

Integrating mechanistic and empirical model projections to assess climate impacts on tree species distributions in northwestern North America

MICHAEL J. CASE  and JOSHUA J. LAWLER

School of Environmental and Forest Sciences, University of Washington, Box 352100, Seattle, WA 98195–2100, USA

Abstract

Empirical and mechanistic models have both been used to assess the potential impacts of climate change on species distributions, and each modeling approach has its strengths and weaknesses. Here, we demonstrate an approach to projecting climate-driven changes in species distributions that draws on both empirical and mechanistic models. We combined projections from a dynamic global vegetation model (DGVM) that simulates the distributions of biomes based on basic plant functional types with projections from empirical climatic niche models for six tree species in northwestern North America. These integrated model outputs incorporate important biological processes, such as competition, physiological responses of plants to changes in atmospheric CO₂ concentrations, and fire, as well as what are likely to be species-specific climatic constraints. We compared the integrated projections to projections from the empirical climatic niche models alone. Overall, our integrated model outputs projected a greater climate-driven loss of potentially suitable environmental space than did the empirical climatic niche model outputs alone for the majority of modeled species. Our results also show that refining species distributions with DGVM outputs had large effects on the geographic locations of suitable habitat. We demonstrate one approach to integrating the outputs of mechanistic and empirical niche models to produce bioclimatic projections. But perhaps more importantly, our study reveals the potential for empirical climatic niche models to over-predict suitable environmental space under future climatic conditions.

Keywords: climate change, correlative, DGVM, niche model, northwestern North America, process-based, species distribution model, species range

Received 20 July 2016; revised version received 29 October 2016 and accepted 2 November 2016

Introduction

Empirical climatic niche models are one of the most commonly used tools for assessing the potential impacts of climate change on tree species distributions. However, empirical niche models do not directly incorporate biotic factors, such as competition, establishment, dispersal, migration, growth, mortality, and evolutionary change (Davis *et al.*, 1998; Pearson & Dawson, 2003; Hampe, 2004; Pearson, 2006). Although climate has been shown to control range limits at upper treeline, recent research suggests that local drivers, such as competition, influence tree growth in closed-canopy forests (Ettinger *et al.*, 2011). Thus, climate-induced range shifts in closed-canopy forests will likely be difficult to accurately predict with conventional empirical niche models.

In contrast to empirical niche models, mechanistic approaches explicitly model processes and relationships that influence a species' geographic range. These

models project species distributions using a set of known or suspected physiological or ecological relationships, rules, and/or limits. Mechanistic models do not rely on known occurrence records but instead are based on current understanding of physiologically or ecologically limiting mechanisms for species. Although mechanistic models have been used to simulate the distribution of individual tree species (e.g., Coops & Waring, 2011), they require a large amount of species-specific information on growth, physiology, and competitive interactions, which is generally not available for most species. Therefore, many mechanistic models are parameterized for coarse classifications of vegetation, such as biomes. For example, dynamic global vegetation models (DGVMs) often simulate the spatial and temporal patterns of vegetation classified into basic plant functional types (Sitch *et al.*, 2003). Plant functional types can be combined with other mechanistic model outputs such as foliar projective cover and plant height to define biomes (e.g., Shafer *et al.*, 2015); however, these basic biome classifications are often too coarse for many conservation and management applications.

Correspondence: Michael J. Case, tel. +1 206 913 1326, fax +1206 685 0790, e-mail: mcase@uw.edu

Given some of the inherent weaknesses of both empirical and mechanistic models, recent studies have begun to integrate the two modeling approaches (Buckley *et al.*, 2010; Dormann *et al.*, 2012; Higgins *et al.*, 2012). For trees in North America, some have combined empirical habitat suitability models with 1) dispersal models to examine the possible colonization of new suitable habitat (e.g., Iversen *et al.*, 2004; McKenney *et al.*, 2007, 2011; Meier *et al.*, 2012), 2) modification factors that incorporate known species attributes to assess potential responses to new climatic conditions and disturbance regimes (e.g., Iversen *et al.*, 2011; Matthews *et al.*, 2011), 3) landscape and population modeling (Hannah *et al.*, 2008), and 4) physiology-based growth models (Coops *et al.*, 2009). Model projections can differ greatly when specific mechanisms are incorporated into simpler empirical niche models. For example, tree species distributions in the Pacific Northwest were projected to contract and shift northward by roughly 330 km under a no-dispersal scenario and by approximately 700 km under a full-dispersal scenario (McKenney *et al.*, 2007, 2011). However, these regional modeling approaches do not address the dynamic processes such as competition among species or the direct and indirect effects of CO₂ enrichment.

Here, we combine the strengths of both empirical climatic niche models and mechanistic models by integrating projections from a DGVM that simulates the distribution of biomes based on plant physiology, interactions between plant functional types, the effects of CO₂ enrichment, and fire, with empirical niche models for six tree species in northwestern North America. The six species included Pacific silver fir (*Abies amabilis*), grand fir (*Abies grandis*), subalpine larch (*Larix lyallii*), western larch (*Larix occidentalis*), Pacific yew (*Taxus brevifolia*), and western redcedar (*Thuja plicata*). Hereafter, we refer to the two sets of model projections as 'unrefined' and 'refined' niche model projections. The unrefined projections define the future locations of the climatic conditions in which the species is found today (and thus areas that are likely to be climatically suitable), whereas the refined projections define the areas that are likely to be climatically suitable in the future and, given the effects of soils, interactions between plant functional types, the effects of CO₂ enrichment, and fire, will likely support the plant functional type to which the species belongs. We then compared the refined and unrefined niche model projections to explore the impact of integrating empirical and mechanistic model outputs on projected climate-induced range shifts.

Materials and methods

General modeling approach

We first determined which of the biome types predicted by the DGVM were likely to be suitable for each of the six tree species (Table 1). This selection of relevant biomes was based on habitat associations and associated forest cover (Table S4; Burns & Honkala, 1990). Although the selection of relevant biomes was largely intuitive and informed by known ecology, nonetheless, it involved some degree of subjectivity. Thus, we explored the impact of biome selection on our results for Pacific silver fir, one of the six species with less overlap between the digital range map and our selected biomes (see Supporting Information). After selecting the relevant biomes for each of the species, we intersected digital tree species range maps with the identified suitable DGVM biomes and used the area of overlap as a map of the current distribution for each species (Fig. S1).

