Climate Change May Trigger Broad Shifts in North America's Pacific Coastal Rainforests

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Introduction

Climate change threatens biodiversity and ecosystem integrity all over the globe (IPCC, 2014) and is already triggering pronounced shifts of species and ecosystems (Chen et al., 2011; Parmesan et al., 2000). Climate change is also expected to exacerbate effects of forest fragmentation (Bossuyt and Hermy, 2002; Opdam and Wascher, 2004), especially where only small fractions of formerly intact ecosystems remain (Heilman et al., 2002), presumably by magnifying local edge effects (Chen et al., 1995; Harper et al., 2005) and by reducing opportunities for dispersal and range expansion (Thompson et al., 2009; Watson et al., 2013). Thus, mitigating such effects in areas of global conservation importance is critical as biodiversity losses are especially significant.

The conservation importance of the coastal temperate rainforest region of North America is exemplified by the inclusion of six World Wildlife Fund Global 200 ecoregions (Ricketts et al., 1999), some of the most carbon dense ecosystems on earth (Leighty et al., 2006; Smithwick et al., 2002), extraordinarily productive salmon (*Oncorhynchus* spp.) runs and relatively intact forests northward (DellaSala et al., 2011). The highest epiphytic lichen biomass of any forest system also occurs here (McCune and Geiser, 2009). Thus, maintaining extant biodiversity in a changing climate has biodiversity significance on a global scale given the region's importance.

Already confirmed climate change effects in this region include elevated temperatures (Karl et al., 2009), declining mountain snowpack (Mote et al., 2005), shifts in species distributions (Wang et al., 2012), and reduced fog levels (Johnstone and Dawson, 2010). Diminished snowpack combined with late winter freezes has triggered dieback of Alaska yellow-cedar (*Cupressus nootkatensis*) in southeast Alaska (Hennon et al., 2012) and northern British Columbia (Wooten and Klinkenberg, 2011).

Vegetation along the northern Pacific coast has been sensitive to climatic changes since the last glaciation, resulting in large shifts in species distributions, and providing strong evidence that future climate change will result in substantial ecological changes (Brubaker, 1988; Heusser et al., 1985). Even small changes in temperature often result in large species displacements, which

explains contemporary pattern of species distributions along the coastal region (Alaback, 1996). A 125 000-year record of vegetation change from the eastern slope of the Cascades, for example, shows that while species movements are individualistic, depending on species characteristics and geography, at the millennial scale global climatic variation is the dominant factor controlling vegetation distribution (Whitlock and Bartlein, 1997). Conifer species' distributions have changed since the glacial maximum reflecting differences in dispersal ability, effects of refugia, and changes in glacial dynamics from central Alaska southward. The physiography of the region, with north-south tending cordillera, has facilitated species movements, helps explain the rarity of species extinctions in the past, and importance of dispersal in the future if species are to adapt to even more abrupt climatic changes. Additionally, dramatic changes in vegetation in the past 20 000 years (Whitlock, 1992) corresponded to warming of 2.5–7.8 °C (median values, including uncertainty) that is similar to what most general circulation models (GCMs) predict for the Western USA by the end of the twenty-first century (IPCC, 2014).

There is no broad adaptation plan that addresses potential range-wide shifts of ecologically and commercially valuable species in this region, although there is a growing body of relevant adaptation work as reflected by the North Pacific Landscape Conservation Cooperative (NPLCC) of the U.S. Fish & Wildlife Service (http://northpacificlcc.org, accessed October 14, 2014). Our primary objectives were therefore to: (1) model current potential distributions of focal conifers considered of commercial importance to land managers and to project future potential distributions of focal species and broad rainforest vegetation types in response to anticipated climate change; (2) identify areas that may exhibit higher vegetation stability, including those in currently protected areas where biodiversity conservation is emphasized; and (3) illustrate how uncertainty can be addressed in designing effective adaptation strategies in a changing climate.

Notably, attempts to predict future shifts in species' ranges have employed a variety of approaches. One widespread approach, climate envelope modeling, considers the climate conditions where a species is currently or historically distributed and estimates where those same suitable climate conditions are expected to be found in the future based on GCM outputs. This approach has both benefits and shortcomings, which have been thoroughly reviewed (Wiens et al., 2009). A criticism of climate envelope modeling is the strict focus on climate variables with little to no consideration of non-climate drivers such as competition, predation, soils, elevation, and dispersal. Thus, in our assessment of potential climate change effects, we employed both climate envelope models and a dynamic vegetation model, despite differences in input data and analysis scales, to qualitatively compare gross differences regarding the spatial patterns produced. Using correlative and mechanistic modeling approaches independently might increase the reliability of predictions (see Coops and Waring, 2011; Kearney et al., 2010), reducing uncertainties inherent in relying on any individual modeling effort.

