

Estimating the vulnerability of fifteen tree species under changing climate in Northwest North America

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ABSTRACT

In the Pacific northwestern (PNW) region of North America, climatic conditions have significantly warmed since a predominantly cool phase of the Pacific North American circulation patterns between 1950 and 1975. What are the implications of this shift in climate for the vulnerability of native tree species? To address this question, we combined mechanistic and statistical models to assess where a variety of native tree species might be more vulnerable within their recorded ranges and where they might potentially migrate. For long-lived species that are well adapted to compete, seasonal differences in photosynthesis and water use offer insights helpful in predicting their distributions. To evaluate the general response of conifers to climatic variation across the region, we previously applied a process-based model (3-PG), to simulate the growth and maximum leaf area index that Douglas-fir could attain within recognized forested areas. We then constructed automated decision tree models to define and map the ecological distributions of 15 tree species based on differences in how photosynthesis was constrained by drought, daytime temperatures, high evaporative demand, and the frequency of frost. For the baseline climate period (1950–1975), the decision tree models predicted presence and absence of each species at ~23,000 observations with an average accuracy of 81%, with an average kappa statistic of 0.74. In this paper the same models were run annually for the period between 1976 and 2006 for each species, and the areas defined as remaining suitable or becoming vulnerable to disturbance were identified based on whether more or less than half of the years fell within the originally defined limits. Based on these criteria, 70% of the species recorded ranges remained suitable, with 30% deemed vulnerable. Results varied notably by species with western red cedar and western hemlock remaining highly adapted, with potential for range expansion in area of up to 50% relative to the baseline period. In contrast, ponderosa pine, lodgepole pine, grand, and noble fir were classified as vulnerable with potential net contractions in their ranges. The analysis was extended through the rest of the 21st century using climatic projections from the Canadian global circulation model with a high fossil fuel emission scenario (A2) and compared to other previously published species range predictions.

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1. Introduction

The impact of increased climate variability on forest vegetation may modify ecosystem processes in a number of ways. Gradual increases in temperature, changes in rainfall patterns, or modification in solar radiation will likely impact growth, regeneration and natural rates of mortality, while more abrupt changes in climate may lead to extensive fires, killing frosts, droughts, and outbreaks of insects and diseases (Chapin et al., 2010). Within the Pacific Northwest (PNW) of North America, the last three decades have seen documented changes in the spatial variation of mean annual temperature and rainfall, with temperatures slightly cooler across

the western U.S. and more than 1.5 °C warmer in much of western Canada in the period 1976–2006 compared to 1950–1975. At the same time, the PNW region has seen extensive outbreaks of fire and insects attributed to these changes (Westerling et al., 2006; Raffa et al., 2008). In some places, tree species appear to be expanding their ranges, while elsewhere, contraction is occurring. This suggests that a resorting of the tree flora is underway as the suitability of the habitat changes, affecting a species' competitiveness and susceptibility to various biological agents. Some of these concepts are incorporated in more formal language by Chapin et al. (2010).

With climatic conditions predicted to continue to change over the rest of the century, conservationist and managers would like to know where species are likely to remain within, or expand from, their current distributions, and conversely, situations where species are likely to become vulnerable. Although coniferous tree

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species differ in their tolerance to frost, drought, humidity deficits and temperature, physiologically, they share much in common. We propose in this paper that knowledge of how one widely distributed species responds to climate can serve as a reference against which to measure and predict the current and future distributions of other, closely related species.

We previously combined the power and simplicity of climate niche species models with the understanding that is provided from mechanistic ones with some success in the Pacific Northwest Region of North America (Coops et al., 2009). This hybrid approach limits the requirement for detailed physiological knowledge to one widely distributed species, Douglas-fir (*Pseudotsuga menziesii*). Provided monthly climatic data, we predicted with a process-based growth model the nearly 10-fold range in maximum canopy leaf area index recorded on forested sites within the region (Runyon et al., 1994; Waring et al., 2005). Seasonal variation in LAI sets limits on light absorbance by photosynthetic pigments in leaves and also constrains the rate at which water can be withdrawn from the rooting zone.

With geographically explicit knowledge of the relative importance of climatic constraints on Douglas-fir photosynthesis, the climatic envelopes in which other species fell were evaluated and interpreted using automated decision tree analyses (De'ath, 2002). For a subalpine species such as lodgepole pine (*Pinus contorta*), its presence or absence on thousands of observations was accurately predicted (68%) with sequential choices related to thresholds based on a suite of growth modifiers (Coops and Waring, 2010). Similar analyses for more than a dozen other species gave good results in predicting presence and absence on 22,771 observations with an average accuracy of 81% (Coops et al., in press). As one might expect, a subalpine species tolerates more frost in the spring, occupies cooler sites in the summer, and experiences less evaporative demand and drought than does the more temperate Douglas-fir. If there is less spring frost, growth conditions may improve more for competing species of trees, insects, and pathogens than for lodgepole pine.

In this paper we expand the hybrid modeling approach to: (a) evaluate the implications of climatic variations over the last three decades in comparison to earlier baseline conditions (1950–1975) for fifteen native tree species, (b) identify the regions within a species range that no longer appear suitable to the species, and (c) note places where the potential for migration is high. In subsequent sections we assess recent climatic variation across the region, describe the process-based model, and the data required to drive it to simulate baseline and transitional extensions and contractions. To put these current movements in perspective for the future, we then use the Canadian general circulation model (CGCM3) to predict climatic conditions through the rest of the century under a high CO₂ emission scenario and examine future species movements.

2. Data and methods

2.1. Major vegetation zones within the study area

The Pacific Northwest Region, which extends from northern California to British Columbia and inland to western Montana, includes portions of four broad (level 1) ecoregions (http://www.epa.gov/wed/pages/ecoregions/na.eco.htm#Level_1) (Fig. 1). The most productive component is represented by the Marine West Coast Forests (MF), which extends from Alaska in a progressively narrowing band to San Francisco. Western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*) are present throughout most of this fog-belt defined ecoregion, with Douglas-fir, coast redwood (*Sequoia sempervirens*) and western red cedar (*Thuja plicata*) locally abundant. The Northwest Forested Moun-