After overlaying all relevant biomes, on average, current mapped ranges were reduced by about 30% in area (i.e., there was 70% overlap in the mapped range and the relevant biomes; Table 1, Fig. S1). However, this reduction varied substantially across species with 59% overlap between the original distribution of western redcedar and the cool forest and coastal cool forest biomes and 90% overlap between the original distribution of subalpine larch and the 1) cold forest, 2) cool forest, 3) cold open forest/woodland, and 4) cool open forest/woodland biomes (see Table 1). The degree that our selected DGVM biomes matched with individual species was dependent on multiple factors, such as how narrow an individual tree species' climatic breadth is and how well the coarse resolution range maps reflect the actual presence of tree species in a given location. We then built empirical niche models using these modified maps of the current species distributions (Fig. 1).

To project changes in potential future species distributions, we first produced future projections by applying the niche models to five future climate projections. We then intersected these future niche projections with the projections of the relevant future biomes from the DGVM (Fig. 1). These areas of intersection are places where the mechanistic DGVM predicts that the basic plant functional type to which the species belongs should be able to exist (given soil types, the effects of increased CO₂ concentrations, interactions with other basic plant functional types, and fire) and where the climate is likely to be suitable for the species.

To assess the effect of integrating DGVM biomes with future species distributions, we compared the percentage of each species distribution that was projected to be stable, to expand, and to contract before and after future biomes were intersected. We considered a portion of the range to be stable if it was projected to be suitable both currently and in the future. Expansion was defined as areas that were projected to become newly suitable in the future and areas of contraction were defined as places that were projected to become unsuitable in the future.

Table 1 Tree species, their relevant biomes, range area as defined by digital range maps (column A), modified range area as defined by the intersection of current range and suitable biomes (column B), and the percentage of range map area that intersects with their relevant biomes, as projected by the dynamic global vegetation model (DGVM) (column C) (Shafer *et al.*, 2015)

| Species | DGVM Biomes | (A) Range area as defined by digital range map (km ²) | (B) Intersection of current range and suitable biomes (km ²) | (C) Percentage of range map area within suitable projected biomes |
|---|--|---|--|---|
| Pacific silver fir (<i>Abies amabilis</i>) | Cold forest, cool forest | 172 756 | 103 649 | 60 |
| Grand fir (<i>Abies grandis</i>) | Cool forest, maritime cool forest, cool open forest/woodland, cool open forest/woodland with broadleaf evergreen component | 211 106 | 182 797 | 87 |
| Subalpine larch (<i>Larix lyallii</i>) | Cold forest, cool forest, cold open forest/woodland, cool open forest/woodland | 32 573 | 29 262 | 90 |
| Western larch (<i>Larix occidentalis</i>) | Cold forest, cool forest, cold open forest/woodland, cool open forest/woodland | 143 450 | 127 460 | 89 |
| Pacific yew (<i>Taxus brevifolia</i>) | Cool forest, coastal cool forest, cool open forest/woodland with broadleaf evergreen component | 349 646 | 246 198 | 70 |
| Western redcedar (<i>Thuja plicata</i>) | Cool forest, coastal cool forest | 385 208 | 227 827 | 59 |

Tree species and distribution maps. We modeled the potential distributions of six tree species: Pacific silver fir, grand fir, subalpine larch, western larch, Pacific yew, and western redcedar. These species represent a wide range of climatic tolerances, and their distributions were fully contained within the study area. The study area encompasses the northwestern United States and southwestern Canada. This region is roughly bounded by the Pacific Ocean to the west, the Great Plains to the east, the southwestern deserts to the south, and the boreal forest to the north.

We downloaded the digital range maps from the U.S. Geological Survey 'Atlas of United States Trees' (US Geological Survey, 1999) and gridded them at approximately 1-km² resolution. We used this relatively fine resolution to strike a balance between the ability to detect large-scale climatic patterns across the study area and the need to provide high resolution projections of potential range shifts.

Climate data. We used historical climate data from the Climatic Research Unit (CRU), University of East Anglia, CL 2.0 (New *et al.*, 2002) and CRU TS 2.1 (Mitchell & Jones, 2005) climatology data sets. Both the CRU CL 2.0 and CRU TS 2.1 data sets were constructed from climate-station records spanning the years 1961 to 1990 and were downscaled to a 10' latitude by 10' longitude global grid. We then clipped the CRU CL 2.0 and CRU TS 2.1 data sets to the study area and downscaled them further to a 30 arc-second resolution grid using a geographic distance-weighted bilinear interpolation method (Shafer *et al.*, 2015). We identified 36 climatic and bioclimatic

variables (Table S1) that are biologically important controls to tree growth (Prentice *et al.*, 1992; McKenzie *et al.*, 2003), and we used these to model current tree distributions.

To model future tree niches, we used future climate projections developed for the IPCC Fourth Assessment Report based on the SRES A2 greenhouse-gas emissions scenario and downscaled by Shafer *et al.* (2015). The A2 emissions scenario represents a world with increasing population growth, regionally oriented economic development, slower development, and implementation of new technologies (Nakicenovic & Swart, 2000). Although updated future climate projections are now available (e.g., CMIP5), the projections that we used (CMIP3) have been shown to have relatively similar climatic boundaries (Wright *et al.*, 2016). We used projections from each of the five following general circulation models (GCMs) for the time period 2070 – 2099: CCSM3 (Collins *et al.*, 2006), CGCM3.1 (T47) (Scinocca *et al.*, 2008), GISS-ER (Schmidt *et al.*, 2006), MIROC3.2 (medres) (Hasumi & Emori, 2004), and UKMO-HadCM3 (Pope *et al.*, 2000).

