the climatic water deficit of plots currently occupied by lodgepole pine increasingly extends beyond the envelope where lodgepole pine currently exists. These projections of deficit suggest that areas with climatic conditions favorable for lodgepole pine will decrease considerably; 27% plots will be subject to more water stress than those under the most stress today.

These projections of deficit suggest that areas with climatic conditions favorable for lodgepole pine will become increasingly rare because trees will be subject to significantly more water stress, with a correspondingly greater VPD. The best statistical model of MPB attack-a Poisson family GLM-found VPD-based variables and their interactions to be the most significant predictors of the number of attacks over the historical period of record, 2000-2003 (Table 3). Interpretation of the models is not straightforward, however, with five predictors and their interactions.

Plots of fitted values against Max VPD and Avg VPD (not shown) suggest that the greatest likelihood of attack comes when mean conditions are hot and dry, but not exceptionally so, and there is a fairly short period of extreme VPD. During such anomalous periods trees are extremely vulnerable, because they are not physiologically adapted to maintain the water balance that is integral not only to survival but also to their capacity to repel beetle attacks (Waring and Running 1998: DeLucia et al. 2000).

Projecting the model into the future clearly suggests that attacks will be concentrated at increasingly higher elevations (Fig. 8) because the climate conducive to outbreaks effectively shifts to higher elevations. By the 2080s under AlB, predictions are outside their feasible range (i.e., > > 4 years with attacks in a 4-year period), indicating a limit to robust extrapolation. Nevertheless, in conjunction with expected elevational shifts of host species (lodgepole pine and ponderosa pine), and

Table 3 Summary statistics for the predictive model of MPB attacks

Predictor	*p* value
MaxVPD (when exceeds 2 kPa)	0.167
Pre-growing season PPT	0.393
AvgVPD (Jun, Jul, Aug)	0.031
DaysVPD exceeds 1.5 kPa	< 0.001
FirstDayVPD (exceeds 1.5 kPa)	< 0.001
Interaction of #1 and #3	0.024
Interaction of #4 and #5	< 0.001

Two predictors were not significant at $\alpha = 0.05$, but were part of highly significant interactions