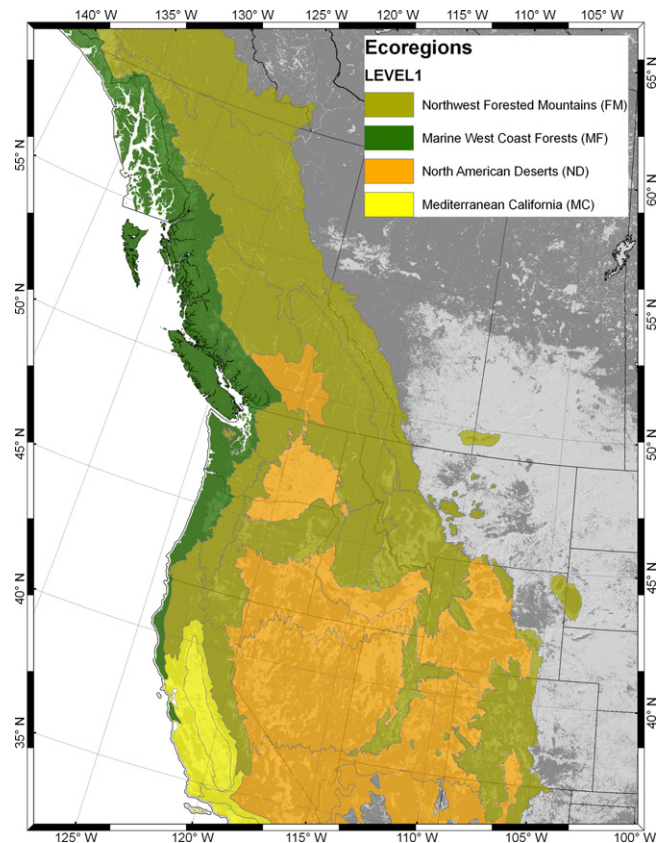


Fig. 1. The Pacific Northwest Region, which extends southward to ~38°N Latitude, include parts of four broadly defined Environmental Protection Agency (EPA) Level I ecoregions. Forested and scrub area as defined from MODIS landcover products are shown in dark gray.

tains (FM) is the second most productive ecoregion in this study. Douglas-fir and western hemlock are frequently abundant in mixtures with many species of pine and true firs. At higher elevations and latitudes, lodgepole pine, mountain hemlock (*Tsuga mertensiana*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*) are characteristic species. On drier sites, ponderosa pine (*Pinus ponderosa*) and incense cedar (*Calocedrus decurrens*) are usually present. Ponderosa pine extends its range into the North American Desert (ND) ecoregion, with further reductions in productivity. In Oregon and northern California, in the rain shadow of the Cascade Mountains, open pine forests grade into western juniper (*Juniperus occidentalis*) woodlands and finally to sagebrush steppe (Franklin and Dyrness, 1973; Runyon et al., 1994). Beyond the influence of summer intrusions of maritime air masses, a small component of the Mediterranean California (MC) ecoregion is included within the PNW region where oaks (*Quercus*), pines and Douglas-fir occur in a transition to grasslands and chaparral (Waring and Major, 1964).

2.2. Historic variation in regional climate

Historically, climatic variation in the Pacific Northwest has been linked with shifts in the warm and cool phases of the Pacific Decadal Oscillations (PDO) in combination with the El Niño Southern Oscillation (ENSO). When both the PDO and ENSO enter a positive phase, winters are much drier and warmer than normal, and summers somewhat more drought-prone. When negative phases of the two oscillations correspond, winters are much cooler and wetter than normal, resulting in higher than average snowpack, more runoff, and a reduced chance of summer drought and late season fires

(Mote et al., 2003). Using correlations with tree rings, Trouet and Taylor (2009) calibrated the combined effects of ENSO and PDO phases on the Pacific North American (PNA) circulation patterns back to 1725, as did Gedalof and Smith (2001) for ENSO phases to 1650.

The PDO was in an extended cool phase from about 1890 to 1925 and for the period from 1945 to 1976. From 1925 to 1946 and from 1977 to 1998, a warm phase of the PDO dominated. Since 1650, there have been 11 major phase shifts in the PDO, each averaging 23 years (Gedalof and Smith, 2001). Recently, the PDO has shifted back and forth from one phase to another, more typical of patterns in the 19th century (Mantua, 2001). Trouet and Taylor (2009) estimated the combined effects of PDO and ENSO on the Pacific North American circulation pattern to be more variable during the 1960s than the PDO record would indicate, but noted that the cool (negative) phase of the PNA extended unbroken from the early 1950s back to 1941. As a result, annual temperatures averaged across the PNW region are steadily increasing by 0.8 °C for the decadal period 1900–2000 (Mote et al., 2003), and are projected to increase by 3.0 °C or more (compared with 1970–1999 values) by the end of the century (Mote and Salathe, 2009). Similarly, annual precipitation averaged across PNW has also increased relative to 1930 values (Mote et al., 2003).

Based on this past evidence and scenario modeling, we conclude that over the past half century the Pacific Northwest has already experienced significant climate variability, especially at the higher latitudes creating conditions that may have altered the vulnerability of native species in much of their currently recorded ranges.

2.3. Climate data, current and projected

Long-term weather observations for stations throughout the region were interpolated spatially using CLIMATE-WNA (<http://www.genetics.forestry.ubc.ca/cfcg/ClimateWNA/ClimateWNA.html>), which includes a bilinear interpolation of the PRISM (Parameter-elevation Regressions on Independent Slopes Model) records, along with adjustments in temperature for mountainous terrain (see Hamann and Wang, 2005). A 90 m-Digital Elevation Model (DEM), obtained from the Shuttle Radar Topography Mission (SRTM), was expanded to 1 km to provide the required elevation data at the same resolution as the climatic data.

Mean monthly atmospheric vapor pressure deficits (VPD) for daylight periods were estimated by assuming that the water vapor concentrations present throughout the day would be equivalent to that held at the mean minimum temperature (Kimball et al., 1997). The maximum VPD was calculated each month as the difference between the saturated vapor pressure at the mean maximum and minimum temperatures. Mean daytime VPD was calculated as two thirds of the maximum value to provide an average daily response rather than one based on the daily extremes (Waring, 2000). The number of days per month with subfreezing temperatures (≤ 2 °C) was estimated from empirical equations with mean monthly minimum temperature (Coops et al., 1998).

Monthly estimates of total incoming short-wave radiation were calculated using a modeling approach detailed by Coops et al. (2000) where the potential radiation reaching any spot is first calculated and then reduced, based on the clarity (transmissivity) of the atmosphere (Goldberg et al., 1979; Bristow and Campbell, 1984; Hungerford et al., 1989). Changes in the atmospheric transmissivity are mirrored in temperature extremes. With a DEM, we adjusted for differences in slope, aspect, and elevation as well as for variations in the fraction of diffuse and direct solar beam radiation (Garnier and Ohmura, 1968; Hungerford et al., 1989). The modeling approach, when compared with direct measurements, predicted both the direct and diffuse components of mean monthly incom-

ing radiation with 93–99% accuracy on flat surfaces, and on sloping terrain accounted for >87% of the observed variation with a mean error $< 2 \text{ MJ m}^{-2} \text{ day}^{-1}$ (Coops et al., 2000).