Dynamic global vegetation model data. Biomes were projected by Shafer *et al.* (2015), using the Lund–Potsdam–Jena (LPJ) dynamic global vegetation model (Sitch *et al.*, 2003). LPJ is a process-based model that uses monthly temperature, precipitation, sunshine, annual atmospheric CO₂ concentrations, and soil characteristics to simulate multiple mechanistic processes, including photosynthesis, growth, resource competition, establishment, mortality, and fire. LPJ uses this information to classify the composition and structure of

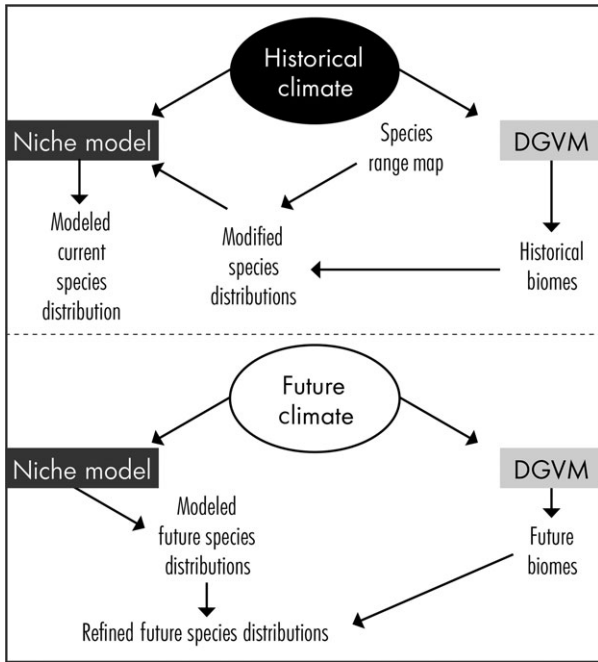


Fig. 1 The general modeling approach of combining historical climate and species range maps to build a niche model and then refining the model projections with mechanistic model output (DGVM). The top panel depicts how the niche models were built and the bottom panel shows how the niche models were used in conjunction with the DGVM outputs to project potential future distributions.

dominant vegetation in the form of plant functional types (PFTs). Each PFT is constrained by bioclimatic limits, which determine whether it can survive or regenerate within a given grid cell (Sitch *et al.*, 2003). LPJ incorporates changes in atmospheric CO₂ concentrations, an important feature for accurately simulating vegetation responses to future climate change. LPJ was run with the same climate data used to build the niche models.

Niche modeling. We used the statistical program, R (R Development Core Team, 2013), and the random forests package 'randomForest' (Liaw & Wiener, 2002) to build models of species' distributions as a function of current climate. Random forest classifiers are nonparametric ensemble models composed of multiple classification trees built with randomly selected subsets of both observations and predictor variables (i.e., resampling) (Breiman, 2001). The result is a 'forest' of classification trees. Because we used categorical data, the majority prediction was tallied across trees. The resampling of predictors and observations reduces the impact of collinearity among predictor variables and allows the model to explore the full range of data space, thereby improving model fit (Elith & Graham, 2009).

We split our data set into a randomly selected 70% of the data for model training and 30% for model evaluation. To test the fit of the models and provide a metric of model accuracy, we resampled the training data set 500 times (i.e., bootstrap

aggregation) and identified the cross-validated error rate reported by the model (i.e., out-of-bag errors). Preliminary analyses showed that a ratio of ten absences to one presence maximized the percent of correctly predicted presences and absences in the model evaluation data set, and therefore, we used that ratio of absences to presences when building our models. The random forest models produce probability estimates ranging from 0 to 1. We converted this range of values to a binary variable representing 'suitable' or 'unsuitable' niche predictions by determining an optimal threshold value for each species model. This threshold value was identified using the 'PresenceAbsence' package in R, which balances the relative costs of false-positive predictions and false-negative predictions by calculating the slope of a line and shifting it from the top left of the receiver operator characteristic (ROC) plot toward the lower right until it first touches the ROC curve (Freeman & Moisen, 2008). The slope of this line is based on the ratio of the relative costs of false-positive predictions and false-negative predictions divided by the prevalence (Fielding & Bell, 1997). We calculated prevalence as the overall proportion of locations where the given tree species was predicted to be present.

We identified models with the fewest number of predictor variables that still successfully predicted at least 70% of the presences and 90% of the absences in the evaluation data set. We used the mean decrease in the Gini index to identify the most important variables and of these selected the least correlated. We then rebuilt the models using these reduced sets of predictors. Most models had two to three predictor variables. Having fewer climate variables in these final models provided more parsimonious models and simplified our inferences as to the climatic controls for each species. We then used the final models to predict potential climatic suitability for each species.

Results

The niche models were able to relatively accurately predict the current ranges of the species. Using the reserved, evaluation data set, the out-of-bag errors averaged 2.0% for refined niche models, whereas the commission errors (i.e., predicting a presence when there is none) averaged 12.8% for refined models. The omission errors – predicting no presence when one is there – averaged 1.4% for refined models (Table 2). The out-of-bag error rate was negatively correlated with range size, with species that have the largest range also having the largest out-of-bag error. With the exception of the model built for the subalpine larch, our models required relatively few predictor variables (Table S2).

Niche model projections refined by mechanistic DGVM projections resulted in smaller future distributions than our unrefined projections for five of the six species, including Pacific silver fir, grand fir, Pacific yew, western larch, and western redcedar (Fig. 2). Neither of our modeling approaches predicted any environmentally suitable areas for subalpine larch in the

Table 2 Classification errors from the confusion matrix, with out-of-bag errors (OOB), commission errors, and omission errors for the refined niche models for six tree species

| Species | Number of climate variables in final model | OOB (%) | Commission errors (%) | Omission errors (%) |
|--------------------|--|---------|-----------------------|---------------------|
| Pacific silver fir | 3 | 1.66 | 10.74 | 1.38 |
| Grand fir | 3 | 1.81 | 12.88 | 1.22 |
| Subalpine larch | 11 | 0.55 | 2.20 | 0.53 |
| Western larch | 3 | 1.88 | 8.96 | 1.62 |
| Pacific yew | 2 | 3.15 | 22.50 | 1.73 |
| Western redcedar | 2 | 3.12 | 19.41 | 1.98 |

future. Refined future projections were also considerably different from unrefined projections for three species – Pacific silver fir, Pacific yew, and western redcedar (Fig. 3). For these species, the refined future projections contained fewer areas that were projected to be stable or newly suitable in the future (i.e., expand) as well as more areas of likely contraction. Although also smaller in extent, the refined projections for western larch and grand fir are somewhat similar in appearance to the unrefined projections (Fig. 3).

