Forest Ecology and Management 362 (2016) 194–204

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Climate-driven changes in forest succession and the influence of management on forest carbon dynamics in the Puget Lowlands of Washington State, USA

Danelle M. Laflower[a], Matthew D. Hurteau[b,*], George W. Koch[c], Malcolm P. North[d], Bruce A. Hungate[c]

[a] IGDP in Ecology and Department of Ecosystem Science and Management, The Pennsylvania State University, University Park, PA 16802, United States
[b] Department of Biology, The University of New Mexico, Albuquerque, NM 87131, United States
[c] Center for Ecosystem Science and Society and Department of Biological Science, Northern Arizona University, Flagstaff, AZ 86011, United States
[d] USDA Forest Service, Pacific Southwest Research Station, Davis, CA 95618, United States

ARTICLE INFO

Article history:
Received 12 October 2015
Received in revised form 8 December 2015
Accepted 14 December 2015
Available online 21 December 2015

Keywords:
Carbon
Climate change
LANDIS-II
Succession
Disturbance

ABSTRACT

Projecting the response of forests to changing climate requires understanding how biotic and abiotic controls on tree growth will change over time. As temperature and interannual precipitation variability increase, the overall forest response is likely to be influenced by species-specific responses to changing climate. Management actions that alter composition and density may help buffer forests against the effects of changing climate, but may require tradeoffs in ecosystem services. We sought to quantify how projected changes in climate and different management regimes would alter the composition and productivity of Puget Lowland forests in Washington State, USA. We modeled forest responses to four treatments (control, burn-only, thin-only, thin-and-burn) under five different climate scenarios: baseline climate (historical) and projections from two climate models (CCSM4 and CNRM-CM5), driven by moderate (RCP 4.5) and high (RCP 8.5) emission scenarios. We also simulated the effects of intensive management to restore Oregon white oak woodlands (*Quercus garryana*) for the western gray squirrel (*Sciurus griseus*) and quantified the effects of these treatments on the probability of oak occurrence and carbon sequestration. At the landscape scale we found little difference in carbon dynamics between baseline and moderate emission scenarios. However, by late-century under the high emission scenario, climate change reduced forest productivity and decreased species richness across a large proportion of the study area. Regardless of the climate scenario, we found that thinning and burning treatments increased the carbon sequestration rate because of decreased resource competition. However, increased productivity with management was not sufficient to prevent an overall decline in productivity under the high emission scenario. We also found that intensive oak restoration treatments were effective at increasing the probability of oak presence and that the limited extent of the treatments resulted in small declines in total ecosystem carbon across the landscape as compared to the thin-and-burn treatment. Our research suggests that carbon dynamics in this system under the moderate emission scenario may be fairly consistent with the carbon dynamics under historical climate, but that the high emission scenario may alter the successional trajectory of these forests.

1. Introduction

Balancing multiple and often competing objectives is a defining characteristic of forest management (Agee and Skinner, 2005; Hudiburg et al., 2009; Turner et al., 2013), a challenge compounded by the uncertainty associated with ecosystem response to changing climate (Millar et al., 2007; Bellassen and Luyssaert, 2014). Abiotic factors, such as temperature and precipitation, influence forest productivity (Keith et al., 2009; Littell et al., 2008) and community composition through the specific climatic constraints associated with different species (Boucher-Lalonde et al., 2012; Hawkins, 2001). Yet, management activities can influence the effects of climate on productivity by altering forest structure, resource availability, and species composition (Millar et al., 2007; Kerhoulas et al., 2013). Informed management

---

* Corresponding author at: The University of New Mexico, MSC03 2020, Albuquerque, NM 87131, United States.

E-mail address: mhurteau@unm.edu (M.D. Hurteau).

http://dx.doi.org/10.1016/j.foreco.2015.12.015
0378-1127/© 2015 Elsevier B.V. All rights reserved.

requires understanding forest responses to projected climate change and how silvicultural practices may alter this response.

Among the myriad objectives that managers are currently tasked with meeting, from species conservation to wood fiber production, there is increased importance placed on forest carbon sequestration because of forests' role in regulating climate (Canadell and Raupach, 2008). The tradeoffs associated with different management objectives are particularly salient in the Pacific Northwestern United States where high carbon density and productivity make the region's forests a large carbon sink and also a high-value source of wood fiber (Hudiburg et al., 2013; Keith et al., 2009; Malmsheimer et al., 2011; Smithwick et al., 2002). This is in large part due to climatic conditions that have shaped the region's forests. The moderate, maritime influenced climate allows for nearly year-round growth at lower elevations (Doehlert and Walker, 1981; Franklin and Waring, 1980; Littell et al., 2008). However, increasing temperature and decreasing growing season precipitation are likely to drive changes in carbon sequestration of these forests (Mote et al., 2013; Rupp et al., 2013).

In the already dry summers of the Pacific Northwest, increasing temperature could further intensify water limitation, especially in forests that occur on the excessively well-drained soils of the Puget Lowlands of Washington state (Crawford and Hall, 1997; Littell et al., 2008). Douglas-fir (*Pseudotsuga menziesii*), a long-lived conifer of intermediate drought-tolerance, dominates much of the Puget Lowland forests, and climate change is projected to have a negative effect on this species, as moisture limitation has the largest influence on its growth (Littell et al., 2010). A reduction in Douglas-fir productivity, due to moisture limitation, may translate to a reduction in overall regional productivity, since the other common large, long-lived species, western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*), are even less drought-tolerant (Burton and Cumming, 1995; Urban et al., 1993).

Active management may provide one option for moderating the effects of changing climate on Puget Lowland forests. Selectively thinning forests can reduce competition for water, nutrients, and space (Bréda et al., 1994; Kerhoulas et al., 2013; Roberts and Harrington, 2008), decrease fire risk and predisposition to insect and disease outbreaks, and thereby increase resilience (Chmura et al., 2011). Manipulating forest structure through management can increase the carbon sequestration rate (Hurteau et al., in press; Latham and Tappeiner, 2002; Martin et al., 2015) and buffer against the effects of species decline due to maladaptation to climate (Rehfeldt et al., 2006). However, these activities impose reductions in the carbon stocks of these forests (Finkral and Evans, 2008; Gray and Whittier, 2014; Hudiburg et al., 2009; Mitchell et al., 2009).

Although forest models for the PNW project shifts in individual species ranges, declines in Douglas-fir, and increases in wildfire (Littell et al., 2010), there is a lack of information regarding how climate- and disturbance-driven changes in species will alter forest-level composition and productivity. We sought to quantify how projected changes in climate and management would alter the composition and productivity of Puget Lowland forests, including the tradeoffs between species conservation and carbon storage. We hypothesized that increasing growing season temperature and decreasing growing season precipitation would decrease productivity, favoring more drought-tolerant species such as ponderosa pine (*Pinus ponderosa*) and Oregon white oak (*Quercus garrayana*), species that occupy the historical woodland habitats in the region. We also hypothesized that management to reduce resource competition would mitigate some climate-driven effects on productivity by diversifying composition of forest stands, and buffer against a state change if dominant species are not well-suited to future climate. We also sought to evaluate the effectiveness of oak restoration treatments to improve habitat for the western gray squirrel (*Sciurus griseus*) under different climate projections and the effects of these treatments on forest C dynamics. We hypothesized that management actions that decreased competition for oaks, coupled with a warmer, drier climate, would reverse the declining trajectory of the species upon the landscape, and that this management would not substantially decrease landscape-scale C sequestration, due to the limited extent of active oak restoration areas. We used a simulation approach to test these hypotheses by modeling forest growth and succession under historical climate and projected climate under two emission scenarios from two climate models through the late 21st century.

2. Materials and methods

2.1. Study area

Joint Base Lewis-McChord (JBLM) is a 36,182 ha military installation located in the Puget Lowlands of western Washington. Natural areas include dense conifer forests, young mixed-conifer forests, and open grasslands (Fig. 1). The oak-conifer ecotone between forest and prairie supports one of three geographically isolated populations of the Washington State-listed western gray squirrel (*S. griseus*) (Washington Department of Fish and Wildlife, 2013). Elevation on the base ranges from 0 to 201 m and generally consists of moderate to rolling topography (Carey et al., 1999). The climate is mild Mediterranean, with a mean annual temperature of 9.7 °C and only 14% of the 1430 mm of mean annual precipitation falling during summer months (National Climate Data Center (NCDC, 2013) GHCND:USC00454486). Soils on the installation are predominantly (77% of the area) well-drained prairie soils (Spanaway series with inclusions of Spana and Nisqually (NRCS, 2013)). The prairie soils have moderately rapid permeability with very low water-holding capacity and support grasslands, woodlands, savanna, and Douglas-fir colonization forest habitats (Zulauf, 1979). Although Douglas-fir is the dominant species, Oregon white oak and ponderosa pine are typically present on drier sites. The principal non-prairie soil is the McChord-Everett complex, a moderately well-drained soil complex that supports the historical moist forests which are dominated by Douglas-fir, with late-successional stands of western hemlock and western redcedar. Broad-leaved trees, such as bigleaf maple (*Acer macrophyllum*), vine maple (*Acer circinatum*), and Oregon ash (*Fraxinus latifolia*), are also present in this forest type. Glacial retreat (7000–10,000 years before present) facilitated the establishment of the region's grasslands, which were maintained through periodic burning by Native Americans (Agee, 1996). Periodic burning was largely abandoned with the advent of European colonization (Foster and Shaff, 2003), facilitating Douglas-fir afforestation, which has converted 8221 ha of JBLM's historical prairie to colonization forest. Much of the installation was extensively harvested prior to Department of Defense acquisition in 1919. The Army conducted clear-cutting and selective harvests from 1947–1952, and shifted to thinning and selection harvests in the 1960s. Current management on the installation includes variable density thinning designed to meet military training and other objectives, such as habitat provision for the western gray squirrel.