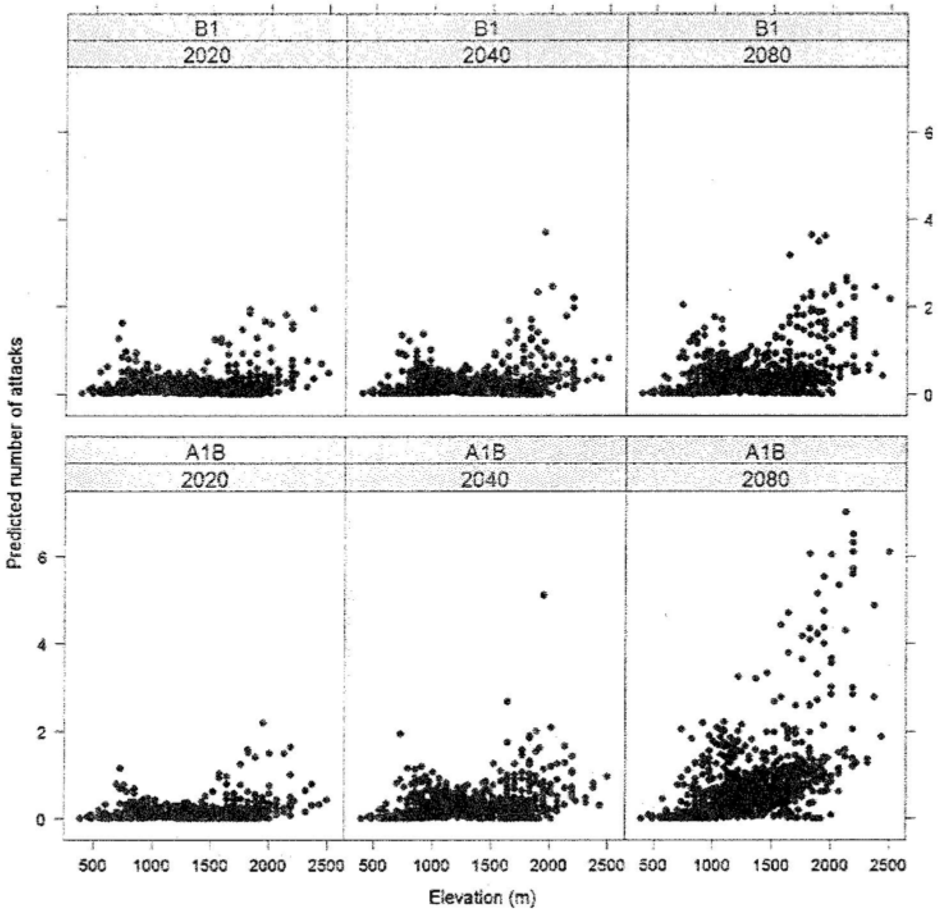

Fig. 8 Changes in the predicted number of mountain pine beetle attacks in a 4-year period (fitted values), with elevation, time, and emissions scenario. Maximum observed value of the response variable was 4, so values $\gg 4$ represent unrealistic extrapolations (see text)

predictions from the adaptive seasonality model (see below), we can clearly expect mountain pine beetle outbreaks to be a continuing concern.

Based on the adaptive seasonality modeling, however, the future area suitable for these outbreaks will decrease (Fig. 9). Temperatures are currently suitable for MPB outbreaks in large areas of the Olympic Mountains, northern Rocky Mountains, in a band of mid-elevation on the west and east sides of the Cascade Mountains, and to a lesser degree in the Blue Mountains of southeastern Washington. However, simulations using climate change scenarios for 2070-2099 predict that the region of climate suitability will move higher in elevation as the climate warms (Fig. 9), thereby reducing the total area of suitability. At lower elevations, increasing temperatures will cause asynchrony in adult emergence through more rapid life stage development, and cause emergence at inappropriate times of year, reducing populations and decreasing the efficacy of mass attacks (Logan and Bentz 1999). Higher elevations will warm enough to allow synchronous population emergence. For the ECHAM5 climate model (moderate warming), temperature suitability will occur at high elevations in the Olympic and Cascade Mountains. The area of adaptive seasonality will be greatly reduced in the Rocky Mountains and eliminated in the Blue Mountains. For the HADCM3 climate model (greater warming), only a few areas of adaptive seasonality will remain, in the highest elevations of the Olympic Mountains and the highest and most northern part of the Cascade Range. These areas of future adaptive