Refining the projections of the niche models with the outputs of the DGVM had the greatest impact on the projected areas of suitability for Pacific silver fir, Pacific yew, and western redcedar (Fig. 3). For these species, the area of projected expansion in suitability was substantially smaller and the area of projected contraction was larger after the projected future biomes were integrated. By contrast, modifying the outputs of the niche models with the DGVM outputs did little to change projected potential future distributions for western larch and grand fir. These two species also had similar projected changes in their distributions (with respect to areas of potential expansion and contraction of suitability) as forecasted by the refined and unrefined model projections. Our results also show that refining species distributions with DGVM outputs had large effects on the geographic locations of suitable habitat. These differences are most evident when examining future areas of expansion for Pacific silver fir in southwestern British Columbia, Canada, and northwestern Washington State, USA (Fig. 4).

Our sensitivity analysis for the Pacific silver fir – in which we expanded the number of biomes included in model – produced larger areas of potential range stability and expansion overall. As one might expect,

including an additional biome in the model reduced the difference between the projected range change produced by refined and unrefined models (Fig. S2). However, despite this modest reduction, the refined model with the addition of a biome still projected less expansion, more contraction, and a larger net change in range than did the corresponding unrefined model.

Discussion

Integrated mechanistic and empirical climatic niche model outputs painted a substantially different picture of potential future niches than did the projections of more conventional empirical climatic niche models. Specifically, using available output from mechanistic models that simulate important biological processes, such as competition, physiological responses of plants to changes in atmospheric CO₂ concentrations, and disturbances generally reduced the area projected by niche models to be climatically suitable for species in the future. These results lend credence to the concern that empirical climatic niche models that are based solely on correlations and hence may not fully reflect the actual processes controlling a species' distribution (Guisan & Zimmermann, 2000), potentially over-predict future areas of suitability (Araújo *et al.*, 2005).

Our results imply that species may be more heavily impacted by climate change than suggested by analyses that rely solely on empirical niche model projections. For instance, other empirical climatic niche models project that Pacific silver fir could lose just 16% of its suitable habitat, western redcedar 8%, Pacific yew 11%, and western larch 61% to 63% by the end of the century (Hamann & Wang, 2006; Rehfeldt *et al.*, 2006). Our results indicate that these studies likely underestimate the true potential change in suitable habitat, by between 12% for western redcedar and 94% for Pacific silver fir, because they do not include mechanistic processes.

Our models projected that western larch and subalpine larch would likely experience the largest overall reductions of their current range as the climate changes. Projections from our unrefined models correspond well with projections from other studies (e.g., Hamann & Wang, 2006; Rehfeldt *et al.*, 2006; McKenney *et al.*, 2007, 2011; Rehfeldt & Jaquish, 2010); however, the projections from our refined models project even larger range reductions. Large areas of potential range contractions were likely driven by warming winter temperatures and declines in the moisture index and snow water equivalent (see Fig. S3). These findings support the notion that high-elevation tree species are at greater risk from climate change than some lower elevation tree species because they are projected to lose a larger