2.2. Field data

Field data for model validation were collected from May–August 2012 on 347 plots distributed across the installation. Sampling was stratified to capture the range of forest conditions prevalent on the installation, and specific training areas were sampled based on accessibility given military training schedules. Prior to sampling, we established a 200 m grid within each training

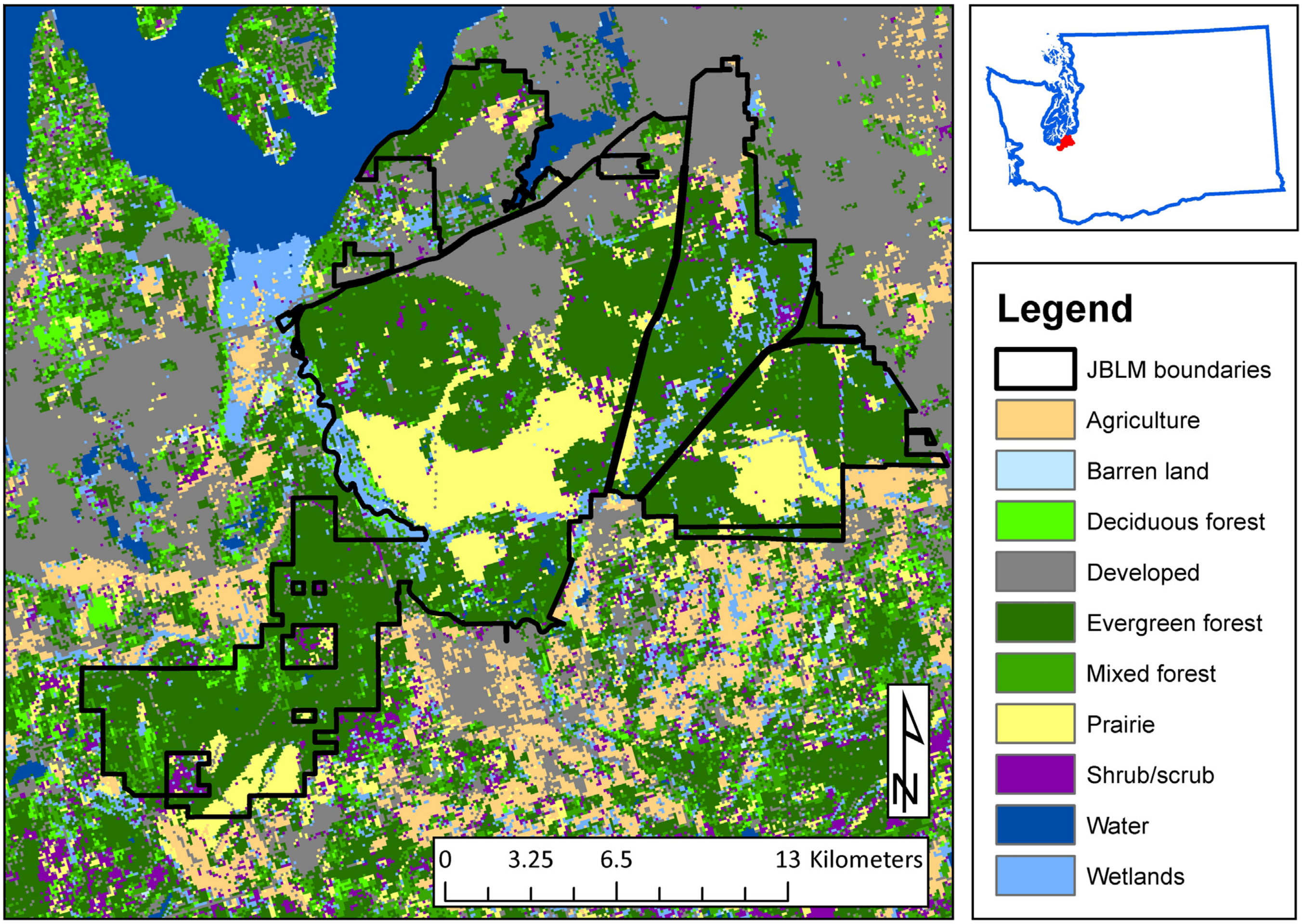

Fig. 1. Regional land cover map of Joint Base Lewis–McChord, and the installation's location in the Puget Lowlands of Washington, USA.

area and sampling was conducted at each grid point. We used a circular 1/5 ha nested plot design to measure all trees >80 cm diameter at breast height (DBH). Trees >50 cm DBH were measured in a 1/10 ha subplot and trees >5 cm DBH were measured in a 1/50 ha subplot. Species, DBH, and height for both live and dead trees were collected within each subplot. Regeneration was tallied by height in a 2 m radius subplot at plot center. Surface fuels and coarse woody debris were measured using three 15 m modified Brown's fuel transects originating from plot center (Brown, 1974). Coarse woody debris measurements included a four decay-class system and included length and end diameter measurements. We used allometric equations from Jenkins et al. (2003) to calculate aboveground biomass for validation of our simulation data.

2.3. Simulation approach

To project forest response to changes in climate, wildfire, and management over time, we used the LANDIS-II model (Scheller et al., 2007). This stochastic, forest disturbance and succession model uses a species-specific, age cohort-based approach to simulate forest succession, where species cohorts are represented by biomass in age classes (Scheller and Mladenoff, 2004; Scheller et al., 2007). Grid cells containing initial species age cohorts and abiotic attributes represent the study area. Within grid cells, species grow, compete, reproduce, and die according to user-defined life history traits (e.g. shade and fire tolerance, dispersal, sprouting, longevity), abiotic conditions, and disturbances (Scheller and Mladenoff, 2004; Scheller et al., 2007). Seed dispersal and disturbances occur within and across grid cells (Scheller and Mladenoff, 2004).

In addition to the base LANDIS-II model, we used the Century Succession, Dynamic Fire and Fuels, and Leaf Biomass Harvest extensions to project C dynamics and species composition resulting from the effects of changing climate, management, and fire. The Century Succession extension (Century) is based on the original CENTURY Soil model (Metherell et al., 1993; Parton et al., 1993). Century simulates above- and belowground C and nitrogen (N) dynamics as influenced by soil characteristics, climate, and species-specific parameters (e.g. growing degree days, C:N ratios, percent lignin, etc.). It projects productivity, C storage, and changes in forest composition (Scheller et al., 2011). One of the factors controlling regeneration is an individual species' shade tolerance. In Century Succession, the site shade class for each grid cell is calculated based on the total biomass present as a percent of the maximum biomass possible for the site (Scheller and Mladenoff, 2004). We used the Dynamic Fire and Fuels extensions to simulate wildfire. The fire extension models frequency, spread, and tree mortality based on local fire weather data and fuel types derived from the Canadian Forest Fire Prediction System (Sturtevant et al., 2009; Van Wagner et al., 1992). The fuels extension assigns and annually updates fuel types based on species composition, age, and post-disturbance information (Sturtevant et al., 2009). We used the Leaf Biomass Harvest extension to simulate both thinning and prescribed burning treatments, as the fire extension cannot implement both wildfire and prescribed fire in the same simulation. The Leaf Biomass Harvest extension can implement multiple, overlapping user-defined prescriptions at variable time steps, as prescription criteria are met (Gustafson et al., 2000).

2.4. Model parameterization

LANDIS-II requires the subdivision of the study area into ecoregions that have similar climate and soils. Given the small elevation gradient and consistent climate across the installation, we used soil type to classify the area into two ecoregions, based on prairie and non-prairie soils, using the Soil Survey Geographic Database (SSURGO; NRCS, 2013). We divided the study area using 4 ha grid cells to match the resolution at which management actions are implemented. We used the Landscape Ecology, Modeling, Mapping & Analysis (LEMMA) Laboratory's Washington Coast and Cascades gradient nearest neighbor (GNN) interpolated map (2 2 1) and database (Ohmann and Gregory, 2002; LEMMA, 2006) to establish JBLM's initial-communities layer of species with their age cohorts. The GNN technique incorporates regional grids of Forest Inventory Analysis (FIA) and USFS Current Vegetation Survey (CVS) plot data, spatially-explicit environmental data (such as geology, topography, climate), and Landsat Thematic Mapper (TM) satellite imagery to predict forest composition at the landscape scale (Ohmann and Gregory, 2002). The LEMMA GNN product has 30 m resolution. We used Arcmap 10.1 (ESRI, 2012) to resample the GNN-based initial communities layer to decrease pixel resolution from 30 × 30 m to 200 × 200 m using a nearest neighbor resampling technique, and further reduced the number of unique communities by binning similar species composition and cohort ages. The aggregated layer included all listed GNN map species that occurred in at least 1% of the grid cells and occupied at least 10% of the basal area in a given GNN grid cell. The initial-communities map included 21 unique, forested or able to be forested (e.g. prairies, shrub swamps), communities and nine tree species. These nine species represented 91% of the individuals sampled in the field.