Most climate models predict that the Pacific Northwest region as a whole will become progressively warmer and perhaps somewhat wetter, with most increase in precipitation during the winter (Mote et al., 2003). The largest changes are predicted to occur to the north, particularly in inland British Columbia and Alberta. In those areas, the frost-free period is expected to increase by at least a month and periods of extremely warm summer days are likely to become more common, based on the fourth assessment report high emission (A2) scenario generated by the Canadian Global Climate Model (version 2) leading to mean annual temperatures increases by 2080s of 3–5 °C (Spittlehouse, 2008).

To simulate conditions under a future projected climate, we utilized the Special Report on Emission Scenarios (SRES) climate scenarios developed by the Intergovernmental Panel on Climate Change (IPCC) Fourth Assessment Report, AR4 (Nakićenović and Swart, 2000; IPCC, 2007). We utilize a range of climate scenarios as well as assessing climate change impacts on the movement of species ranges and quantifying species adaptation. This information can then be used to categorise species vulnerability based on the range of responses to potential future climatic conditions and in doing so we are applying a vulnerability-based approach as recommended by the Intergovernmental Panel on Climate Change (IPCC, 1998). We contrasted two extremes: “a business as usual” scenario (A2) and a scenario (B1) that assumes current emissions rates will remain steady until around 2040, and then slowly drop to about half of the current rate by the end of the century. We used scenarios from the Canadian Climate Centre’s Modeling and Analysis (CCCma) third generation general circulation model (CGCM3), which includes improvements in the treatment of clouds, solar radiation, and land surface processes along with a simple ocean mixed-layer model with a thermodynamic sea ice component (McFarlane et al., 2005; Scinocca et al., 2008). Downscaling of the GCM was undertaken within CLIMATE-WNA (see Hamann and Wang, 2005). We contrasted changes among three standard 30-year periods, the 2020s (2011–2040), 2050s (2041–2070) and the 2080s (2071–2100) provided by the global climate model.

2.4. Choice of a physiologically-based forest growth model

The most common approach to modeling a species’ distribution is to define its niche or bioclimatic envelope from which its presence or absence can be predicted and compared with empirical data (Austin, 1985; Iverson and Prasad, 1998; McKenzie et al., 2003; Thuiller et al., 2008). Although such models are usually quite successful in defining current ranges of species, their ability to forecast shifts in geographic distributions under new and possibly novel climatic conditions is unclear (Williams et al., 2007). To assess how changes in day length, temperature and soil water balances actually affect photosynthesis and growth requires more mechanistic models. Such models are able to predict growth performance outside a species’ native range (Sands et al., 2000; Rodriguez et al., 2002; Dye et al., 2004). At the same time, more mechanistic models, through sensitivity analyses, provide a means to evaluate the relative importance of different climatic and soil variables on a species’ performance (Waring, 2000; Coops et al., 2005; Waring et al., 2008). Lastly, mechanistic models provide a link to total plant photosynthesis which varies seasonally. Upper limits of photosynthesis are set by the amount of light absorbed by green leaves (LAI). Thus, a day of subfreezing temperatures in the winter when the day length is short (in the Northern Hemisphere) has much less effect than in May when the day length is much longer (assuming equivalent LAI).

The potential drawback of mechanistic models is that a detailed knowledge is required to define a species’ physiological response

to seasonal variation in solar radiation, precipitation, temperature, atmospheric humidity deficits, and soil properties.

There are a wide variety of physiologically-based process models available but only a few have been designed to scale projections of photosynthesis, structural growth, and annual mortality across landscapes (see reviews by Mäkelä et al., 2000; Nightingale et al., 2004). Among the most widely used is the 3-PG model (Physiological Principles Predicting Growth) developed by Landsberg and Waring (1997) which, when coupled with a decomposition model, provides estimates of net carbon exchange (Peng et al., 2002). 3-PG provides a reasonable compromise between highly complex, fine-temporal scale process models, and those applied at annual time-steps. It is based on a number of established biophysical relationships and constants and incorporates simplifications that have emerged from studies conducted over a wide range of forests (Landsberg et al., 2003). The model includes the following simplifications: (a) that climatic data are adequate when averaged at monthly time steps, (b) that autotrophic respiration (R_a) and net primary production (NPP) are approximately equal fractions of gross photosynthesis (GPP), (c) that maximum canopy conductance approaches a constant as LAI exceeds 3.0, and (d) that the proportion of photosynthate allocated to roots increases with drought and decreases with nutrient availability.

The 3-PG model calculates gross photosynthesis, transpiration, growth allocation and litter production at monthly intervals, and takes into account deficiencies in precipitation in previous months and years by sequentially updating a soil water balance. Each month, the most limiting climatic variable on photosynthesis is selected, based on departure from conditions that are defined as optimum (expressed as unity) or completely limited (expressed as zero) for a particular species or genotype. The ratio of actual/potential photosynthesis decreases in proportion to the reduction in the most limiting environmental factor. The fraction of production not allocated to roots is partitioned among foliage, stem and branches based on allometric relationships and knowledge of annual leaf turnover (Landsberg et al., 2003).

The model works as follows: Absorbed photosynthetically active radiation (APAR) is estimated from total incoming solar radiation and LAI; and the utilized portion is calculated by reducing APAR by an amount determined by a series of modifiers that take values between 0 (system 'shutdown') and 1 (no constraint) to limit gas exchange via canopy stomatal conductance (Landsberg and Waring, 1997). The monthly modifiers include: (a) averaged day-time vapor pressure deficits, (b) the frequency of subfreezing conditions, (c) soil drought and (d) mean daily temperature. Drought limitations are imposed as a function of soil properties and a simple water balance that calculates when soil water supply is less than transpiration estimated with the Penman-Monteith equation.

Details of model parameterization and predictions are described in detail in Coops et al. (in press) and are briefly summarized here for completeness. The 3-PG model for Douglas-fir was parameterized using data from both conventional forestry yield tables and other literature (Waring and McDowell, 2002; Waring et al., 2008) with some notable exceptions. Although 3-PG normally requires information on soil water holding capacity and soil fertility, accurate information on these properties is generally unavailable for mountainous areas. Regional scale mapping of soil attributes is available in both the United States (STATSGO) and in British Columbia, however, the development of a consistent and seamless soil attribute coverage across these two jurisdictions using the same attributes was not possible due to different soil classification systems and spatial resolutions. As a result the analysis was limited to climatic effects and the available water holding capacity set at 200 mm for a sandy loam soil which has been demonstrated to relate to pre-dawn water potential measurements (a surrogate

Table 1

Scientific and common names for species analyzed in this paper.