Also, in this paper, our findings are used to illustrate some key concepts in climate adaptation planning for managers wishing to maintain extant biodiversity in a changing climate for a rainforest region that straddles two countries (USA and Canada) and large swaths of public and private lands. Additional analyses not presented, including detailed appendices and datasets, are available online (http://databasin.org/articles/172d089c062b4fb686cf18565df7dc57; accessed October 28, 2014).

North America Pacific Coast Temperate Rainforest Region

The Pacific Coast of North America contains the largest proportion of temperate rainforests in the world, representing 35% of the global total (DellaSala et al., 2011). Stretching from the coast redwoods (38° N), California to northern Kodiak Island and Prince William Sound (61° N), Alaska, these rainforests span a wide climatic gradient (Alaback, 1996). Coastal rainforests are associated with cool, moist oceanic air masses, a narrow range of temperature extremes, high frequency of clouds and fog, and high annual precipitation, with most precipitation in the winter (Redmond and Taylor, 1997) and up to 20% in the summer in northern latitudes (DellaSala et al., 2011). The region consists of four distinct rainforest zones that differ climatically and floristically: (1) subpolar – north of southeast Alaska to Prince William Sound and Kodiak Island; (2) perhumid – southeast Alaska to northern Vancouver Island; (3) seasonal – central Vancouver Island to southern Oregon; and (4) warm – southern Oregon coast to San Francisco Bay area (Alaback, 1996; **Figure 1**).

Climate Data

In order to predict potential shifts in species and rainforest distributions, we used the downscaled WorldClim dataset at 30 arc-s (1-km) resolution (Hijmans et al., 2005). We obtained 19 climatic variables for baseline conditions (1950–2000) and for two future time periods (2050s, 2080s) under the A2A ensemble-high-emissions scenario. This scenario assumes continued global population growth and focus on regional economic growth rather than global collaboration. It is one of the scenarios that most closely tracked the emissions trajectory at the time of our 2012 study. Thus, we used three GCMs: CCCMA-CGCM2 (third assessment, Flato and Boer, 2001), CSIRO-MK2 (third assessment, Gordon et al., 2002), and HADCM3 (third assessment – Johns et al., 2003) that covered a broad range of temperature and precipitation projections spanning dry and wet projections.

For climate envelope modeling, we employed a 1000-km buffer on the coastal rainforest study area to capture the entire current ranges of focal species and potential future shifts. Due to the small distribution of coast redwood, the buffer for the baseline model was set to 100 km around the most outer available localities.