The Century Succession extension requires species-specific life history characteristics, soil, and climate data. We parameterized life history and functional type data for the nine species in the initial communities layer using the scientific literature and the CENTURY user guide (Supplementary Tables 1–5). The soil layer, including initial C and N values, was developed using NRCS SSURGO data (NRCS, 2013). We partitioned soil C into pools and estimated N as a function of soil C using the methodology from the Century Soil Model (Metherell et al., 1993) (Supplementary Table 4). We adjusted N deposition to reflect annual N deposition for LaGrande, Washington (NADP, 2012) and estimated rates of biological N_2 fixation (Heath et al., 1987). Following Loudermilk et al. (2013) and Martin et al. (2015), we calibrated soil decay parameters so that at the initial time-step of the simulation, simulated soil carbon was similar to SSURGO values. We used 51 years (1962–2012) of climate data from the Landsburg, WA weather station for initial parameterization and validation (NCDC GHCND: USC00454486).

To generate simulation data for model validation comparison with aboveground biomass measurements from field data, we subtracted 100 years from current cohort ages and ran simulations from 1912 to 2012 using climate data from the Landsburg, WA weather station. From this output, we extracted aboveground biomass (AGB) values in 2012 from the 5533 pixels that contained forests. Field data biomass ranged from 1510 to 82,414 g m^{-2}, with a mean of 36,988 g m^{-2}. Simulated biomass ranged from 416 to 65,535 g m^{-2}, with a mean of 41,100 g m^{-2}, indicating that the model simulated the influence of climate and site variables on forest productivity (Fig. 2).

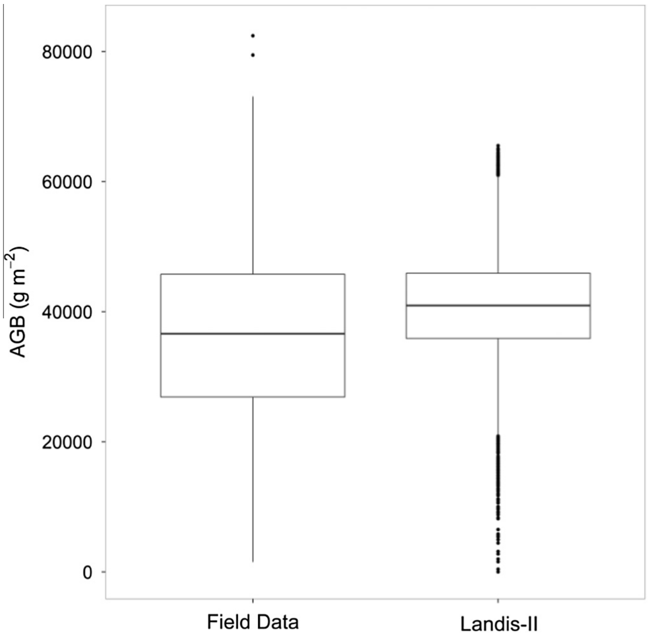

Fig. 2. Comparison of aboveground biomass (Mg ha^{-1}) of field data ($n = 346$) and LANDIS-II simulations of all forested pixels ($n = 5533$).

We parameterized the Dynamic Fire extension by creating three fire regions: prairie, forests on prairie-soil, and forests on non-prairie-soil, as defined by ecoregion and cover type. We used wildfire occurrence data from JBLM prairie fires (2007–2011) and USFS forest fires within 100 km of JBLM (1995–2005) to estimate parameters for fire size. To estimate frequency, we reclassified the LANDFIRE mean fire return interval (MFRI) data product to represent our three fire regions (LANDFIRE, 2013). To parameterize fire weather (wind speed, direction, etc.) and fuel conditions, we obtained data from the Enumclaw, WA Remote Automatic Weather Station (RAWS; 451702) and processed it with Fire Family Plus 4.1 (Bradshaw and McCormick, 2000). To refine fire spread patterns, we created spatial layers for slope and aspect using the Spatial Analyst extension in ArcMap (ESRI, 2012) from Washington State GIS digital elevation model raster layers (http://wagda.lib.washington.edu/data/geography/wa_state/#elevation). To define fuel types, we binned general forest types that exhibited similar behavior following Sturtevant et al. (2009) and calibrated them according to the methodology outlined in Scheller et al. (2011). We included wildfire in all of our simulations.

We parameterized timber harvest in the Leaf Biomass Harvest extension based on JBLM's current land management practices, which set annual harvest at approximately 40% of net annual growth (45,000–54,000 m^3 biomass annually; Griffin, 2007). To remove this amount of biomass, we simulated a harvest that targeted 67% of the 70–180 year old Douglas-fir cohorts and occurred annually on 1% of the area on prairie soils and 0.5% of the area on non-prairie soils. To account for unintended mortality during harvesting operations, we removed 2% of all other species from these areas targeted for harvesting. We excluded stands that contained cohorts over 300 years old, riparian communities, and wooded wetlands to incorporate JBLM's priority management goals. To increase landscape heterogeneity and maintain regeneration sources, we limited harvest to once during the simulation period in any given grid cell, and did not harvest on sites that had been burned by wildfire within the last 10 years or were adjacent to sites harvested within the last 40 years.

We used Leaf Biomass Harvest to simulate prescribed burning by implementing a thin from below prescription that preferentially removed young, fire-sensitive cohorts following Syphard et al. (2011). Because the harvest extension simulates prescribed burning, areas that received a prescribed burn were excluded from the thinning treatment. To simulate fire-induced mortality, the decadal treatment removed 85% of 1–26 year old Douglas-fir cohorts, 90% of 1–5 year old Oregon white oak cohorts, 5% of 1–24 year old ponderosa pine cohorts, 90% of 1–15 year-old cohorts for all other species, and a smaller fraction of older cohorts. Prescribed burning treatments were limited to prairies and Douglas-fir forests on prairie soils. We did not simulate prescribed burning in areas where the initial communities contained late-successional conifers, cohorts over 300 years old, or were in riparian buffer areas. We implemented prescribed fire treatments, if sites had not experienced a disturbance for ten years, by ranking grid cells based on the Dynamic Fuels extension fire-hazard index fuel type, with the highest ranked cells being treated first. To reflect increased canopy base height following prescribed burn treatments, we modified fuel types for a 10-year duration after application, following Martin et al. (2015). We used a 5-year fire return interval for prairie and a 20-year fire return interval for forest, such that 20% of qualifying prairie and 5% of qualifying forest was available to burn annually.

To test our hypothesis that intensive management to favor Oregon white oak would increase its frequency on the landscape, we used the Leaf Biomass Harvest extension to simulate an oak restoration treatment. We created a 708 ha management area that met three criteria: prairie soil, away from riparian areas, and included extant oaks. Within this area we conducted intensive management that replicated thinning and burning to reduce conifer biomass and the resultant shade class to a level that would allow oaks to regenerate. Our treatment thinned 85% of the non-pine conifers between 20 and 230 years old and included prescribed burning with a 10-year fire return interval. The entire management area was eligible for treatment annually, and management occurred on stands that were at least 11 years old and had not been harvested or burned within ten years.

2.5. Climate data and projections

To investigate the effects of projected changes in climate on forest dynamics, we used NASA Earth Exchange US Downscaled Climate Projections for Pierce County, Washington (Thrasher et al., 2013). These climate projections, downscaled using the Bias-Correction Spatial Disaggregation algorithm from two Coupled Model Intercomparison Project Phase 5 general circulation models (CNRM-CM5 (CNRM) National Centre of Meteorological Research, France and CCSM4 (CCSM) National Center of Atmospheric Research, USA), were found to best simulate regional climate over the 20th century (Rupp et al., 2013). Both models showed simulated mean annual precipitation that was higher than the 20th century mean. CNRM-CM5 had simulated mean temperature that was lower than the 20th century mean, while the ensemble mean annual temperature from CCSM4 showed no deviation from the observed mean (Rupp et al., 2013). We selected two emission scenarios (Representative Concentration Pathways, RCPs) to bracket the range of potential future emission pathways. RCP 4.5 is a moderate scenario where greenhouse gas emissions (GHG) stabilize at 650 ppm carbon dioxide (CO_2) by 2100, and RCP 8.5 is a high, or business-as-usual, scenario where GHG emissions do not stabilize by 2100 (Moss et al., 2008, Supplemental Figs. 1 and 2). We binned projected climate data by decade for each scenario to develop distributions for use in LANDIS-II.

2.6. Simulation experiment and data analysis

We used a full factorial design to quantify the effects of management and changing climate on C dynamics and species composition. We simulated four management scenarios: control (no management), burn-only, thin-only, and thin-and-burn treatments under current climate (baseline) and four projected climate scenarios (CNRM 4.5, 8.5; CCSM 4.5, 8.5). We ran 25 replicates of each of the 20 treatment-climate scenarios to capture the stochastic variability of individual simulations.