Species	Common name	Code
<i>Pseudotsuga menziesii</i>	Douglas-fir	DF
<i>Thuja plicata</i>	Western redcedar	WRC
<i>Tsuga heterophylla</i>	Western hemlock	WH
<i>Tsuga mertensiana</i>	Mountain hemlock	MH
<i>Pinus contorta</i>	Lodgepole pine	LPP
<i>Pinus ponderosa</i>	Ponderosa pine	PP
<i>Picea sitchensis</i>	Sitka spruce	SS
<i>Pinus albicaulis</i>	Whitebark pine	WBP
<i>Chamaecyparis nootkatensis</i>	Alaska yellow cedar	YC
<i>Abies procera</i>	Noble fir	NF
<i>Picea engelmannii</i>	Engelmann spruce	ENG
<i>Larix occidentalis</i>	Western larch	WF
<i>Abies lasiocarpa</i>	Subalpine fir	SAF
<i>Abies amabilis</i>	Pacific silver fir	PSF
<i>Abies grandis</i>	Grand fir	GF

measurement for soil water availability) at drought-prone sites (Waring and Clear, 1967; Running, 1994). The relative low value for soil water storage assures that if drought occurs, it will be recognized (Nightingale et al., 2007). A soil fertility rank of 50% of maximum, which results in an even partitioning of growth above- and belowground was also set.

2.5. Predicting baseline, transitional, and future ranges of Northwest tree species

Coops et al. (in press) applied the 3-PG model across the region to predict stand growth and LAI, using the mean baseline climate derived from CLIMATEWNA from 1950 to 1975. Model simulations were run for 50 years of stand development by which time stands have obtained maximum LAI and maximum canopy closure. The model was then stopped. Using observations of species occurrence, collected by from the USDA Forest Inventory and Analysis (FIA) and a combination of field and other observation data (such as aerial photographic interpretation) from the Province of British Columbia, the monthly climatically-restricting modifiers to photosynthesis were extracted for each of the four modifiers at the 22,771 observations across the region. Decision tree models were then used to predict the ranges of the fifteen coniferous species in reference to their presence and absence recorded on the survey plots with accuracies ranging from 70% to 93% with a mean accuracy of 81% and a mean kappa statistic, a conservative measure of concordance, of 0.74 (Coops et al., in press).

In this research we applied the decision trees, developed for each species (Table 1), to evaluate the extent that conditions have become more or less suitable for each species, first over the transitional interval from 1976 to 2006, and then at 30-year intervals to the end of the 21st century based on projections for the A2 and B1 (high and low) emission scenarios from the Canadian GCM.

2.6. Statistical analyses

Nitschke and Innes (2008) propose that resilience can be used as a measure of a species response to climate change and is inversely proportional to the modeled probability of presence. As a result, a species which has an increasing probability of occurring at a site is considered well adapted to climatic change, whereas a species whose probability is declining is becoming less competitive and more vulnerable to disturbance (Nitschke and Innes, 2008). We utilize this definition and evaluated the fitness of 15 coniferous species in reference to their equilibrium ranges in a number of ways. We first calculated the fraction of a species' range that was no longer deemed suitable for each of the years between 1976 and 2006. We then defined as "vulnerable" those cells within a