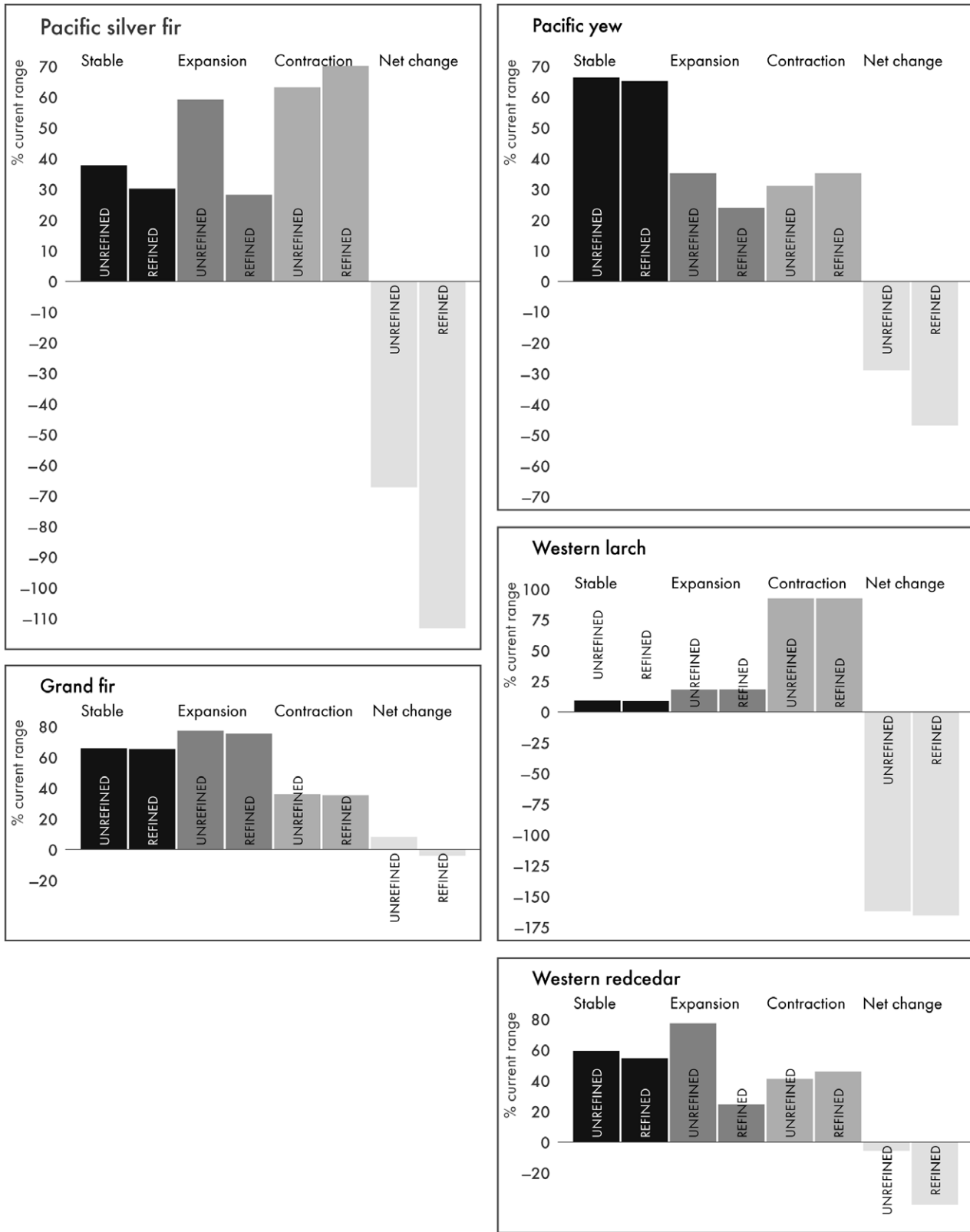
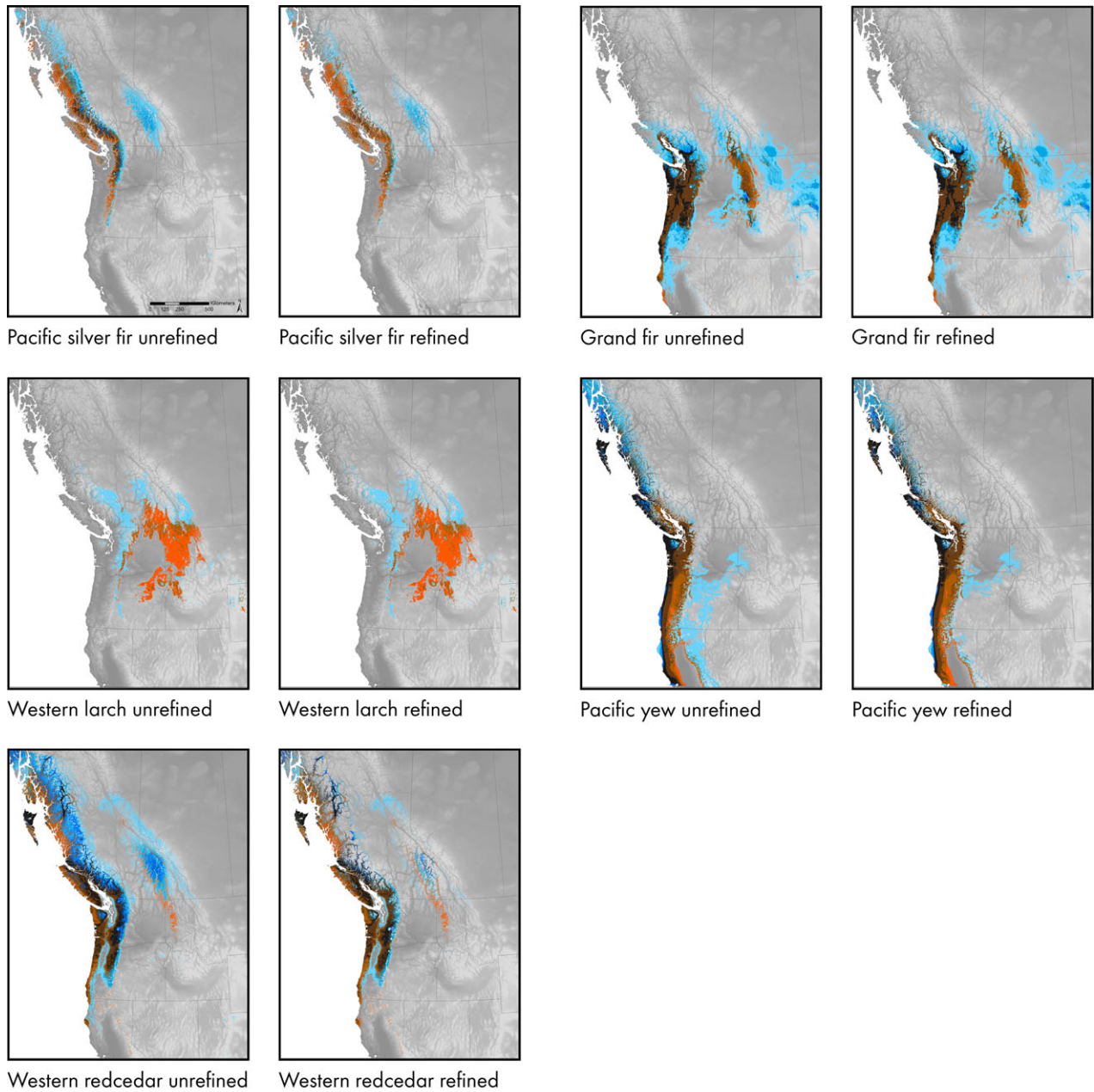


Fig. 2 Area as a percentage of the current range extent projected to remain stable, expand, and contract, as well as the net change of future suitable environmental space for five tree species for both the refined and unrefined niche models.



Legend

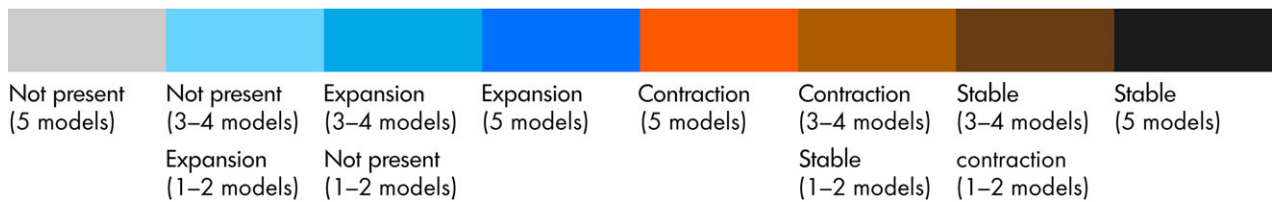


Fig. 3 Future projections for the refined distributions of five tree species and agreement of the ensemble of five general circulation models for the time period 2070 to 2099 for the A2 greenhouse-gas emissions scenario. [Colour figure can be viewed at wileyonlinelibrary.com].