To quantify treatment and climate effects on carbon pools and fluxes, we calculated net ecosystem carbon balance (NECB, calculated as net primary productivity minus heterotrophic respiration and fire emissions) and total ecosystem carbon (TEC). To quantify changes in successional dynamics, we calculated the ratio of aboveground carbon for the mid-seral Douglas-fir to late-successional tree species (western hemlock and western redcedar). For each of the 20 scenarios, we calculated landscape-scale mean and 95% confidence intervals from the replicates for between-scenario comparisons of NECB, TEC, and ratios of Douglas-fir to late-successional species. To quantify changes in species composition, we calculated year 2100, mean grid-cell-level richness and 95% confidence intervals to create species richness frequency distributions for each of the scenarios. We used ArcMap 10.1 (ESRI, 2012) and R 3.0.01 (R Core Team, 2013) with the ggplot2, plyr, and raster packages (Wickham, 2009, 2011; Hijmans, 2014) to process the simulation data and produce figures.

To quantify differences in the probability of oak presence under baseline climate for each of our four treatments, we compared the empirical cumulative distribution for probability of oak on the landscape using the Kolmogorov–Smirnov goodness-of-fit test (K-S test). We also ran a K-S test comparison of oak presence between the controls of each climate scenario against the control of the baseline climate scenario to test if climate was influential for determining the probability of oak occurrence. To evaluate the effects of treatment on the probability of oak presence under projected climate, we ran K-S tests comparing each treatment to the control within each climate scenario. We created year 2100 oak probability surfaces of all simulations to visualize effects of climate and management on oak presence. To quantify differences in landscape-scale carbon sequestration when managing to favor oaks, we compared TEC for each thin-and-burn treatment-climate scenario, with and without the 708 ha oak management block being managed to favor oak. We calculated mean TEC and 95% confidence intervals for the replicate simulations.

3. Results

3.1. Effects of climate on carbon balance

NECB increased for the first 20 years of the control simulation, regardless of climate scenario (Fig. 3). As the forest matured, respiration increased and NECB began to decline under all climate scenarios. The effects of changing climate on carbon flux began at mid-century, with a substantial deviation from baseline NECB occurring under the high emission projections in late-century (Fig. 3).

The late-century decline in NECB under the high emission scenario was due to the effects of higher temperature and decreased precipitation on NPP. By late century, moderate climate change did not alter tree species richness, but more severe climate change did reduce richness (Fig. 4). In addition, the high emission scenarios altered the transition to late-successional species. The typical trajectory for this system, under baseline climate, is a gradual decline in Douglas-fir regeneration as late-successional tree species (western hemlock and western redcedar) establish and account for a larger fraction of aboveground carbon (Fig. 5). This successional pattern held under the moderate emission scenario. However, under the high emission scenarios, the rate of increase

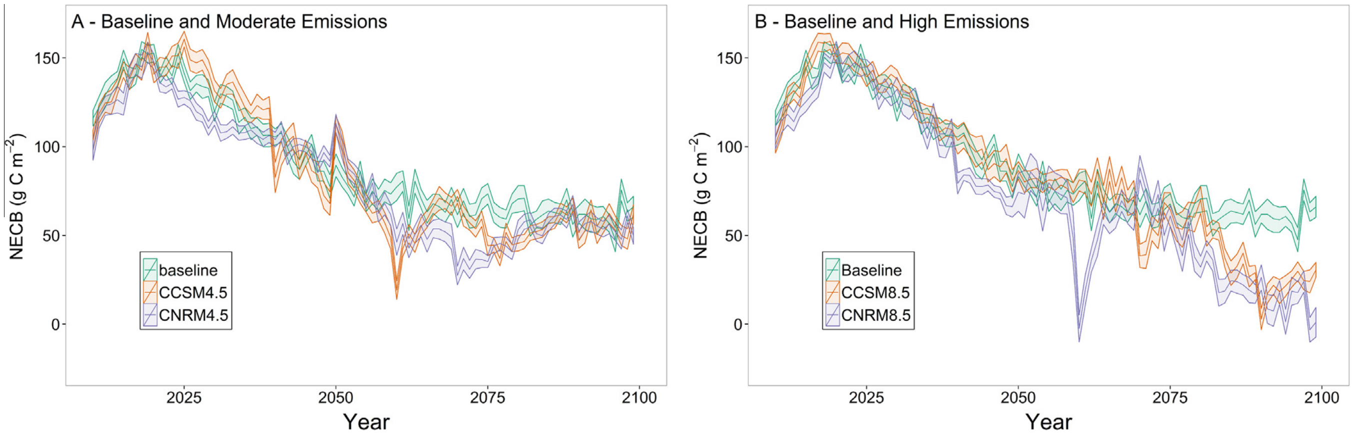

Fig. 3. Net Ecosystem Carbon Balance (NECB) for the no management (control) simulations under baseline climate and climate projections from two general circulation models (CCSM and CNRM), driven by moderate (RCP 4.5) and high (RCP 8.5) emission scenarios. Lines are the mean NECB and shading the 95% confidence intervals from 25 replicate simulations.

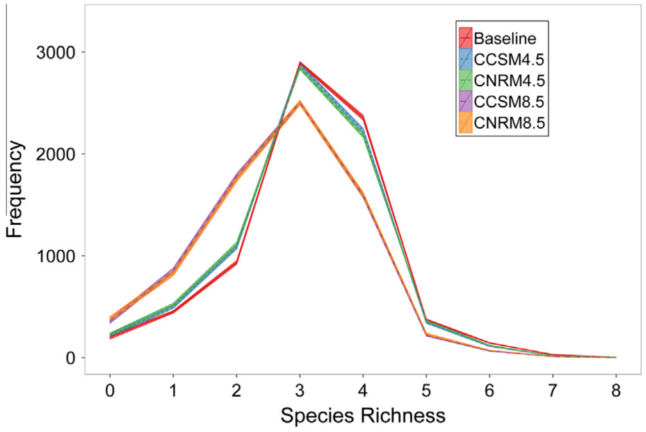

Fig. 4. Year 2100 comparison of species richness frequency distributions for baseline climate and climate projections from two general circulation models (CCSM and CNRM), driven by moderate (RCP 4.5) and high (RCP 8.5) emission scenarios. Lines are the total number of grid cells within the study area that had a given mean species richness calculated from the 25 replicate simulations. Shading is the 95% confidence intervals from the 25 replicate simulations. Total number of forested grid cells within the study area is 5533.

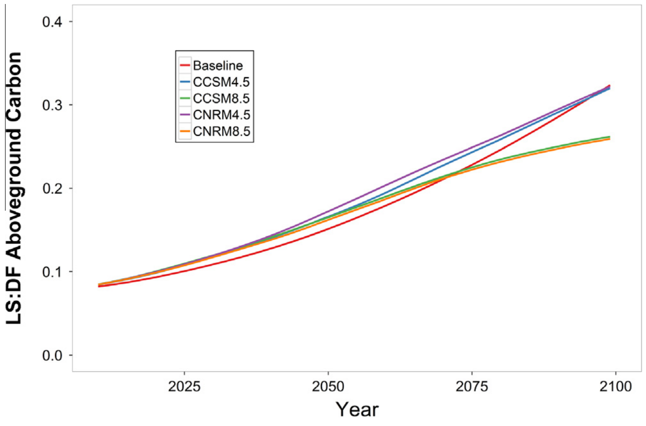

Fig. 5. Ratio of late successional species (LS; western hemlock and western redcedar) to Douglas-fir (DF) aboveground carbon stocks for the no management (control) simulations under baseline climate and projected climate from two general circulation models (CCSM and CNRM) driven by moderate (RCP 4.5) and high (RCP 8.5) emission scenarios. Values are means of 25 replicate simulations.

of late-successional species aboveground carbon declined relative to the baseline climate and moderate emission scenarios (Fig. 5).

3.2. Effects of management on forest carbon balance

By 2030 under baseline climate, all three active treatments had higher NECB than the control. Before 2030, only the thin-only treatment had NECB comparable to the control. Under baseline climate, the thin-and-burn and burn-only treatments sustained NECB at a higher rate than the control, once respiration became more influential under the control scenario (Fig. 6a). The burn-only and thin-and-burn treatments caused an early century decrease in NECB relative to the control because of the initial fuel loads and the C flux to the atmosphere from burning (Fig. 6a).

Although the control NECB had the largest decline under baseline climate, control total ecosystem C was the largest of the four management scenarios because the only C losses were from wildfire (Fig. 7). Total ecosystem C decreased with increasing management intensity. As expected, the thin-and-burn treatment reduced TEC more than either thinning or burning alone (Fig. 7). The TEC decline in both thinning treatments was driven primarily by the harvest of Douglas-fir.