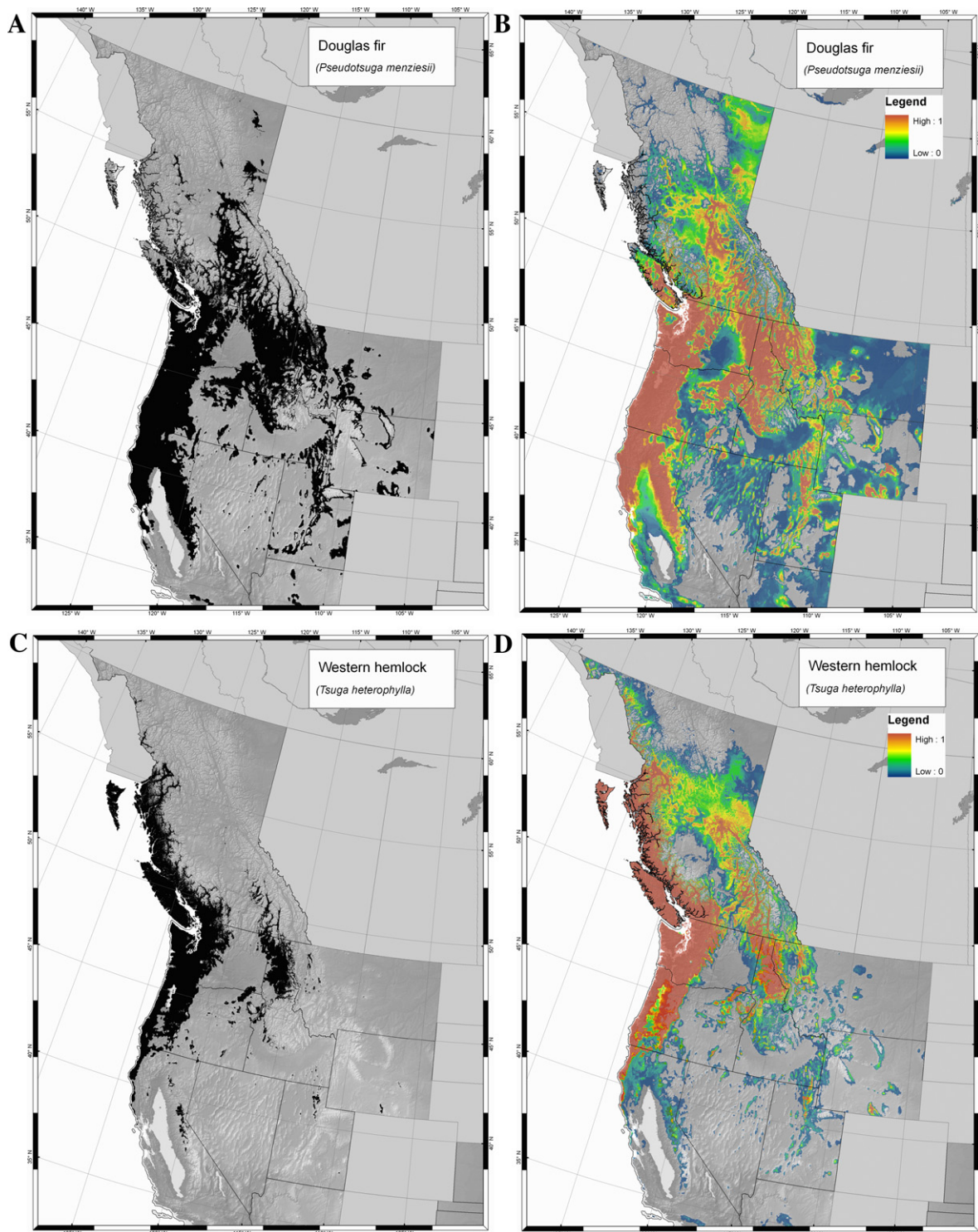


Fig. 2. (Left) Modeled distributions of (A) Douglas-fir and (C) western hemlock based on mean climatic conditions during the calibration period (1950–1975). (Right) Probability of occurrence of the two species during the transitional period (1976–2006) (B and D).

species' baseline range that were unsuitable for 15 years or more of the 1976–2006 timeframe. Using the same threshold, species were mapped as resilient or adapted in each cell if they were predicted to occur for more than 15 years over the time period. This number of years suitable for the species compared to the total time period (30 years) resulted in the calculation of the probability of occurrence. We then extended the comparison from 2010 into 30-year periods to the end of the 21st century. Finally, we compared the areas designated as vulnerable in reference to baseline climatic conditions

(1950–1975) by latitude, longitude and elevation, as well as within designated ecoregions to contrast differences in species' vulnerable and resilience range expansion.

3. Results

The ranges predicted for Douglas-fir and western hemlock, based on simulations for the baseline period (1950–1975), are shown in Fig. 2(A) and (D). As previously stated, this period

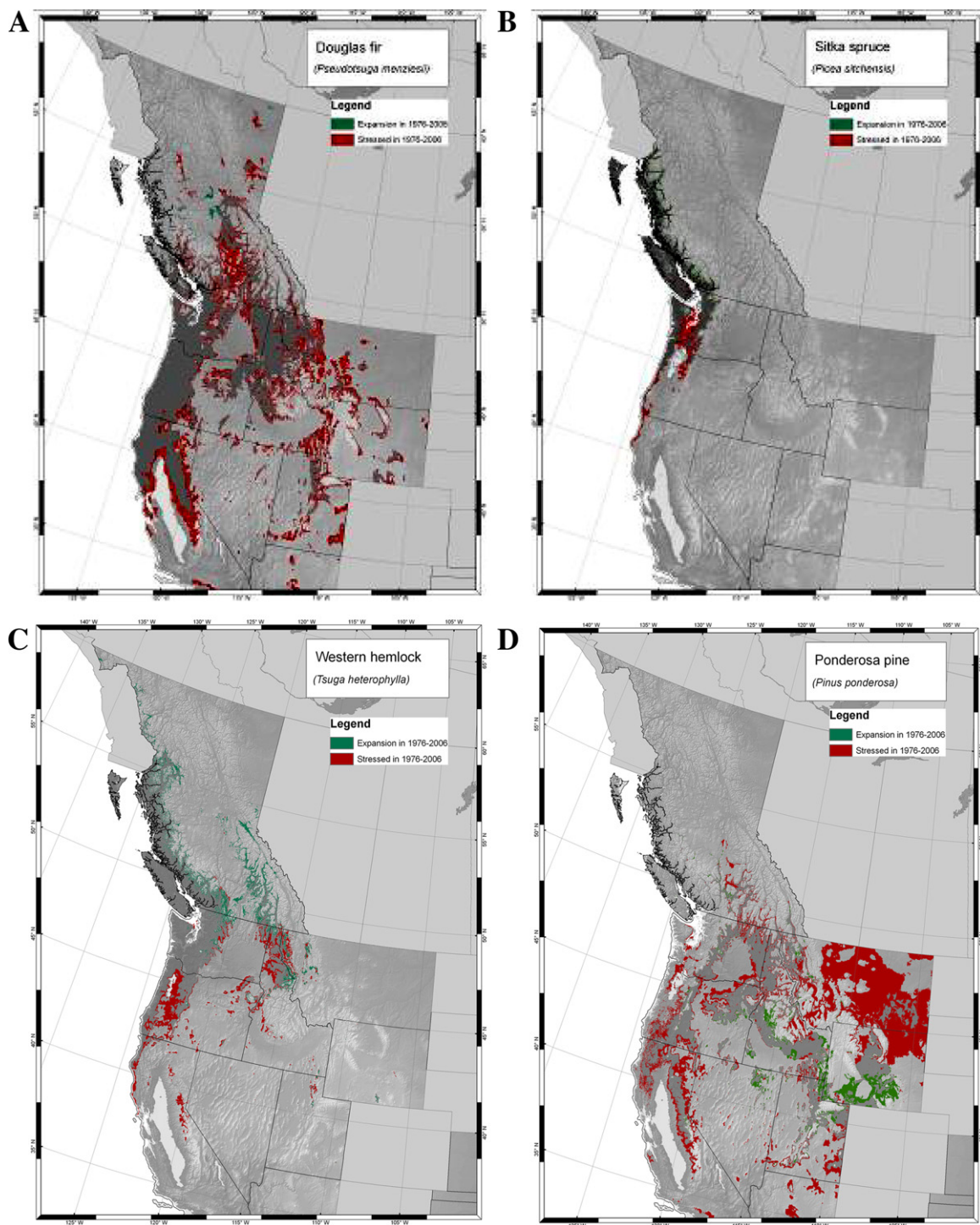


Fig. 3. Modeled distributions of tree species are delineated in gray and red for the period from 1950 to 1975. In the transitional period, 1976–2006, areas are identified for potential range expansion (green) and for contraction (red) based on the proportion of years that fell within or outside the previously defined climatic niche more or less than 50% of the time, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

represented generally cool, moist phases of the ENSO and PDO. We mapped a mosaic of favorable and unfavorable conditions for the two species by applying these calibrated decision tree models annually for the transitional period between 1976 and 2006 (Fig. 2(B)–(D)). Areas where each species remains resilient (i.e. high probability of occurrence) to the observed climate variation from 1976 to 2006 are shown in orange, whereas locations where the species is most vulnerable (i.e. low probability of occurrence) are shown in green and blue colors and repre-

sent areas for which climatic conditions are predicted to have become progressively less favorable for the species. Two cases are presented in Fig. 2 based on their dominance in the Pacific Northwest landscape. In the case of Douglas-fir, the species is resilient to the climate variability in parts of northeastern British Columbia and eastern Montana. Similarly, western hemlock is resilient in parts of interior B.C. east to the Rocky Mountains, along the coast and in some areas of northern California and Idaho.