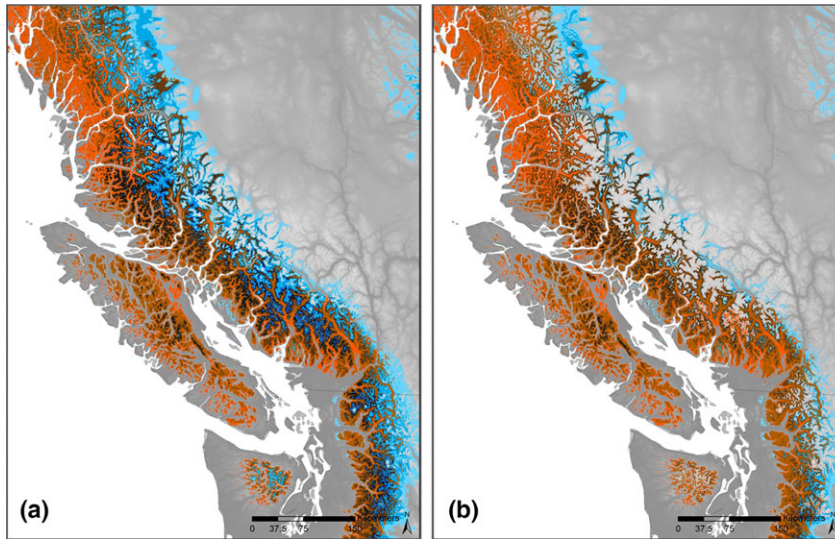


Fig. 4 Close-up future projections for the (a) unrefined and (b) refined distributions of Pacific silver fir and agreement of the ensemble of five general circulation models for the time period 2070 to 2099 for the A2 greenhouse-gas emissions scenario. The color scheme is the same as in Fig. 3. [Colour figure can be viewed at wileyonlinelibrary.com].

portion of their suitable habitat (Bell *et al.*, 2014). Although we did not assess dispersal, western larch seeds are small and lightweight and can disperse greater distances than the heavier seeds of some of its competitors, such as Douglas-fir (*Pseudotsuga menziesii*) and subalpine fir (*Abies lasiocarpa*) (Shearer, 1959). Nevertheless, it is potentially unlikely that even tree species with greater dispersal abilities will be able to track their suitable habitat (McKenney *et al.*, 2011). Furthermore, it is likely that changes in disturbances, such as fire, will play an increasing role in determining which tree species persist. Large fires are projected to become more frequent and intense in western North America (Littell *et al.*, 2010; Rogers *et al.*, 2011; Westerling *et al.*, 2011), and many of these events may be too severe for western larch establishment.

The lack of suitable habitat for subalpine larch in the future corresponds with other studies (e.g., Hamann & Wang, 2006; Crookston *et al.*, 2010) and is supported by ecological information about the species. For instance, subalpine larch has been found to be relatively sensitive to changes in climate and occupies some of the coldest high-elevation sites on which trees grow (Case *et al.*, 2015). Therefore, a change in snowfall or the seasonal duration of snowpack will likely influence the ability of this species to persist in some areas. Subalpine larch also has a disjunct distribution, with a portion in the Rocky Mountains and another portion in the Cascade Range (Arno & Habeck, 1972), providing a barrier to gene flow.

Others have suggested that niche models are generally more useful for conservation planning when

predicting areas of future habitat than predicting areas of future contraction (Schwartz 2012; Iverson & McKenzie, 2013). Subsequently, both our modeling approaches show that most species analyzed here are projected to potentially increase at the northern margins of their current distributions, a pattern generally consistent with other studies in the region (e.g., Hamann & Wang, 2006; Rehfeldt *et al.*, 2006; McKenney *et al.*, 2007; McKenney *et al.*, 2011). Our two modeling approaches indicate areas of expansion for grand fir and Pacific yew to the north of their current distributions, largely driven by warming temperatures and an increasingly moist climate. Also, grand fir's very small net decrease in suitable habitat as projected by the refined model is attributed to the projected increase in precipitation and moisture throughout the region. Moreover, both the refined and unrefined projections for grand fir were largely driven by spring precipitation, which is projected to increase in western Washington, western British Columbia, and the Canadian Rockies (Fig. S3). LPJ, the mechanistic model used, also indicates that the extent of cool forests and coastal cool forests are projected to expand, and therefore, we have more confidence that there will be suitable habitat for grand fir to the north. As the optimal environmental space for trees continues to change, this type of information may be useful to forest managers who seek to maximize growth and productivity.

We have presented one approach for integrating empirical climatic niche and mechanistic model projections; however, other studies have explored alternative modeling techniques and methods (e.g., Iverson &

McKenzie, 2013 for a review). Some of these other approaches have incorporated dispersal (Iverson *et al.*, 2004), competition (Meier *et al.*, 2012), and the effects of disturbance regimes (Lawson *et al.*, 2010; Iverson *et al.*, 2011); however, none, to our knowledge, have explicitly incorporated the effects of CO₂ enrichment and the subsequent species responses. For instance, higher concentrations of CO₂ are likely to have profound effects on the growth of plants by increasing the rate of photosynthetic carbon fixation by leaves as shown by a range of free-air carbon dioxide enrichment (FACE) experiments (Ainsworth & Rogers, 2007).

Although there are clearly advantages of integrating the outputs of mechanistic and empirical climatic niche models as we have done here, there are three key places where a modeling approach such as ours could be improved. First, because alternative empirical nichemodeling techniques tend to provide different future projections for a given species (Elith & Graham, 2009), it may be useful to use an ensemble of outputs from multiple niche-modeling techniques to provide more robust projections (Araújo & New, 2007). Second, the selection of which biomes are most relevant for each tree species likely affected our results. The distributions of some species, such as grand fir, subalpine larch, and western larch matched their respective biomes relatively well; however, the distributions of other species, particularly western redcedar and Pacific silver fir, did not. Although our selection of biomes was shown to have an effect on the future projections for Pacific silver fir (see Fig. S4), it appears that the model with an additional biome selected tends to overestimate areas of suitability (see Fig. S5) giving us cause for concern when projecting into the future. Nevertheless, the Pacific silver fir models that included an additional biome had relatively similar percent differences between refined and unrefined models compared our models with the original selection of biomes (see Fig. S2). This indicates that our conclusion – that species may be more heavily impacted by climate change than suggested by analyses that rely solely on empirical niche model projections – is robust, to a reasonable degree, to the potential effects of the process of biome selection. Finally, it is possible that our analyses underestimate the potential for a species to move into areas that are outside of its current climatic envelope. Because we modeled suitability as a subset of a species' climate envelope, we were unable to capture potential fundamental niche shifts resulting from processes such as increased water-use efficiency or changes in the factors that determine the realized niche (e.g., reduced competition). There is ample evidence of species being able to live outside of their current climate envelopes (e.g., eucalypts, Booth *et al.*, 2015; Booth, 2016). Thus, it is

possible that these types of fundamental and realized ecological niche expansions could offset the projected contractions as forecasted by our refined vs. unrefined model projections.