When we included projected climate in the simulations, the effects of treatment on NECB were still present, with treatments having higher NECB than the control after 2030 (Fig. 6). However, the influence of changing climate caused both increased interannual NECB variation and a late-century decline, relative to the baseline climate scenario. The influence of rising temperature and precipitation variability is evident in year 2060 under the CCSM moderate emission scenario and CNRM high emission scenarios (Fig. 6c and d). During 2060, under both scenarios, a warm, wet fall caused a substantial increase in respiration. The climate-driven declines in NECB resulted in reduced TEC across management scenarios (Table 1). While under the baseline and moderate emission scenarios TEC continued to increase throughout the simulation period, under the high emission scenarios TEC leveled-off at lower total carbon for all treatments (Table 1).

Under baseline climate, aboveground carbon of late-successional species continued to increase through the simulation period (Fig. 5). We found slightly lower ratios of late-successional to Douglas-fir aboveground biomass in simulations that included prescribed burning, which was expected given that these species are fire-intolerant (Table 2). However, projected climate under the high emission scenario caused a substantial decline in the rate of late-successional species aboveground carbon increase,

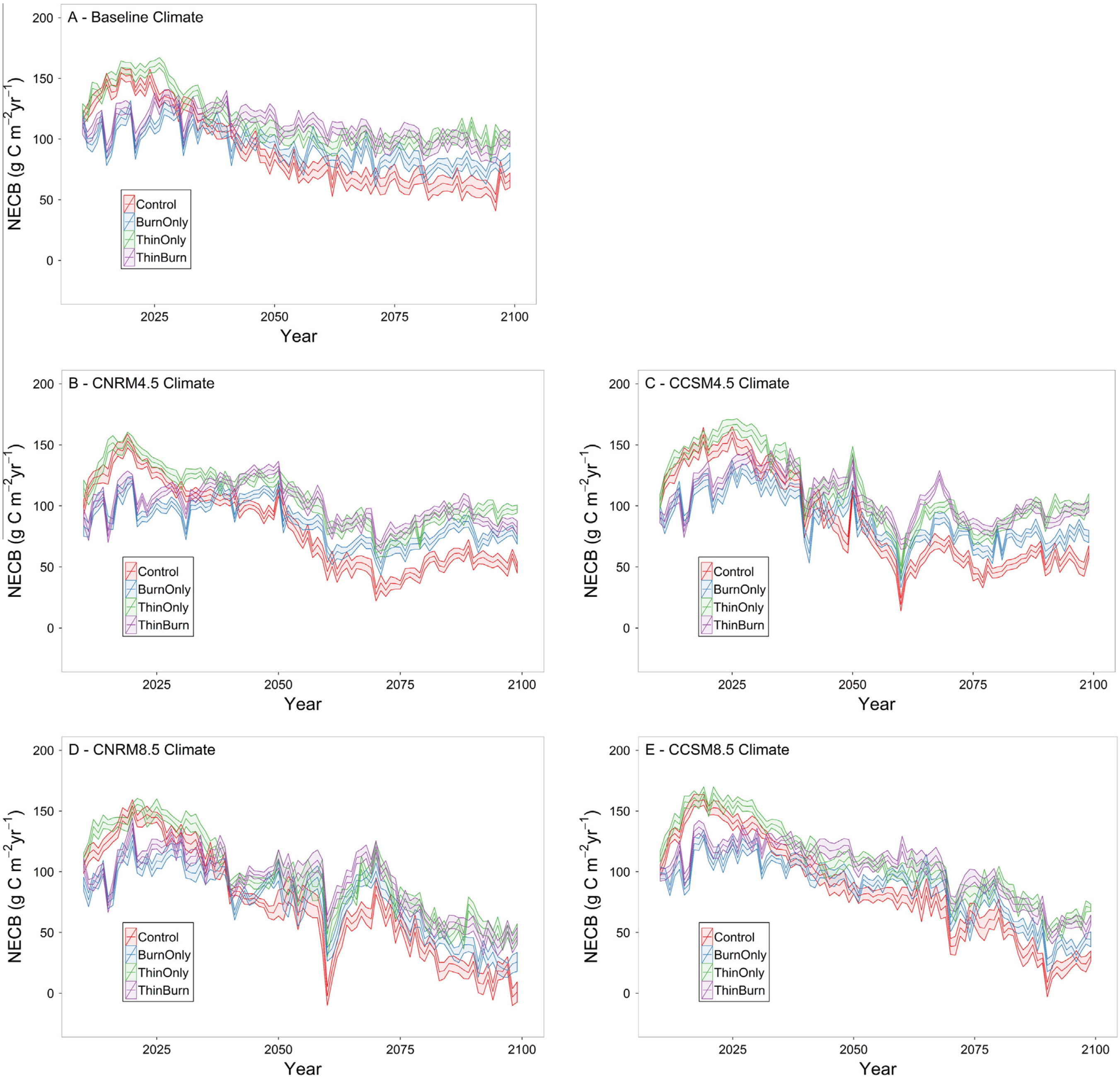

Fig. 6. Net Ecosystem Carbon Balance (NECB) of simulated forest management treatments (control, burn-only, thin-only, thin-and-burn) under baseline climate and climate projections from two general circulation models (CCSM and CNRM), driven by two emission scenarios (moderate (RCP 4.5) and high (RCP 8.5) emissions). Lines are the mean NECB and shading the 95% confidence intervals from 25 replicate simulations.

regardless of management, leading to a decline in the ratio of late successional species to Douglas-fir (Table 2).

3.3. Carbon tradeoffs of oak restoration

Across the installation, under baseline climate, we found that the thin-only and thin-and-burn treatments had a larger proportion of cells with higher year 2100 probability of oak occurrence than the control (K-S test: thin-only $D = 0.069$, $p < 0.001$; thin-and-burn $D = 0.0467$, $p < 0.001$; Fig. 8), because oak regeneration is light-limited. Although we expected a warmer, drier climate to favor oaks under the control scenario, we found no significant differences between the baseline climate control and the projected climate controls, regardless of emission scenario. We found that treatments had the same effect on the year 2100 probability of oak occurrence, regardless of climate scenario, emphasizing the dominant influence of treatments increasing light availability for oak regeneration. We compared the treatments with the control for each climate scenario and found significantly greater probability of occurrence for the thin-only and thin-and-burn than for the control and burn-only (Supplementary Table 6).

Within the intensive oak management area, the harvest prescription removed ~85% of overstory conifers and reduced conifer regeneration, resulting in a substantial increase in the probability of oak presence (Fig. 9). Late-century projections in the oak management area showed a 5- to 6-fold increase in oak aboveground carbon over the installation-wide thin-and-burn treatment (Supplemental Table 7). Intensive treatments within the 708 ha site

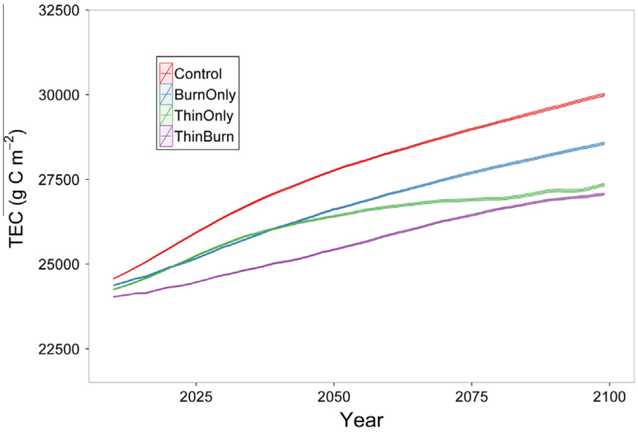

Fig. 7. Total Ecosystem Carbon (TEC) of simulated forest management treatments (control, burn-only, thin-only, thin-and-burn) under baseline climate. Lines are the mean TEC and shading the 95% confidence intervals from 25 replicate simulations.

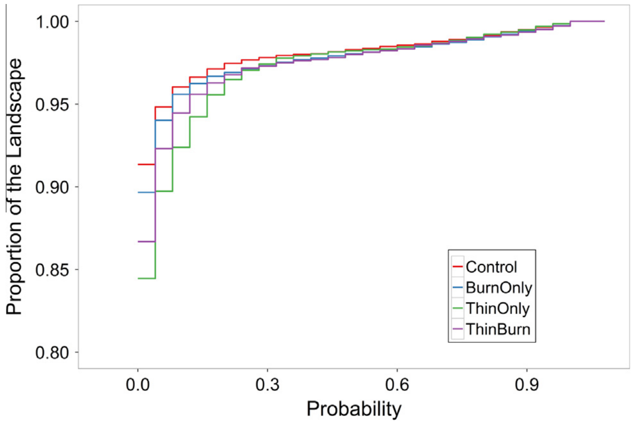

Fig. 8. Year 2100 empirical cumulative distribution of simulated forest management treatments (control, burn-only, thin-only, thin-and-burn) under baseline climate for the probability of oak existence. For each treatment $n = 7386$ grid cells.

decreased landscape-scale TEC between 355–380 g C m^{-2} (approximately 1.5%) compared to the thin-and-burn treatment, but a faster overall growth rate minimized the difference over time (Fig. 10).