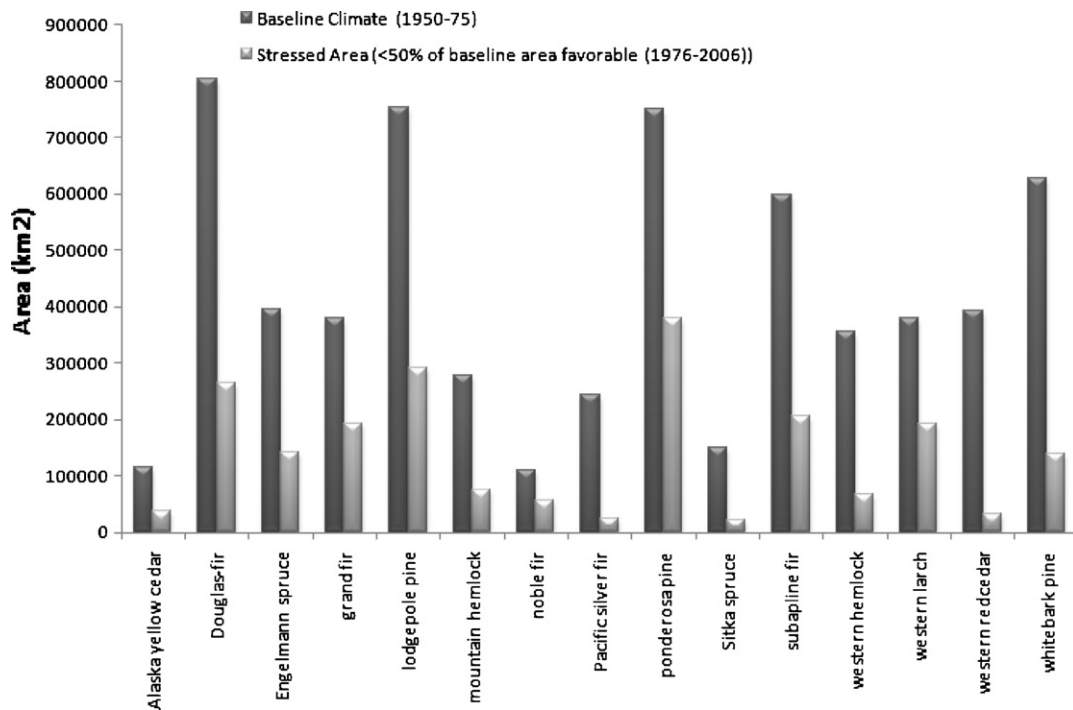


Fig. 4. Species distribution ranges based on the baseline climate (1950–1975) and the area within the baseline for each species stressed/vulnerable.

3.1. Defining areas of species resilience and vulnerability

From annual analyses during the transitional period, we defined as vulnerable areas within a species' baseline range that have less than a 50% probability of species occurrence from 1976 to 2006. Using the same threshold, areas which are resilient for the species occur if there is >50% probability of species occurrence (Fig. 3). From the examples shown, Douglas-fir exhibits the least potential for expansion, and western hemlock the most. Vulnerable areas within the baseline established range of Douglas-fir and ponderosa pine represent, for the most part, lower elevation sites where drought stress appears to be the major cause. In contrast, Sitka spruce and western hemlock are predicted to be able to move northward while becoming vulnerable at their southern limits as a result of increasing in temperature.¹

Over the 30-year transitional period, our climatically-driven decision-tree models predict on average that 30% of the 15 tree species' ranges have become vulnerable to climate change (Fig. 4). There is, however, considerable variation, with up to 50% of the range becoming vulnerable for ponderosa pine, noble fir, grand fir and western larch, and <10% for Pacific silver fir and western red cedar. When the areas of vulnerable forests are combined and plotted as a function of geographic location and elevation, striking trends emerge. Higher elevation sites appear to contain far more species characterized as "vulnerable" than do lower and mid-elevation sites. Inland and southern extremities of the Pacific Northwest Region are also more likely to show vulnerable areas for a majority of species than areas nearer the coast and at more northern latitudes (Fig. 5).

¹ Maps showing the modeled baseline-defined ranges, contractions and expansions during the transition period are available for all fifteen species: <http://www.pnwspecieschange.info/>.

3.2. Analysis by ecoregion

The percentage of observations in which each tree species was recorded is tabulated by level I ecoregion in Table 2. In addition, we provide the percent of these observations which are predicted to be vulnerable for each species (outside the ecological niche established under the baseline climate), as well as the % increase in observations that are resilient and thus will potentially expanded during the transitional period. Within the Northwest Forested Mountains, where all of the 15 species occur except Sitka spruce, most of the species have only moderate areas of their range classified as vulnerable (between 5 and 30%), with the exception of grand fir and ponderosa pine. Some species, such as whitebark pine remain well adapted within their predicted baseline range for the period 1976–2006. Within the cool, moist, coastal ecoregion (Marine West Coast Forests) both noble fir and subalpine fir, although recorded infrequently on observations, are predicted to become highly vulnerable during the transitional period. Alaska yellow cedar is predicted to be vulnerable over 25% of its baseline-defined range. Observations within the North America deserts, incorporating the drier plateaus in British Columbia and extending through Washington and Oregon, offer a range of conditions. Species such as western hemlock, whitebark pine and western larch, although infrequent, are predicted to remain well within their current range. In contrast, ponderosa pine and Douglas-fir, although widely distributed, are predicted to become more vulnerable in many places. In the Mediterranean California ecoregion within the Pacific Northwest, ponderosa pine and Douglas-fir were occasionally recorded as present at observations, with an increase in the vulnerable area likely during the transition period.

3.3. Shifts in species' distributions under projected climate change

The predicted contraction and expansion of each of the 15 modeled species under the A2 emission scenario using the Canadian GCM are presented in Fig. 6. The B1 emission scenario is less

Table 2
Percentage of observations within four major bioclimatic zones (ecoregions) occupied by the 15 tree species and the fraction of observations modeled to be stressed >50% of the years during the transition period 1975–2006, compared with the baseline period (1950–1975) and the proportion of observations where the species' range is predicted to have expanded during the transition period. Background code: clear 0–10%, light gray 10–25%, medium gray 25–50%, black >50% of predicted range either unsuitable during transition period, or expanding in the transition period. Species codes listed in Table 1.