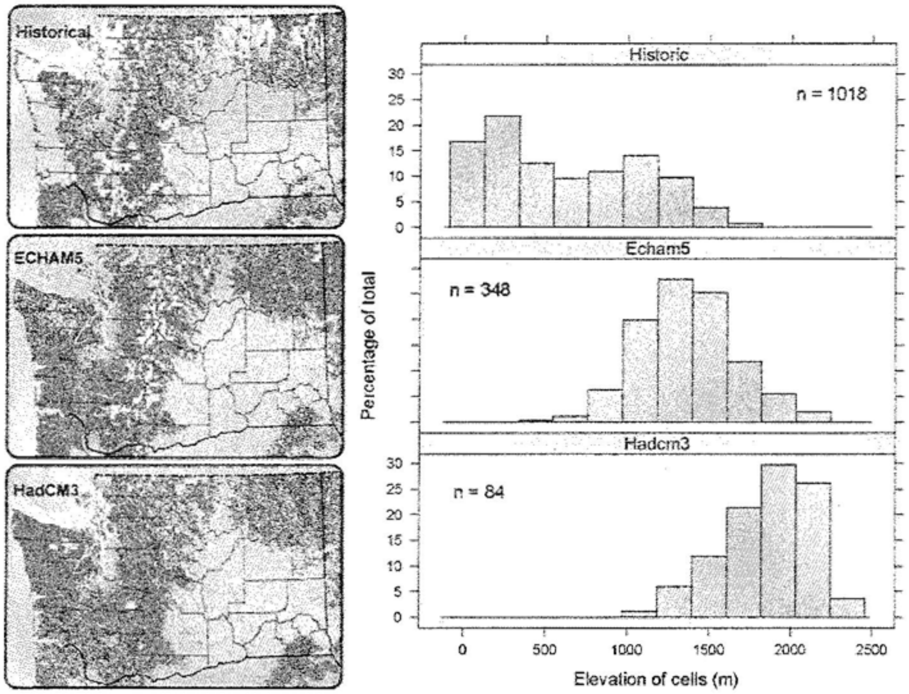

Fig. 9 Adaptive seasonality of mountain pine beetle in Washington forests for historical (1970–1999), ECHAM5, and HadCM3 future scenarios for the 2080s (SRES scenario A1B). Yellow cells are suitable space for the beetle. Histograms show the change in elevation distribution across scenarios for suitable cells with n = total cells with suitable climate for the MPB. Figure: Robert Norheim

seasonality coincide with the current distribution of white bark pine, but are mostly above the current elevation range of other susceptible species.

These figures are, of course, snapshots in time. In fact, outbreaks of mountain pine beetle could occur across the areas "traversed" by the beetle between now and the late twenty-first century as their climatic suitability moves upward in elevation (subject to host tree species availability). The low area of adaptive seasonality presented using the HadCM3 projection for the 2080s therefore belies the much larger area suitable for outbreaks at some time between the present and the 2080s. Furthermore, the average climate used does not capture interannual variability in future temperatures that may initiate outbreaks of mountain pine beetle earlier in time than suggested by these results.

4 Discussion

4.1 Importance of disturbance as principal player in forest change

The direct impacts of climate change on tree species (e.g., productivity, distribution) are important. However, given the projected increases in fire area and MPB attacks at higher elevations, the indirect impacts of climate change on ecosystems through disturbance are likely to be greater, notwithstanding that disturbance has a more immediate impact on the ecological integrity of forest ecosystems and associated ecosystem services. It is likely in the future that the rate of forest change (forest type, species composition, productivity) in response to climate change will be driven more by disturbance than by gradual changes in tree populations (driven by impacts on life-history characteristics and phenology) and will therefore be more rapid than suggested by climate-based analyses of future species range shifts.

The combined projected increases in water limitation, area burned, increase in high elevation area of adaptive seasonality, and increase in host vulnerability suggest that few areas are immune to increasing disturbance. For example, although we were unable to build strong predictive models of future west-side fire, increasing summer Tmax and potential evapotranspiration suggest that large disturbances are likely in west-side forests that have not traditionally been thought of as "fire prone". Elsner et al. (2010), found that west of the Cascade crest, summer soil moisture is likely to decline substantially due to increasing temperature. Some global climate models project decreases in summer precipitation for the region, whereas others project little change-few suggest increased precipitation. This implies that future climatic conditions will decrease fuel moisture, and it is therefore reasonable to expect increased fire activity. Evidence from stand age classes also indicates that fires much larger than those in the modem record occurred in past centuries (Henderson and Peter 1981; Agee and Flewelling 1983). The impacts of increasing disturbance, whether east-side or west-side, are worthy of further study.

Some areas may also face novel disturbance interactions. Synergistic interactions between disturbances are producing larger effects than would occur from either disturbance independently (McKenzie et al. 2009). For example, MPB outbreaks have been linked to the increased likelihood of stand-replacing fire and changes in fire behavior, although the nature of the effect depends on the time since infestation (Lynch et al. 2006; Jenkins et al. 2008). Combined with increasing climatic stress on tree populations and growth, such disturbance interactions can alter forest structure and function more rapidly than could be predicted from models of species redistribution or disturbance alone. Simultaneous climatically driven shifts in the locations of species' optima, ecosystem productivity, disturbance regimes, and the interactions between them could reset forest succession over large areas and short time frames compared to changes observed during the twentieth century. Human disturbance, such as twentieth century land management (younger stands and possible loss of genetic diversity), may exacerbate the effects of fire and insect disturbance. The increasing tendency toward water limitation on the edges of the Columbia River Basin and the projections for modified climatic ranges for ponderosa pine, Douglas-fir, and lodgepole pine strongly suggest that post-disturbance regeneration will proceed along different successional trajectories and different genotypes or species will be favored.