4. Discussion

Given the uncertainty surrounding the sign and strength of the global forest C sink, Bellassen and Luyssaert (2014) have suggested that the lowest risk path forward is a strategy that increases the sequestration rate and retains C in forests. The risk associated with this approach is dependent upon forest response to projected climate. We found that climate under the moderate emission scenario caused insignificant changes in carbon stocks, fluxes, and species richness compared to baseline climate simulations (Figs. 3, 4 and 6). However, under the high emission scenario carbon stocks and fluxes declined (Fig. 6, Table 1) and the ecosystem was simplified as measured by increased frequency of low tree species richness grid cells (Fig. 3). These results partially supported our hypothesis that a warmer, drier climate would decrease productivity and favor drought-tolerant species. Increasing temperature and decreasing summer precipitation impacted the successional transition from Douglas-fir to late-successional western hemlock and western redcedar (Table 2), which contributed to productivity declines. However, the inability of more drought-tolerant species to compete for light precluded their establishment and growth at rates sufficient to compensate for the climate-driven declines of the drought-intolerant species.

Our findings are supported by empirical research highlighting the role of moisture limitation in successional development. Western hemlock is particularly susceptible to drought-induced mortality during regeneration (Christy and Mack, 1984), making the water-holding capacity of the soil and the amount of incoming solar radiation important factors influencing its establishment (Dodson et al., 2014; Gray and Spies, 1997). Although western hemlock is often the dominant species in infrequent fire systems, Douglas-fir may dominate when soil moisture is limiting (Franklin and Hemstrom, 1981). Given the moisture controls on late-successional species regeneration and the low water-holding capacity of the prairie soils at JBLM, these areas are likely to be the first to experience a shift to a Douglas-fir climax community. This transition would likely result in a less productive forest because of climate and shade limitations on Douglas-fir regeneration (Van Tuyl et al., 2005).

Management effects on carbon stocks were consistent across climate scenarios, with stocks decreasing as management intensity increased (Fig. 7, Table 1). As we hypothesized, treatments that

Table 1
Total ecosystem carbon (g m^{-2}) of simulated forest management treatments (control, burn-only, thin-only, thin-and-burn) under baseline climate and climate projections from two general circulation models (CCSM and CNRM), driven by two emission scenarios (moderate (RCP 4.5) and high (RCP 8.5) emissions) in year 2100. Values are mean and 95% confidence intervals for total ecosystem carbon from 25 replicate simulations.

Treatment	Baseline	CNRM4.5	CCSM4.5	CNRM8.5	CCSM8.5
Control	30000 ± 19	28840 ± 13	29330 ± 24	28337 ± 18	28980 ± 18
Burn-only	28566 ± 17	27610 ± 17	27948 ± 18	27131 ± 13	27676 ± 19
Thin-only	27349 ± 17	26497 ± 16	26806 ± 14	25686 ± 19	26263 ± 12
Thin-and-Burn	27065 ± 14	26179 ± 15	26577 ± 21	25661 ± 14	26237 ± 16

Table 2
Ratio of late successional species (LS; western hemlock and western redcedar) to Douglas-fir (DF) aboveground carbon stocks by treatment (control, burn-only, thin-only, thin-and-burn) under baseline climate and projected climate from two general circulation models (CCSM and CNRM) driven by moderate (RCP 4.5) and high (RCP 8.5) emission scenarios in year 2100. Ratios are of mean aboveground carbon values from 25 replicate simulations.

Treatment	Baseline	CNRM4.5	CCSM4.5	CNRM8.5	CCSM8.5
Control	0.32	0.32	0.32	0.26	0.26
Burn-only	0.28	0.29	0.29	0.24	0.24
Thin-only	0.36	0.37	0.37	0.30	0.30
Thin-and-Burn	0.31	0.31	0.31	0.26	0.26

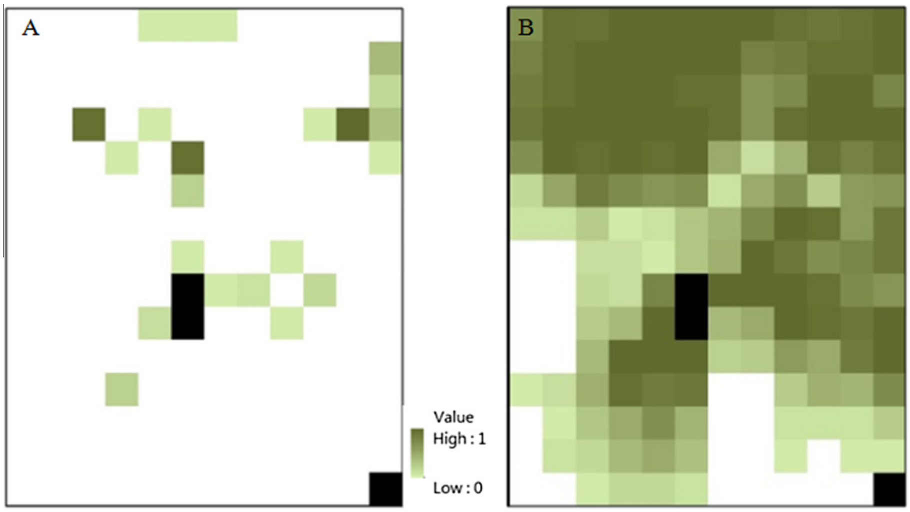

Fig. 9. Year 2100 oak probability surface for the 708 ha oak restoration area for the thin-and-burn (A) and the oak restoration treatment that included more intensive thinning and burning (B) under baseline climate. Darker green pixels have a higher probability of oak occurrence. Black areas not managed by Joint Base Lewis–McChord and were excluded. For each treatment $n = 25$ replicate simulations. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

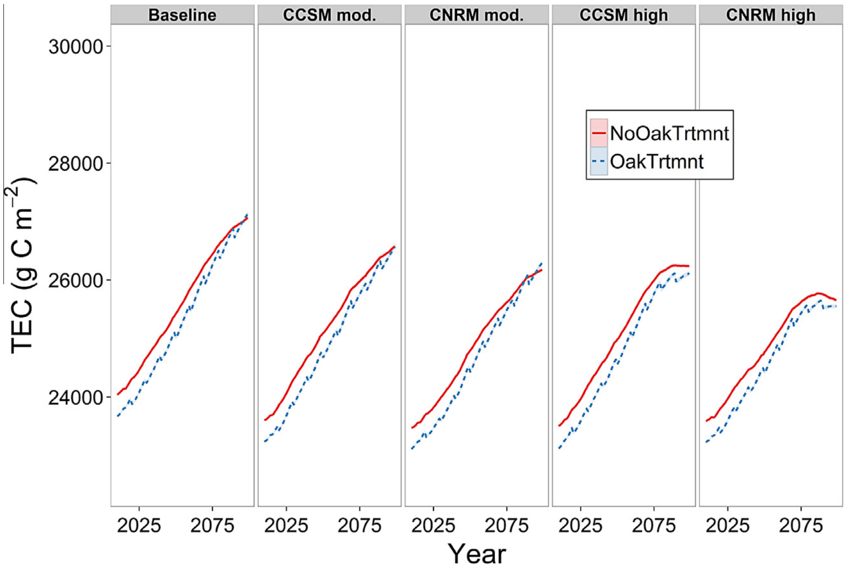

Fig. 10. Total ecosystem carbon (TEC) of treatment simulations (thin-and-burn, intensive oak restoration coupled with thin-and-burn) under baseline climate and climate projects from climate models (CCSM and CNRM), driven by two emission scenarios (moderate (RCP4.5) and high (RCP8.5) emissions). Lines are mean TEC and shading the 95% confidence intervals from 25 replicate simulations.

reduced competition increased NECB relative to the control over the long-term (Fig. 6). However, the increase was insufficient to counteract the climate-driven NECB decline under the high emission scenario (Fig. 6). Our results are similar to those of previous studies in the Pacific Northwest (Hudiburg et al., 2009; Mitchell et al., 2009) where excluding management yields the largest forest carbon stock (Fig. 7, Table 1). Thus, if managers implement treatments to meet some other objective, there will be carbon tradeoffs.

At Joint Base Lewis-McChord, the objective of habitat provision for the western gray squirrel exemplifies one case of carbon tradeoffs. The thin-only and thin-and-burn treatments did increase the probability of oak, the species most associated with squirrel use, over the control (Supplemental Table 6), but at a carbon cost of 2651 g m^{-2} for the thin-only and 2935 g m^{-2} for the thin-and-burn by 2100 under baseline climate. The magnitude of the carbon cost was consistent across climate scenarios (Table 1). When we evaluated the effects of the more intensive oak restoration treatment we found that, relative to the thin-and-burn, both the probability of oak presence and the amount of oak biomass increased significantly and the effect of the oak restoration treatment on landscape-scale total ecosystem carbon was minimal by late-century (Fig. 10). These results suggest that the effects of intensive management on carbon storage can be minimized when the treatments only influence a small fraction of the landscape.