Although there are several areas in which an approach such as ours could be improved, our integration of empirical climatic niche and mechanistic model outputs addresses one of the greatest challenges of anticipating potential future climate impacts on species and populations – namely the need to incorporate ecological mechanisms into models for large numbers of species. It is generally accepted that models that better reflect ecological mechanisms will better capture potential responses of species to climate change, but researchers rarely have the data to build highly mechanistic models for more than a few well-studied species. Having more mechanistic projections of potential future climate impacts on species has the potential to lead to more informed climate-adaptation planning and more effective management in the face of climate change.

Acknowledgements

This work was partially supported by grants from the U.S. Geological Survey and the U.S. Park Service. Thomas Hinckley and Don McKenzie provided insightful and helpful comments on an early draft of the manuscript. Climate data and DGVM projections were developed by Sarah Shafer (U.S. Geological Survey). We are also grateful to the lovely Carole Guizzetti who assisted with maps and figures. The authors declare no conflict of interest.

References

- Ainsworth EA, Rogers A (2007) The response of photosynthesis and stomatal conductance to rising [CO₂]: mechanisms and environmental interactions. *Plant, Cell & Environment*, **30**, 258–270.
- Araújo MB, New M (2007) Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*, **22**, 42–47.
- Araújo MB, Pearson RG, Thuiller W, Erhard M (2005) Validation of species-climate impact models under climate change. *Global Change Biology*, **11**, 1504–1513.
- Arno SF, Habeck JR (1972) Ecology of alpine larch (*Larix lyallii* Parl.) in the Pacific Northwest. *Ecological Monographs*, 417–450.
- Bell DM, Bradford JB, Lauenroth WK (2014) Mountain landscapes offer few opportunities for high-elevation tree species migration. *Global Change Biology*, **20**, 1441–1451.
- Booth TH (2016) Estimating potential range and hence climatic adaptability in selected tree species. *Forest Ecology and Management*, **366**, 175–183.
- Booth TH, Broadhurst LM, Pinkard E *et al.* (2015) Native forests and climate change: lessons from eucalypts. *Forest Ecology and Management*, **347**, 18–29.
- Breiman L (2001) Random forests. *Machine Learning*, **45**, 5–32.
- Buckley LB, Urban MC, Angilletta MJ, Crozier LG, Rissler LJ, Sears MW (2010) Can mechanism inform species' distribution models? *Ecology Letters*, **13**, 1041–1054.
- Burns RM, Honkala BH (1990) *Silvics of North America: Volume 1. Conifers: Volume 2. Hardwoods*. Washington, D.C., U.S. Department of Agriculture, Forest Service.
- Case MJ, Lawler JJ, Tomasevic JA (2015) Relative sensitivity to climate change of species in northwestern North America. *Biological Conservation*, **187**, 127–133.
- Collins WD, Bitz CM, Blackmon ML *et al.* (2006) The community climate system model version 3 (CCSM3). *Journal of Climate*, **19**, 2122–2143.
- Coops NC, Waring RH (2011) Estimating the vulnerability of fifteen tree species under changing climate in Northwest North America. *Ecological Modelling*, **222**, 2119–2129.