The projected increase in area burned is robust to a point, but statistical models of area burned have some important limitations. Area burned cannot increase indefinitely, because of a finite forested area within the state. At some point, enough forests will be disturbed and climate will change to the point where the climate/disturbance association can no longer resemble the modeled relationships. For example, some ecosection models (e.g., Okanogan Highlands, Eastern Cascades) show evidence of hydro climatic facilitation of fire, probably via increased fine fuels (Littell et al. 2009), and future area burned could decrease if precipitation increases were insufficient to offset expected potential evapotranspiration or if spring/summer precipitation decreased. The climate models we used are a hedge against such uncertainties-they are the models best able to reproduce the region's observed climate and the average of many possible future realizations, ensuring the most robust estimates of mean area burned. The variablity in future fire regimes has been underestimated, however, by using the composite mean and not an ensemble composed of all the available future climate models.

Most evidence suggests that mountain pine beetle attacks in the future are likely to be more successful and beetle populations will be moving to higher elevations. An important uncertainty here is the timing of species range changes and the timing of beetle populations range changes-for beetle attacks to achieve epidemic status, a sufficient population of well established mature trees must be present to sustain the insects. If species turnover proceeds quickly, accelerated by increased fire, spatial heterogeneity of age classes on the landscape may reduce beetle impacts significantly.

The strength of the relationships between climate and fire and climate and mountain pine beetles supports a hypothesis of climate-driven disturbance as the primary mechanism of change in the future forests of Washington. We were not able to assess the interaction between fire and mountain pine beetles quantitatively, but it is likely, for example, that MPB outbreaks will affect fuel structure and availability to fire (Lynch et al. 2006). A process model that considers this interaction and any potential synergies for impacts to forest ecosystems would be useful to project future conditions. Such a model should consider the relative importance of the two disturbances in future synergistic interactions, which depends on the presence of suitable host species and the fire regimes expected in those forest types. For example, high-elevation whitebark pine ecosystems may have severe MPB mortality in the future without greatly influencing the area burned by fire because fuel availability would not necessarily change dramatically in such low-density forests. On the other hand, nearly pure lodgepole pine forests, which are already strongly fire dependent, will potentially have altered fuel characteristics conducive to relatively rapid rates of fire spread, thereby increasing the potential size of fires.

A further complication, which we did not study, is disturbance interactions with forest management goals, such as wildlife habitat, timber products, or other ecosystem services, but because the area susceptible to disturbance impacts will be large, and strategies to mitigate the potential resource risks will need to carefully consider potential novel effects of altered disturbance regimes.

4.2 Broad characteristics of future forests in Washington

Increasing water limitation appears likely across a significant portion of the northern Columbia River Basin and eastern Cascades, if other factors (e.g., CO_2 driven increases in water use efficiency) do not offset the climatically driven changes. Our definition of water limitation is conservative, and emphasizes the most severe limitation; much of the forested area we defined as energy-limited in Washington is water limited for some portion of the year, but that limitation is not as severe as the areas highlighted in Fig. 3. For those areas where annual precipitation is less than annual potential evapotranspiration (a less conservative definition of water limitation) there may still be important limitations on productivity and regeneration.

A caveat to the projections of future species-appropriate climate envelopes is that they fail to consider ecological factors that can exacerbate or mitigate the projected changes. For example, such models assume the climatic ranges they describe are equally applicable across all parts of a species' life cycle (McKenzie et al. 2003), but the models are constructed on the presence or absence of established trees of many ages-not on seedlings, which are likely most susceptible to climate variability. We also do not consider the impacts of local soil limitations, nutrient limitations, changes in nitrogen deposition, all of which could affect productivity and species distribution locally in the future.