Species	Northwest Forested Mountains			Marine West Coast Forests			North American Deserts			Mediterranean California		
	Pres.%	Stress%	Exp. %	Pres.%	Stress%	Exp. %	Pres.%	Stress%	Exp. %	Pres.%	Stress%	Exp. %
DF	64	19	2	25	9	0	11	38	0	1	22	0
WRC	41	1	150	55	0	5	4	3	110			
WH	36	12	80	62	2	17	2	0	480			
MH	62	8	390	36	12	86	2	18	646			
LPP	80	12	6	11	16	2	9	5	0			
PP	80	27	6				18	36	8	2	64	0
SS				100	2	56						
WBP	83	0	0	3	0	4	14	0	4			
YC	6	8	0	94	25	0						
NF	94	13	21	6	100	395						
ENG	80	12	15	1	16	392	19	5	7			
WF	91	2	0				9	0	5			
SAF	91	16	4	3	57	15	6	11	27			
PSF	38	2	26	58	0	18	4		19			
GF	91	27	1	9	7	41						

extreme but in a similar direction, results not shown. The area predicted to be suitable for the 15 tree species during the calibration period ranged from <100,000 to >800,000 km² (Fig. 6a). Douglas-fir (DF), western hemlock (WH), whitebark pine (WP) and western red cedar (WRC) are all predicted to expand their individual ranges, potentially, beyond 800,000 km² before the end of the century. These widely distributed species, with the exception of whitebark pine (WP), are projected to maintain most or all of their originally defined ranges (Fig. 6b). Of the species investigated, only ponderosa pine (PP) and lodgepole pine (LPP) are predicted to occupy smaller total areas near the end of the century than they now do.

4. Discussion

4.1. Defining baseline and transitional climatic periods

The year 1976, which defines the start of the transitional period, corresponds to an abrupt shift in the surface temperature of the tropical Pacific Ocean from cooler than normal to warmer than normal that propagated to the North Pacific (Giese et al., 2002). One effect of this shift in ocean temperatures was a significant increase in wildfire activity across much of the western U.S. by the mid-1980s, associated with a concurrent reduction in snowpack and an earlier start of the growing season (Westerling et al., 2006). Although some FIA surveys were initiated in 1930 in the West, we started our calibration period in 1950 when surveys were first completed for all western states.

4.2. Preliminary evidence supporting model predictions

As presented in Fig. 2 and Fig. 3, many species during the transitional years became vulnerable, within their baseline (modeled) ranges. Changes in species distributions do not necessarily infer loss but rather provide an indication of the species vulnerability to changes in the underlying physiological modifiers to growth and while species will not necessarily disappear from the landscape species will likely decrease in abundance over time (Nitschke and Innes, 2008). If true, we would expect an increase in disturbance during the transitional years in areas designated as vulnerable. One way to test this assumption is to compare the proportion of species predicted to be vulnerable in different ecoregions with the amount of forest cover recently confirmed as disturbed via remote sensing, such as potentially using the approach of Mildrexler et al. (2009). This will form the basis of future work. A more conclusive test

of model predictions requires inspections on the ground. Huang (1998) followed this course in the Cascade Mountains of central Oregon by documenting that grand fir, a temperate forest species, has established itself under the canopy of what had been previously a subalpine forest composed of older age classes of mountain hemlock, lodgepole pine, and western white pine. At lower elevations, he recorded grand fir present in a range of age classes, without observing any subalpine species. A more definitive study in the Santa Rosa Mountains of southern California documented over a similar 30 year period that ten perennial species of trees and shrubs have migrated upward in elevation an average of 65 m in association with climatic warming and a reduction in snowpack (Kelly and Goulden, 2008).

4.3. Forecasting future climates

The emphasis in this paper is on recent (transitional) variation in climatic conditions and the implication of that variation on species' distributions. To put these analyses in perspective for the future, we used the Canadian general circulation model (CGCM3) to predict climatic conditions through the rest of the century under a high CO₂ emission scenario. The CGCM3 model starts with a lower mean temperature than most models at the beginning of the last century but simulates a more rapid increase (Mote et al., 2005). On average, the temperature in the Pacific Northwest increased approximately 0.1 °C per decade through the 20th century. The average warming during the rest of this century is expected to be in the range from 0.1 to 0.6 °C per decade, with a value of 0.3 °C per decade most likely (Mote et al., 2005). Essentially all climate models predict acceleration in warming (Mote et al., 2005). At the same time, projected changes in precipitation are modest for the PNW region and unlikely to be above natural variability until late in the 21st century. With warmer winters there should be a progressive reduction in snowpack, particularly where temperatures fluctuate near freezing (Mote et al., 2003). This should lead to substantially more wildfires in late summer and fall in areas where summer precipitation is well below the potential evaporative demand, as reported by Meyn et al. (2010) over the last 70 years in British Columbia. Based on recent trends, we expect disturbances to become increasingly more frequent as the century progresses (Flannigan et al., 2005; Kurz et al., 2008), providing an opportunity for more rapid migration of species than might otherwise be expected.

To assess the validity of the species range predictions into the future we compared the area estimates to other studies. Hamann