- Coops NC, Waring RH, Schroeder TA (2009) Combining a generic process-based productivity model and a statistical classification method to predict the presence and absence of tree species in the Pacific Northwest, U.S.A. *Ecological Modelling*, **220**, 1787–1796.
- Crookston NL, Rehfeldt GE, Dixon GE, Weiskittel AR (2010) Addressing climate change in the forest vegetation simulator to assess impacts on landscape forest dynamics. *Forest Ecology and Management*, **260**, 1198–1211.
- Davis AJ, Jenkinson LS, Lawton JH, Shorrocks B, Wood S (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature*, **391**, 783–786.
- Dormann CF, Schymanski SJ, Cabral J *et al.* (2012) Correlation and process in species distribution models: bridging a dichotomy. *Journal of Biogeography*, **39**, 2119–2131.
- Eilith J, Graham CH (2009) Do they? How do they? WHY do they differ? On finding reasons for differing performances of species distribution models. *Ecography*, **32**, 66–77.
- Ettinger AK, Ford KR, HilleRisLambers J (2011) Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. *Ecology*, **92**, 1323–1331.
- Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38–49.
- Freeman EA, Moisen G (2008) PresenceAbsence: an R package for presence absence analysis. *Journal of Statistical Software*, **23**, 1–31.
- Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.
- Hamann A, Wang T (2006) Potential effects of climate change on ecosystem and tree species distribution in British Columbia. *Ecology*, **87**, 2773–2786.
- Hampe A (2004) Bioclimate envelope models: what they detect and what they hide. *Global Ecology and Biogeography*, **13**, 469–471.
- Hannah L, Midgley G, Davies I *et al.* (2008) *BioMove-Creation of a Complex and Dynamic Model for Assessing the Impacts of Climate Change on California Vegetation*. California Energy Commission, Sacramento, CA, USA.
- Hasumi H, Emori S (2004) *K-1 Coupled GCM (MIROC) Description*. Center for Climate System Research, University of Tokyo, Tokyo.
- Higgins SI, O'Hara RB, Bykova O *et al.* (2012) A physiological analogy of the niche for projecting the potential distribution of plants. *Journal of Biogeography*, **39**, 2132–2145.
- Iverson L, McKenzie D (2013) Tree-species range shifts in a changing climate: detecting, modeling, assisting. *Landscape Ecology*, **28**, 879–889.
- Iverson L, Schwartz MW, Prasad A (2004) Potential colonization of newly available tree-species habitat under climate change: an analysis for five eastern US species. *Landscape Ecology*, **19**, 787–799.
- Iverson L, Prasad A, Matthews S, Peters M (2011) Lessons learned while integrating habitat, dispersal, disturbance, and life-history traits into species habitat models under climate change. *Ecosystems*, **14**, 1005–1020.
- Lawson DM, Regan HM, Zedler PH, Franklin J (2010) Cumulative effects of land use, altered fire regime and climate change on persistence of *Ceanothus verrucosus*, a rare, fire-dependent plant species. *Global Change Biology*, **16**, 2518–2529.
- Liaw A, Wiener M (2002) Classification and regression by randomForest. *R News*, **2**, 18–22.
- Littell J, Oneil E, McKenzie D, Hicke J, Lutz J, Norheim R, Elsner M (2010) Forest ecosystems, disturbance, and climatic change in Washington State, USA. *Climatic Change*, **102**, 129–158.
- Matthews SN, Iverson LR, Prasad AM, Peters MP, Rodewald PG (2011) Modifying climate change habitat models using tree species-specific assessments of model uncertainty and life history-factors. *Forest Ecology and Management*, **262**, 1460–1472.
- McKenney DW, Pedlar JH, Lawrence K, Campbell K, Hutchinson MF (2007) Beyond traditional hardness zones: using climate envelopes to map plant range limits. *BioScience*, **57**, 929–937.
- McKenney DW, Pedlar JH, Rood RB, Price D (2011) Revisiting projected shifts in the climate envelopes of North American trees using updated general circulation models. *Global Change Biology*, **17**, 2720–2730.
- McKenzie D, Peterson DW, Peterson DL, Thornton PE (2003) Climatic and biophysical controls on conifer species distributions in mountain forests of Washington State, USA. *Journal of Biogeography*, **30**, 1093–1108.
- Meier ES, Lischke H, Schmatz DR, Zimmermann NE (2012) Climate, competition and connectivity affect future migration and ranges of European trees. *Global Ecology and Biogeography*, **21**, 164–178.
- Mitchell TD, Jones PD (2005) An improved method of constructing a database of monthly climate observations and associated high-resolution grids. *International Journal of Climatology*, **25**, 693–712.
- Nakicenovic N, Swart R (eds.) (2000) *Emissions Scenarios: A Special Report of Working Group III of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.
- New M, Lister D, Hulme M, Makin I (2002) A high-resolution data set of surface climate over global land areas. *Climate Research*, **21**, 1–25.
- Pearson RG (2006) Climate change and the migration capacity of species. *Trends in Ecology & Evolution*, **21**, 111–113.
- Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.
- Pope DV, Gallani LM, Rowntree RP, Stratton AR (2000) The impact of new physical parametrizations in the Hadley Centre climate model: hadAM3. *Climate Dynamics*, **16**, 123–146.
- Prentice IC, Cramer W, Harrison SP, Leemans R, Monserud RA, Solomon AM (1992) A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography*, **19**, 117–134.
- R Development Core Team (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available online: <http://www.R-project.org>. R version 3.0.1 (2013-05-16) – “Good Sport” Copyright (C) 2013 The R Foundation for Statistical Computing Platform: x86_64-w64-mingw32/x64 (64-bit).
- Rehfeldt GE, Jaquish BC (2010) Ecological impacts and management strategies for western larch in the face of climate-change. *Mitigation and Adaptation Strategies for Global Change*, **15**, 283–306.
- Rehfeldt GE, Crookston NL, Warwell MV, Evans JS (2006) Empirical analyses of plant-climate relationships for the western United States. *International Journal of Plant Sciences*, **167**, 1123–1150.
- Rogers BM, Neilson RP, Drapek R, Lenihan JM, Wells JR, Bachelet D, Law BE (2011) Impacts of climate change on fire regimes and carbon stocks of the U.S. Pacific Northwest. *Journal of Geophysical Research*, **116**, G03037.
- Schmidt GA, Ruedy R, Hansen JE *et al.* (2006) Present-day atmospheric simulations using GISS ModelE: comparison to in situ, satellite, and reanalysis data. *Journal of Climate*, **19**, 153–192.
- Schwartz MW (2012) Using niche models with climate projections to inform conservation management decisions. *Biological Conservation*, **155**, 149–156.
- Scinocca JF, McFarlane NA, Lazare M, Li J, Plummer D (2008) Technical Note: the CCCma third generation AGCM and its extension into the middle atmosphere. *Atmospheric Chemistry and Physics*, **8**, 7055–7074.
- Shafer SL, Bartlein PJ, Gray EM, Pellier RT (2015) Projected future vegetation changes for the northwest United States and southwest Canada at a fine spatial resolution using a dynamic global vegetation model. *PLoS ONE*, **10**, e0138759.
- Shearer RC (1959) Western larch seed dispersal over clear-cut blocks in northwestern Montana. *Montana Academy of Science, Proceedings*, **19**, 130–134.
- Sitch S, Smith B, Prentice IC *et al.* (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, **9**, 161–185.
- US Geological Survey (1999) Digital representation of “Atlas of United States Trees” by EL Little, Jr. Available at: <http://gsc.cr.usgs.gov/data/little>. (accessed 1 August 2015).
- Westerling AL, Turner MG, Smithwick EAH, Romme WH, Ryan MG (2011) Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. *Proceedings of the National Academy of Sciences*, **108**, 13165–13170.
- Wright AN, Schwartz MW, Hijmans RJ, Bradley Shaffer H (2016) Advances in climate models from CMIP3 to CMIP5 do not change predictions of future habitat suitability for California reptiles and amphibians. *Climatic Change*, **134**, 579–591.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. A list of climate variables used in the species distribution models.

Table S2 and S3. Additional modeling results.

Table S4. Detailed information on the selection of species and relevant biomes.

Figure S1. Maps of the geographic distributions of six tree species and their relevant DGVM-projected biomes.

Figure S2. Bar charts representing the percent change for modeling Pacific silver fir with two different selections of biomes.

Figure S3. Maps of the difference between historical climate and the ensemble of five general circulation models for 15 climate variables.

Figure S4. Maps of the future distribution of Pacific silver fir using two different selections of DGVM biomes.

Figure S5. Maps of predicted presences of the current distribution of Pacific silver fir using two different selections of DGVM biomes.

Figure S6. Maps of the predicted presences for the current distribution of Pacific silver fir using models with a different number of climate variables.

Figure S7. A map showing the overlap between the distribution of Pacific silver fir and the coastal cool forest biome.