Many of Washington's future forests may look much like the forests that are currently present, but the most vulnerable forests may look radically different due to increased frequency and severity of disturbances. Eventually, species and stand densities that are resistant to increased summer water deficit and increased disturbance will be favored, and landscape structure and pattern will change. Particularly in places where vegetation types shift from forest to woodland or from tundra to forest, fire regimes will be influenced by the shift in vegetation. Dynamic vegetation models that address the feedbacks between vegetation, climate, fire, and biogeochemistry are required to understand such processes. In the near term, however, such uncertainties are less important than the considerable impacts on Washington's current forest ecosystems.

All of the impacts assessed in this study are likely to occur by the 2040s at the northern edge of the Columbia Basin in the Okanogan Highlands and in the northeastern North Cascades. The impacts of climate on fire regimes, insect attacks, tree water stress and both Douglas-fir and pine species' ranges will likely interact strongly in the northeastern Cascade Range, Okanogan Highlands, and Blue Mountains earlier rather than later in the twenty-first century. Although less area burned is projected in the western Cascades and the Olympics and there is less area dominated by pines susceptible to MPB, it would be a mistake to conclude that impacts and their interactions will not be important in those ecosystems. For example, Douglas-fir will be outside of its optimal climate range over considerable areas, and there are almost certainly thresholds of water deficit past which large areas of west-side forests would be at risk for large fires. Such fires do not occur in the twentieth century historical record, so our statistical fire models are incapable of projecting them. However, even though we are unable to model large west-side fires, hotter and drier summers unequivocally increase the chance that such fires will occur.

4.3 Adaptation options

Adaptation options depend greatly on the scale in question (Table 4, Millar et al. 2007; Joyce et al. 2008). Regional adaptation is necessarily an exercise in forest policy and planning as much as it is engaging in land-management actions; it must be sufficiently flexible to facilitate adaptation locally but also capable of organizing regional responses. Local adaptation must be tailored to local conditions to succeed (all adaptation is necessarily local), but decisions that determine local action may be made at the state or federal level, requiring a regional or national viewpoint. Furthermore, given climate change and globalization, adaptation proceeds in a context defined as much by regional and global pressures as by local conditions. No successful strategy can be crafted without awareness of these outside pressures.

Regional adaptation consists of strategies likely to promote conditions that increase resilience to expected changes and thereby increase the likelihood of a specific objective. Thinking about adaptation for forests is in many ways in its infancy, but examples might include stronger emphases on: reducing anthropogenic stresses on forest ecosystems, promoting resilience to likely impacts, landscape and biological diversity, planning for projected future conditions, and assessing the decision context in terms of barriers and opportunities that limit or facilitate local adaptation (Millar et al. 2007; Joyce et al. 2008).

Local adaptation consists of application of tools (existing or new) to affect conditions. First one must identify management objectives, assess capacity to alter conditions for the objectives, and then develop appropriate tools. For example, targeted thinning in drier forests in which fire suppression has led to fuel accumulations

Table 4 Examples of adaptation options (after Millar et al. 2007)

Adaptation strategy	Regional actions (policy)	Local actions (management)
Resist change	Minimize impacts of disturbance, suppress fire in systems where fire is rare, but maintain Wildland Fire Use (WFU)	Suppress wildfire in wildland-urban interface;
Promote resilience to change	Thin stands from below (to increase fire resilience); create uneven-aged structures or reduce density (to increase resilience to insects)	Use large disturbances as opportunities to establish new genotypes, and forest heterogeneity and diversity
Allow forest ecosystems to respond to change	Plant new species expected to respond favorably to warmer climate	Use new genotypes, or even species, in forestry plantations

capable of sustaining a high severity fire (novel in those ecosystems) may increase the resilience of that forest to a fire. In wetter forests where twentieth century harvest practices have decreased age class diversity and altered patch structure, targeted thinning and cutting could simultaneously create appropriate fuel breaks and increase canopy and age-class diversity. In water-limited forests, it is possible that tailoring stand density to the expected water conditions of the future will increase resilience to insect attack and climate change in general by increasing stand water supply to counteract the projected increased atmospheric demand.