We did not include increasing atmospheric CO_2 in our simulations. Higher CO_2 generally stimulates photosynthesis while reducing stomatal conductance and transpiration, thereby increasing water use efficiency (Keenan et al., 2013; Norby et al., 2005) except in cases of severe water limitation when stomatal conductance is reduced regardless of CO_2 level. However, over time nitrogen limitation reduces the CO_2 fertilization effect (Norby et al., 2010). Thus, while not including the effects of rising atmospheric CO_2 may have resulted in an underestimate of NECB during late-century under the high emission scenario, increased growth is unlikely to be sustained because nitrogen inputs in this system are relatively small. Another potential limitation of our study is that we held wildfire probability constant throughout the simulations and did not include insect and pathogen disturbance. Littell et al. (2010) found that the area burned by wildfire in Washington state could increase threefold by the late-21st century. Yet for the Puget lowlands, they concluded that fire data were insufficient to adequately model the change in area burned over time. If area burned does increase at JBLM, we would expect a transition toward early-successional forest types and a potential opportunity for increased establishment of more drought-tolerant species. Insect and pathogen disturbances could be exacerbated by a warmer, drier climate because drought-stressed individuals can be more susceptible to attack (Sturrock et al., 2011). Schmitz and Gibson (1996) found that Douglas-fir beetle outbreaks were coincident with periods of drought. Increased frequency of insect outbreaks with changing climate could drive substantial declines in NECB. Finally, we did not account for the effects of competition from the invasive shrub Scotch broom (*Cytisus scoparius* L.), which occurs on approximately 5% of the study area. Scotch broom can form dense monocultures and reduce Douglas-fir establishment (Peterson and Prasad, 1998), which could negatively affect post-disturbance regeneration, causing declines in NECB. Our results should also be considered in the context of only including projections from two GCMs. While projections from both models included multiple ensemble members which helps address uncertainty associated with initial conditions, only including projections from two GCMs does not account for uncertainty due to model structure (Rupp et al., 2013).

Unlike other ecosystems where extreme drought events are already causing community composition changes (Allen et al., 2015), relatively moderate climatic changes through mid-century are unlikely to cause substantial changes in forest composition or carbon dynamics at JBLM. However, by late-century under the high emission scenario, the increase in evaporative stress from warmer, drier summers may shift the successional climax from a mesic conifer to a Douglas-fir community, especially on the well-drained prairie soils. Drier conditions and Douglas-fir's inability to regenerate in its own shade could slow productivity, favoring a landscape more similar to historical conditions. In the context of future climate uncertainty and the current need to provide habitat for listed species, a strategy that produces heterogeneous ecological conditions presents the best opportunity for building a resilient ecosystem.

Acknowledgements

Funding for this research was provided by the US Department of Defense's Strategic Environmental Research and Development Program (SERDP, project RC-2118). We thank the JBLM field crew for assistance with data collection and Jeff Foster for providing data and facilitating access to field locations. We also thank M. Kaye and K. Shea for providing feedback on an earlier version of this manuscript.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.12.015.

References

Agee, J.K., 1996. Achieving conservation biology objectives with fire in the Pacific Northwest. Weed Technol. 10, 417–421.

Agee, J.K., Skinner, C.N., 2005. Basic principles of forest fuel reduction treatments. For. Ecol. Manage. 211, 83–96.

Allen, C.D., Breshears, D.D., McDowell, N.G., 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6 (8), 129.

Bellassen, V., Luyssaert, S., 2014. Managing forests in uncertain times. Nature 506, 153–155.

Boucher-Lalonde, V., Morin, A., Currie, D.J., 2012. How are tree species distributed in climatic space? A simple and general pattern. Glob. Ecol. Biogeogr. 21, 1157–1166.

Bradshaw, L., McCormick, E., 2000. FireFamily Plus user's guide, Version 2.0. Gen. Tech. Rep. RMRS-GTR-67WWW. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Bréda, N., Granier, A., Aussenack, G., 1994. Effects of thinning on soil and tree water relations, transpiration and growth in an oak forest (*Quercus petraea* (Matt.) Liebl.). Tree Physiol. 15, 295–306.

Brown, J.K., 1974. Handbook for inventorying downed woody material. USDA Forest Service General Technical Report INT-16. Ogden, UT.

Burton, P.J., Cumming, S.G., 1995. Potential effects of climatic change on some western Canadian forests, based on phenological enhancements to a patch model of forest succession. Water Air Soil Pollut. 82, 401–414.

Canadell, J.G., Raupach, M.R., 2008. Managing forests for climate change mitigation. Science 320, 1456–1457.

Carey, A.B., Thysell, D.R., Brodie, A.W., 1999. The forest ecosystem study: background, rationale, implementation, baseline conditions, and silvicultural assessment. USFS PNW-GTR-457. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.

Chmura, D.J., Anderson, P.D., Howe, G.T., Harrington, C.A., Halofsky, J.E., Peterson, D. L., Shaw, D.C., St.Clair, J.B., 2011. Forest responses to climate change in the northwestern United States: ecophysical foundations for adaptive management. For. Ecol. Manage. 261, 1121–1142.

Christy, E.J., Mack, R.N., 1984. Variation in demography of juvenile *Tsuga heterophylla* across the substratum mosaic. J. Ecol. 72, 75–91.

Crawford, R., Hall, H., 1997. Changes in the south Puget Prairie Landscape. In: Dunn, P., Ewing, K. (Eds.), Ecology and Conservation of the South Puget Sound Prairie Landscape. The Nature Conservancy, Seattle, Washington, pp. 11–15.

Dodson, E.K., Burton, J.I., Puettmann, K.J., 2014. Multiscale controls on natural regeneration dynamics after partial overstory removal in Douglas-fir forests in western Oregon, USA. For. Sci. 60, 1–8.

Doehlert, D.C., Walker, R.B., 1981. Photosynthesis and photorespiration in Douglas-fir as influenced by irradiance, CO_2 concentration and temperature. For. Sci. 27, 641–650.

ESRI, 2012. ArcMap desktop. Release 10.1. Environmental Systems Research Institute, Redlands, CA, USA.

Finkral, A.J., Evans, A.M., 2008. The effects of a thinning treatment on carbon stocks in an Arizona ponderos pine forest. For. Ecol. Manage. 255, 2743–2750.

Foster, J.R., Shaff, S.E., 2003. Forest colonization of Puget Lowland grasslands at Fort Lewis, Washington. Northwest Sci. 77, 283–296.

Franklin, J.F., Hemstrom, M.A., 1981. Aspects of succession in the coniferous forests of the Pacific Northwest. In: West, D.C., Shugart, H.H., Botkin, D.B. (Eds.), Forest Succession: Concepts and Application. Springer-Verlag, New York, pp. 212–229.

Franklin, J.F., Waring, R.H., 1980. Distinctive Features of the Northwestern Coniferous Forest: Development, Structure, and Function. Oregon State University Press, Corvallis, Oregon, pp. 59–86.

Gray, A.N., Spies, T.A., 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. Ecology 78, 2458–2473.

Gray, A.N., Whittier, T.R., 2014. Carbon stocks and changes on Pacific Northwest national forests and the role of disturbance, management and growth. For. Ecol. Manage. 328, 167–178.

Griffin, S., 2007. Forest Management and Stump-to-forest Gate Chain-of-custody Certification Evaluation Report for the Forestlands Managed by the Forestry Branch, Fort Lewis Military Installation, Department of Defense. Scientific Certification Systems, Emeryville, CA.

Gustafson, E.J., Shifley, S.R., Mladenoff, D.J., Nimerfro, K.K., He, H.S., 2000. Spatial simulation of forest succession and timber harvesting using LANDIS. Can. J. For. Res. 30, 32–43.

Hawkins, B.A., 2001. Ecology's oldest pattern? TRENDS Ecol. Evol. 16, 470.

Heath, B., Sollins, P., Perry, D.A., Cromack Jr., K., 1987. Asymbiotic nitrogen fixation in litter from Pacific Northwest forests. Can. J. For. Res. 18, 68–74.

Hijmans, R.J., 2014. Raster: Geographic data analysis and modeling. Version 2.2-12. <http://CRAN.R-project.org/package=raster>.

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

Hudiburg, T.W., Luyssaert, S., Thorton, P.E., Law, B.E., 2013. Interactive effects of environmental change and management strategies on regional forest carbon emissions. Environ. Sci. Technol. 47, 13132–13140.

Hurteau, M.D., Liang, S., Martin, K.L., North, M.P. Koch, G.W., Hungate, B.A., in press. Restoring forest structure and process stabilizes forest carbon in wildfire-prone southwestern ponderosa pine forests. Eco. App., http://dx.doi.org/10.1890/15-0337.1.

Jenkins, J.C., Chojnacky, D.C., Heath, L.S., Birdsey, R.A., 2003. National-scale biomass estimators for United States tree species. For. Sci. 1, 12–35.

Keenan, T.F., Hollinger, D.Y., Bohrer, G., Dragoni, D., Munger, J.W., Schmid, H.P., Richardson, A.D., 2013. Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise. Nature 499, 324–328.

Keith, H., Macke, B.G., Lindenmayer, D.B., 2009. Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. Proc. Nat. Acad. Sci. 106, 11635–11640.

Kerhoulas, L.P., Kolb, T.E., Hurteau, M.D., Koch, G.W., 2013. Managing climate change adaptation in forests: a case study from the U.S. Southwest. J. Appl. Ecol. 50, 1311–1320.

LANDFIRE, 2013. LANDFIRE Mean Fire Return Interval layer. U.S. Department of Interior, Geological Survey. <http://landfire.cr.usgs.gov/viewer/> Accessed 1 October 2014.