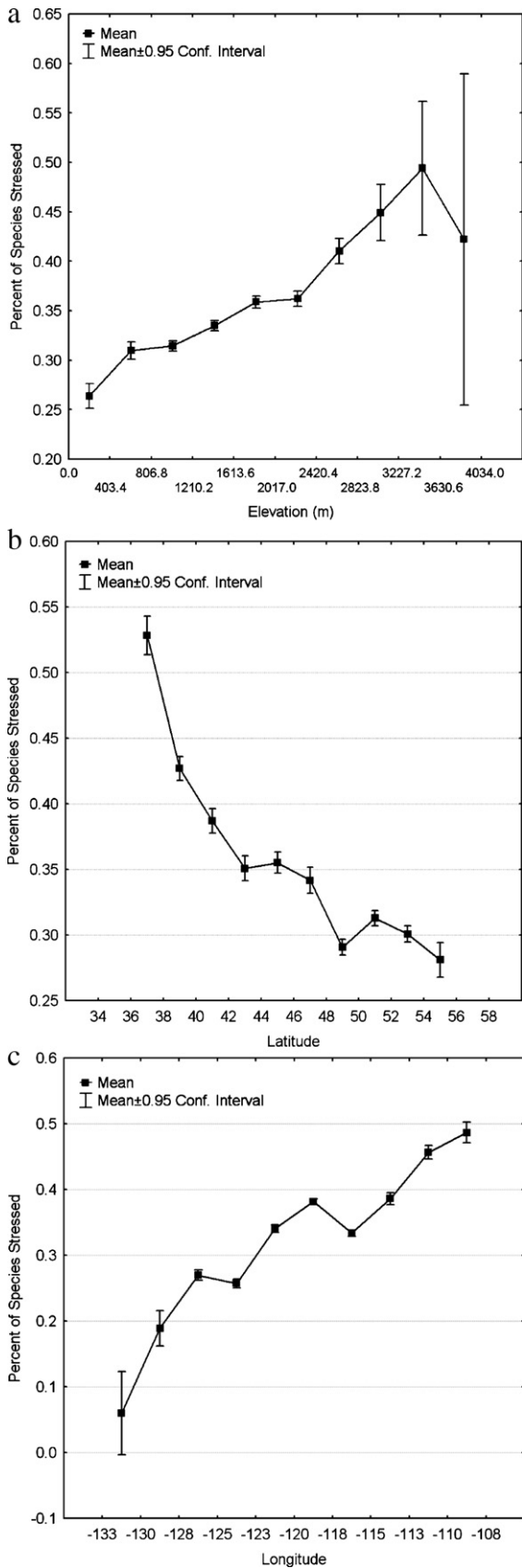


Fig. 5. Based on decision tree models, vulnerable areas of forests composed of 15 native tree species increased with a rise in (a) elevation, fell with increases in latitude (b), and the more western the longitude (c) during the transitional period (1976–2006).

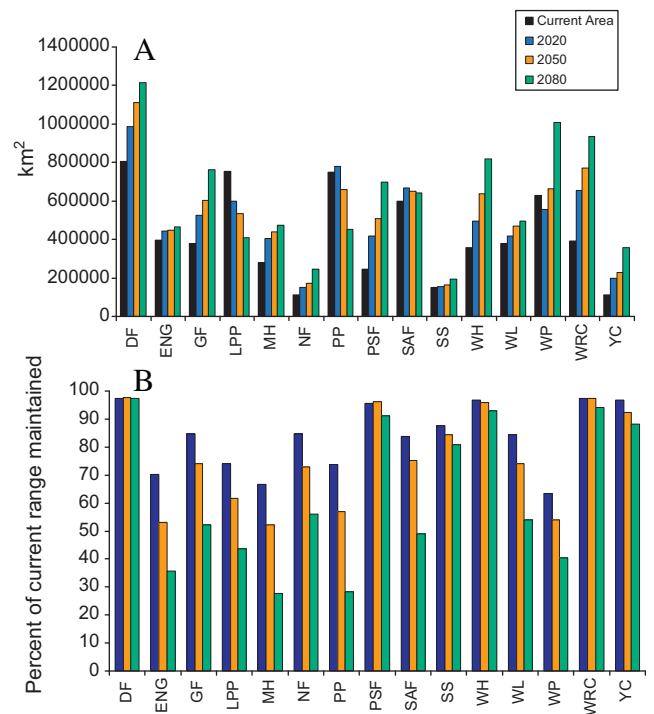


Fig. 6. (a) Predicted changes in species' ranges over the rest of the 21st century (a) expressed in area (b) as a percentage of the historical range maintained. Species codes defined in Table 1.

and Wang (2006) assessed distribution changes for a number of ecosystems and PNW tree species for the same three time periods this century. Likewise McKenney et al. (2007) assessed the potential impact of climate change on the distribution of 130 tree species in North America for the same A2 and B1 climate scenarios. Encouragingly the results for many of the species were similar. In the case of Hamann and Wang (2006) the area for each species which had become vulnerable by 2080 corresponded exceptionally very well ($R^2 = 0.70, N = 14$) with these results except for Ponderosa pine which, in our models, was predicted to have a large component of the current range becoming vulnerable in the inland, eastern, range of its distribution, whereas Hamann and Wang (2006) show no change in the species distribution. The relationship of these results of McKenney et al. (2007) were also strong with good agreement ($R^2 = 0.48, N = 12$) with the total change in area of species again with the exception of Ponderosa pine and Engelmann Spruce. The results are also consistent with our previous research with Lodgepole pine which also indicated a reduction in the area suitable for the species by 2080. In the case of Coops and Waring (2010) the analysis included a significant reduction of the species in Alberta which was not included in this analysis which reduced the overall species range to 17% of the current baseline by 2080.

We did not include the effects of increasing atmospheric CO₂ concentrations in this analysis, although we recognize that continual increases in atmospheric CO₂ are projected and may enhance photosynthesis and water-use efficiency (Marshall and Monserud, 1996). In areas likely to encounter increased drought, we would expect little response to rising atmospheric concentrations in CO₂, taking into account an increase in partitioning of photosynthate below ground (Eamus and Jarvis, 2004). Otherwise, the CO₂ enhancement effect may be sufficient to compensate, at least in part, for predicted increases in evaporative demand and drought (Almeida et al., 2009). Another important function in process-based models is the relation between water use and water storage. In this study we assume that all trees have access to 200 mm of available soil water storage, a value similar to that reported by Running

(1994) that gave good results across a forested gradient in Oregon. Models that calculate monthly water balances carry over any surplus or deficit in soil water balance, not only from one month to the next, but from one year to another, which permits recognition of multi-year drought effects. Refinements in model parameterization in the future, should consistent, fine scale data become more available, can recognize differences in soil depth and texture (Landsberg and Waring, 1997) as well as variation in rooting depth associated with tree size (Irvine et al., 2002).

4.4. Implications for management

Although models are far from perfect, they offer conservationist and managers reasons to expect where disturbances are mostly likely associated with climate change and how the composition of forests may change. The opportunity to confirm or refute model predictions therefore exists. If model predictions are supported by field surveys, adaptations to accommodate regional changes should have priority. Because of the accelerated projected rates of climate change, establishment of corridors to accommodate migration across ownerships may not prove adequate. As a result, we advocate that some effort be made to select seed sources that could be planted in areas where range expansion is predicted (Rehfeldt et al., 1999) recognizing that other issues such as seed dispersal and production are also key determinants of species movements.

5. Summary

Climatic conditions across the Pacific NW region have significantly warmed between the cool (1950–1975) and warm phase (1976–2006) of the Pacific North American (PNA) circulation patterns, and projections through the 21st century suggest warming will continue and accelerate. As a result of these trends, many Northwest tree species, according to our model predictions, are becoming less adapted (averaging 30%) within their baseline modeled (1950–1975) ranges. Over the last three decades, relatively large areas outside the modeled ranges of 13 out of 15 native trees species have become more favorable for potential migration. Although models are far from perfect, they offer conservationist and managers reasons to expect where disturbances are mostly likely associated with climate change and how the composition of forests may change.

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