The management implications of climate impacts to forests are manifold, and the need to anticipate those impacts in the state of Washington is paramount. "Forest types", "communities", disturbance return intervals, and historic ranges of variability are all concepts that attempt to define the state of a forest, but that state is inherently dynamic and thus defies easy categorization. Climate change will only increase the necessity of recognizing such dynamism in ecosystems. Reference conditions and historic ranges of variability are also concepts that will need to be re-evaluated as management tools because the trajectories of forest ecosystems will be away from conditions we are familiar with and future disturbance regimes will likely exceed the range of historic variability. All this does not mean that there is no utility in planning-quite the opposite. It means planning for expected conditions and what they mean for resource management. It may well mean changing the mandates and goals of land management agencies to reflect new conditions and priorities, planning for unexpected conditions, and experimenting with novel ideas (or reviving old ideas), particularly when there is too much uncertainty in projections. It quite likely also means using available tools now (silviculture, cross-agency collaboration) while considering the barriers to using other tools (e.g., prescribed fire). In order to accomplish this, however, a concerted effort to increase communication between scientists, managers, and policy makers is required. The rates of change expected and the nature of the impacts will require .broad collaboration.

4.4 Uncertainty and limitations

Projections of future climate and subsequent impacts on forest ecosystems are necessarily subject to some limitations and uncertainty. We have constrained the uncertainty associated with using one or a few climate models by using an ensemble projection of future climate and its hydrologic outcomes. We have also approached these questions at regional to sub-regional scales to avoid the problems associated with making climate and impacts projections at inappropriately fine scales. The strengths of these projections are in regional patterns and trends. One of the chief limitations of the projections is that after the middle of the twenty-first century, the differences between climate models and emissions scenarios are likely more important than the uncertainty surrounding modeled forest processes. However, there are some important uncertainties worth noting beyond those associated with climatic uncertainty. First, in our comparison of water and energy limited forests, water limitation is defined in this work in a general biophysical way; different species requirements, or the adaptation of different vegetation types to new conditions, are not considered. The reported shifts are therefore a way of emphasizing places with most vulnerability, not necessarily where particular vegetation is vulnerable. Second, in our future species climatic suitability analyses, the projections do not consider ecological interactions that may affect outcomes of future conditions as much or more than climate, particularly in forests, where establishment, growth, and mortality are more limited by competition than by climate. Third, the future fire analysis assumes a constantly log-linear dependence of area burned on climate, and it is reasonable to expect that towards the end of the century, novel forest-climate-vegetation relationships would create new fire regimes inconsitent with the projections. These uncertainties all increase with time. However, given that emissions scenario AlB is considered moderate (e.g., less forcing than either A2 or AlFI) and we employ a climate model ensemble for most of projections, we are confident that the projections are within the realm of plausibility.

5 Research needs

5.1 Understanding future microclimate in mountain and forest ecosystems

Spatial variability of climate in the complex terrain associated with forest ecosystems is poorly understood. Much more needs to be known about how to downscale regional climate to local conditions and whether such downscaling could decrease the uncertainty in key outcomes for forest management. In particular, will there be substantial differences in the way climate will change in different geographic areas (e.g., for maritime vs. continental) or at different elevations. Current data resources and future scenarios are generally inadequate to assess impacts at scales useful for managers.

5.2 Understand the geographic distribution of genetic variability and climatic tolerances for tree species

Planning for future resilience and responses to disturbance require well developed knowledge of genotypic variability and sub-species climatic tolerances so that seed stock well adapted to likely future conditions can be selected. The geographic variability of sub-species genotypes and how those genotypes perform in different climatic conditions is poorly documented for most species. Some climatic changes could have substantial differences in their impacts on different species within the same stand due to differences in physiology, life history, or morphology, and the implications of these need to be better understood in the context of energy and water limitation.

5.3 Understand the role of climate in tree establishment generally, but particularly post-fire and at lower treeline, to prioritize post-disturbance treatments and planting efforts

The success of tree establishment after disturbance likely varies with climate, but the degree to which elimate limits establishment is not well known. Most of the bioclimatic approaches to future vegetation response to climate change do not account for this potential sensitivity in early life-history stages and instead focus on climate relationships for established trees. Because establishment is more sensitive than persistence of established trees, it is likely that important tree species will fail to establish after disturbance when the climate has shifted sufficiently.