Latham, P., Tappeiner, J., 2002. Response of old-growth conifers to reduction in stand density in western Oregon forests. Tree Physiol. 22, 137–146.

LEMMA. Landscape Ecology, Modeling, Mapping & Analysis, 2006. <http://lemma.forestry.oregonstate.edu/data/structure-maps>. Accessed 4 April 2013.

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

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

Loudermilk, E.L., Scheller, R.M., Weisberg, P.J., Yang, J., Dilts, T.E., Karam, S.L., Skinner, C., 2013. Carbon dynamics in the future forest: the importance of long-term successional legacy and climate-fire interaction. Glob. Change Biol. 19, 3502–3515.

Malmsheimer, R.W., Bowyer, J.L., Fried, J.S., Gee, E., Izlar, R.L., Miner, R.A., Munn, I.A., Oneil, E., Stewart, W.C., 2011. Managing forests because carbon matters: integrating energy, products, and land management policy. J. For. 109, S7–S51.

Martin, K.M., Hurteau, M.D., Hungate, B.A., Koch, G.W., North, M.P., 2015. Carbon tradeoffs of restoration and provision of endangered species habitat in a fire-maintained forest. Ecosystems 18, 76–88.

Metherell, A.K., Harding, L.A., Cole, C.V., Parton, W.J., 1993. CENTURY soil organic matter model environment technical documentation. Agroecosystem Version 4.0. Fort Collins, CO:USDA-ARS.

Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and the forests of the future: managing in the face of uncertainty. Ecol. Appl. 17, 2145–2151.

Mitchell, S.R., Harmon, M.E., OConnell, K.E.B., 2009. Forest fuel reduction alters fire severity and long-term storage in three Pacific Northwest ecosystems. Ecol. Appl. 19 (30), 643–655.

Moss, R., Babiker, M., Brinkman, S., Calvo, E., Carter, T., Edmonds, J., Elgizouli, I., Emori, S., Erda, L., Hibbard, K., Jones, R., Kainuma, M., Kelleher, J., Lamarque, J.F., Manning, M., Matthews, B., Meehl, J., Meyer, L., Mitchell, J., Nakicenovic, N., O'Neill, B., Pichs, R., Riahi, K., Rose, S., Runci, P., Stouffer, R., van Vuuren, D., Weyant, J., Wilbanks, T., van Ypersele, J.P., Zurek, M., 2008. Towards new scenarios for analysis of emissions, climate change, impacts, and response strategies. Technical Summary. Intergovernmental Panel on Climate Change, Geneva 25 pp.

Mote, P.W., Abatzoglou, J.T., Kunkel, K.E., 2013. Climate. In: Dalton, M.M., Mote, P. W., Snover, A.K. (Eds.), Climate Change in the Northwest: Implications for our Landscapes, Waters, and Communities. Island Press, Washington, D.C., pp. 25–40.

NADP. 2012. National Atmospheric Deposition Program, National Trends Network 2012 annual and seasonal data summary for site WA21 Part 1: summary of sample validity and completeness criteria. NADP Program Office, Illinois State Water Survey, Champaign, IL. nadp.sws.uiuc.edu/NTN/ntnData.aspx. Accessed 1 APR 2014.

NCDC, 2013. National Oceanic and Atmospheric Administration, National Climatic Data Center. www.ncdc.noaa.gov. Accessed 1 May 2013.

Norby, R.J., DeLucia, E.H., Glelen, B., Calfapietra, C., Giardina, C.P., King, J.S., Ledford, J., McCarthy, H.R., Moore, D.J.P., Ceulemans, R., DeAngelis, P., Finzi, A.C., Schlesinger, W.H., Oren, R., 2005. Forest response to elevated CO_2 is conserved across a broad range of productivity. Proc. Nat. Acad. Sci. 102, 18052–18056.

Norby, R.J., Warren, J.M., Iversen, C.M., Medlyn, B.E., McMurtrie, R.E., 2010. CO_2 enhancement of forest productivity constrained by limited nitrogen availability. Proc. Nat. Acad. Sci. 107, 19368–19373.

NRCS, 2013. Web Soil Survey. U.S. Department of Agriculture, Natural Resources Conservation Service. <http://websoilsurvey.nrcs.usda.gov>. Accessed 1 October 2013.

Ohmann, J.L., Gregory, M.L., 2002. Predictive mapping of forest composition and structure with direct gradient analysis and nearest-neighbor imputation in coastal Oregon, U.S.A. Can. J. For. Res. 32, 725–741.

Parton, W.J., Scurlock, J.M.O., Ojima, D.S., Gilmanov, T.G., Scholes, R.J., Schimel, D.S., Kirchener, T., Menaut, J.-C., Seastedt, T., Moya, E.G., Kamnalrut, A., Kinyamario, J. I., 1993. Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. Glob Biogeo Cycles. 7, 785–803.

Peterson, D.J., Prasad, R., 1998. The biology of Canadian weeds. 109. *Cytisus scoparius* (L.) Link. Can. J. Plant Sci. 78, 497–504.

R Core Team, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. <http://www.R-project.org/>.

Rehfeldt, G.E., Crookston, N.L., Warwell, M.V., Evans, J.S., 2006. Empirical analyses of plant-climate relationships for the western United States. Int. J. Plant Sci. 167, 1123–1150.

Roberts, S.D., Harrington, C.A., 2008. Individual tree growth response to variable-density thinning in coastal Pacific Northwest forests. For. Ecol. Manage. 255, 2771–2781.

Rupp, D.E., Abatzoglou, J.T., Hegewisch, K.C., Mote, P.W., 2013. Evaluation of CMIP5 20th century climate simulations for the Pacific Northwest USA. J. Geophys. Res.: Atmos. 118, 10884–10906.

Scheller, R.M., Domingo, J.B., Sturtevant, B.R., Williams, J.S., Rudy, A., Gustafson, E.J., Mladenoff, D.J., 2007. Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. Ecol. Model. 201, 409–419.

Scheller, R.M., Hua, D., Bolstad, P.V., Birdsey, R.A., Mladenoff, D.J., 2011. The effects of forest harvest intensity in combination with wind disturbance on carbon dynamics in Lake States Mesic Forests. Ecol. Model. 222, 144–153.

Scheller, R.M., Mladenoff, D.J., 2004. A forest growth and biomass module for a landscape simulation model, LANDIS: design, validation, and application. Ecol. Model. 180, 211–229.

Schmitz, R.F., Gibson, K.E., 1996. Douglas-fir beetle. Forest Insect & Disease Leaflet 5 U.S. Department of Agriculture. Washington, D.C.

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

Sturrock, R.N., Frankel, S.J., Brown, A.V., Hennon, P.E., Kliejunas, J.T., Lewis, K.J., Worrall, J.J., Woods, A.J., 2011. Climate change and forest diseases. Plant Pathol. 60, 133–149.

Sturtevant, B.R., Scheller, R.M., Miranda, B.R., Shinneman, D., Syphard, A., 2009. Simulating dynamic and mixed-severity fire regimes: a process-based fire extension for LANDIS-II. Ecol. Model. 220, 3380–3393.

Syphard, A.D., Scheller, R.M., Ward, B.C., Spencer, W.D., Strittholt, J.R., 2011. Simulating landscape-scale effects of fuels treatments in the Sierra Nevada, CA, USA. Int. J. Wildland Fire 20, 364–383.

Thrasher, B., Xiong, J., Wang, W., Melton, F., Michaelis, A., Nemani, R., 2013. New downscaled climate projections suitable for resource management in the U.S. Eos. Trans. Am. Geophys. Union 94, 321–323.

Turner, M.G., Donato, D.C., Romme, W.H., 2013. Consequences of spatial heterogeneity for ecosystem services in changing forest landscapes: priorities for future research. Landsc. Ecol. 28, 1081–1097.

Urban, D.L., Harmon, M.E., Halpern, C.B., 1993. Potential response of Pacific Northwestern forests to climatic change, effects of stand age and initial composition. Clim. Change 23, 247–266.

Van Tuyl, S., Law, B.E., Turner, D.P., Gitelman, A.I., 2005. Variability in net primary production and carbon storage in biomass across Oregon forests—an assessment integrating data from forest inventories, intensive sites, and remote sensing. For. Ecol. Manage. 209, 273–291.

Van Wagner, C.E., Stocks, B.J., Lawson, B.D., Alexander, M.E., Lynham, T.J., McAlpine, R.S., 1992. Development and Structure of the Canadian forest fire Behavior Prediction System. Fire Danger Group, Forestry Canada, Ottawa, Ontario.

Washington Department of Fish and Wildlife. 2013. Threatened and endangered wildlife in Washington: 2012 annual report. Listing and Recovery Section, Wildlife Program, Washington Department of Fish and Wildlife, Olympia, WA. 251 p.

Wickham, H., 2009. Ggplot2: Elegant Graphics for Data Analysis. Springer, New York.

Wickham, H., 2011. The split-apply-combine strategy for data analysis. J. Statist. Software 40, 1–29.

Zulauf, A.S., 1979. Soil survey of Pierce County area, Washington. U.S. Department of Agriculture, Natural Resources Conservation Service.