5.4 Move from fire area burned to landscape fire effects and fire severity

The area burned by fire is not the best metric of ecological impact. The role of future fire in forested landscapes depends as much or more on fire effects and fire severity as on the area burned. Physically based models at finer spatial scales are needed to address impacts of changing fire regimes on vegetation and watershed hydrology. Fire also has important implications for short-term hydrologic response after disturbance, which may include important feedbacks to biological effects in forest and aquatic systems.

5.5 Understand how other insects (e.g., spruce and fir beetles or defoliators) and pathogens respond to climatic change

The mountain pine beetle is not the only insect species of concern in a warming climate, and the role of climate in other insects' life cycles and host vulnerabilities must be better understood if we are to anticipate future impacts.

5.6 Understand the effects of silvicultural treatments on fire behavior and stand vigor

Forest managers need tools for climate change adaptation, and a tool that is available now is silviculture. Appropriate silvicultural prescriptions require knowledge of expected local impacts and stand and tree physiological thresholds that may not have historical analogues. The potential impacts identified in this paper point to two silvicultural research needs. First we must better understand the physiological response of mature trees to changing climate conditions to determine if silvicultural treatments could stem those impacts. Second we need to understand how different silvicultural treatments can be used in anticipation of different projected climatic changes. The impacts and benefits of silvicultural treatments on forest ecosystem processes such as fire severity are generally poorly quantified.

5.7 Understand the implications of impacts for overarching management strategies and institutional structure

Forest management strategies and institutional structures are products of the evolving pressures on forest ecosystems and how they relate to external societal demands for resources and services. To that end, the new (or altered) pressures on forests expected with climate change will likely require rethinking old models of forest ecosystems (e.g., community or vegetation types, fire regimes, forest health, and other norms) as well as management strategies (e.g., adaptive management vs. scenario planning, resilience, etc.). Research needs therefore include not only the response of forest ecosystems to future climate, but also what those impacts mean for human systems that depend on and affect forests (Millar et al. 2007; Joyce et al. 2008).

6 Conclusions

- Spatial patterns of productivity will change-state-wide productivity may initially increase due to warmer temperatures but will then decrease due to increased drought stress. Douglas-fir productivity appears to vary with climate across the region and will potentially increase in energy-limited forests in the near term. Climatic variability will continue to mediate productivity.
- Species composition will be affected by climate, and the consequences for lower elevation forests and for species susceptible to mountain pine beetle are potentially substantial. Climate will be inconsistent with the establishment of Douglas-fir, ponderosa pine, and lodgepole pine in many areas by the middle of the twenty-first century. Forest species composition will likely change chiefly in the wake of large disturbances and may be affected by climatic limitation of regenerating trees.
- Regional fire area burned may increase two- or three-fold. Fire regimes in different ecosystems in the PNW have different sensitivities to climate. Year-to-year variation will continue and potentially increase, and will also be a challenge for planning.
- Due to climatic stress on host trees, mountain pine beetle outbreaks may increase in frequency and levels of tree mortality. Mountain pine beetles will reach higher elevations due to an increase in favorable temperature conditions for the beetles in these areas as the region warms. Conversely, this species may become less of a threat at middle and lower elevations as the region warms, due to less favorable temperature conditions. Other insect species may emerge in areas that are no longer suitable for the mountain pine beetle.
- Disturbance will be a key player in the future of Washington's forests. Sudden changes to forest structure and composition caused by stand-replacing disturbances will speed up species turnover and transitions to new structural characteristics of stands and landscapes, and maintain positive feedbacks between rates of change in disturbance regimes and forest succession.

Climate change will clearly impact the forests of Washington through multiple processes, with major consequences to ecosystem structure, function, and services. Carbon storage, timber production, habitat for plant and animal species, and mass and energy fluxes, among other processes, will be substantially modified in the coming decades. Furthermore, it seems reasonable to assume that Washington is not unique: other forest regions of the western United States, and indeed of the Earth, will probably experience equal or greater impacts. Quantifying the magnitude of the expected change win be necessary for land managers needing to plan for climate change.

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