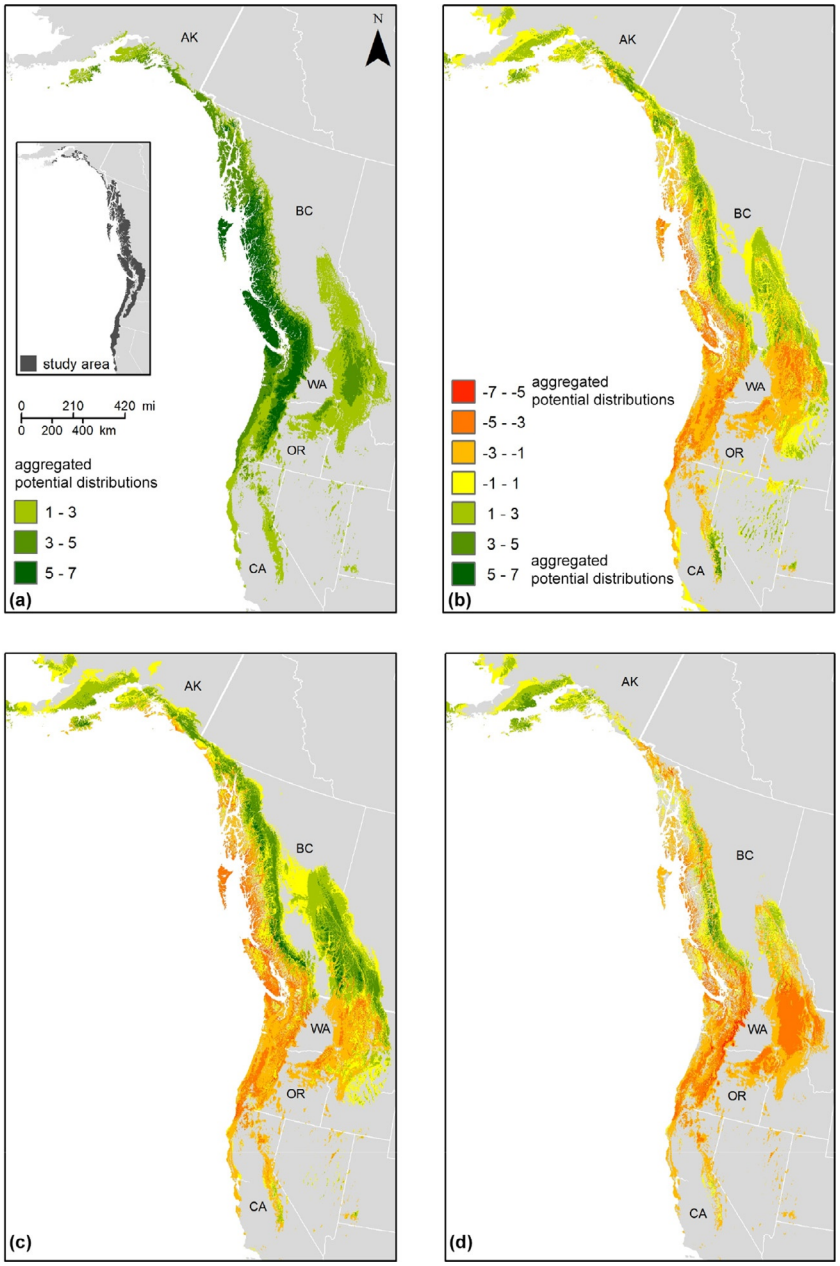

Figure 1 Aggregated potential distribution of eight focal conifer species (Pacific silver and grand fir, Alaska yellow-cedar, Sitka spruce, western red cedar, western and mountain hemlock, coast redwood) for the baseline period (a) and the richness changes for 2080s under scenario A2A ensemble-emissions based on three General Circulation Models (CSIRO (b), CCCMA (c), and HADCM3 (d)).

Selection of Focal Species of Commercial Importance

Based on prior discussions with land managers, we selected eight dominant conifer species of commercial, conservation, and cultural importance to model potential range shifts related to climate change. These species also were chosen because there was readily available location data and their geographic range overlapped primarily with our study area. They included Sitka spruce (*Picea sitchensis*), western and mountain hemlock (*Tsuga heterophylla*, *T. mertensiana*), western red cedar (*Thuja plicata*), Alaska yellow-cedar, Pacific silver and grand fir (*Abies amabilis*, *A. grandis*), and coast redwood (*Sequoia sempervirens*). We did not include other conifers with wide distributions that extended well outside our study area buffer such as Douglas-fir (*Pseudotsuga menziesii*, see Coops and Waring, 2011) or hardwoods (see Hamann and Wang, 2006) given their lower importance to land managers in this region.

Presence-only Modeling of Focal Species

To build the baseline species distribution models, we obtained presence-only data (point and polygon locations) for focal species from numerous databases (USDA Forest Inventory Assessment DataMart v5.1 – apps.fs.fed.us/fiadb-downloads/datamart.html; Biogeoclimatic Ecosystem Classification Program – www.for.gov.bc.ca/hre/becweb/resources/codes-standards/standards-becdb.html, active October 14, 2014; herbaria collections; museum records; published atlases) and from regional specialists that provided more than 30 000 species localities ranging from 710 occurrence points for coast redwood to 7999 points for western hemlock.

Presence-only models outline areas that are predicted as suitable space for a given species according to the predictor dataset (Soberón and Peterson, 2005); these models are known to overestimate realized distributions due to missing information of unvisited locations (Kent and Carmel, 2011). To examine the impact of climate change on species distributions, we only took climatic predictors into account, therefore, focusing on a species' climate envelope (Pearson and Dawson, 2003). Potential distribution was thus determined by projecting this climate envelope across the geographic study area (Soberón and Peterson, 2005).

We applied Maxent 3.3.3k (Elith et al., 2011; Phillips et al., 2006) to model current and future potential distribution for each focal species. Maxent frequently outperforms other presence-only modeling algorithms (Wisz et al., 2008). Instead of real absences, Maxent uses random background points to approximate the best fitting probability distribution for estimating habitat suitability (Elith et al., 2011). We used area under curve (AUC) statistics to assess model discrimination performance (Phillips et al., 2006). All models were replicated 25 times using the bootstrap replicate run type. The final average outputs were used for further analyses. The species datasets were split into 70% training and 30% test data sets randomly chosen for each model run.

We used jackknife procedures from initial model runs to exclude predictors that showed low importance in predicting included presence points when modeled in isolation, expressed by low values of model gain. We activated the 'fade by clamping' option in Maxent to mitigate clamping issues arising from projection values extending beyond the range of training data (Phillips et al., 2006) and chose the logistic output format. The automatic feature selection was applied since it has been validated with respect to a broad range of species, environmental conditions, numbers of occurrences, and degrees of sample selection bias (Phillips and Dudík, 2008). Using ARCGIS 10, the continuous grid outputs of the Maxent models were transformed into binary data showing either potential presence or modeled absence of a given species based on species-specific thresholds that minimized falsely excluded presences while retaining the similarity to published ranges (Little, 1978). Thus, for every species we created one baseline (1950–2000) potential distribution layer and six future potential distribution layers based on the two time periods (2050s, 2080s) and three GCMs.

Identifying Areas of Persistence, Gain, and Loss

For each focal species, we analyzed and mapped differences and commonalities between current and all variants of future potential distributions that were categorized as: (1) 'persistent distribution' where baseline and future potential distributions overlap, (2) 'distribution gain' where baseline potential distributions are absent but future potential distributions are present, and (3) - 'distribution loss' where baseline potential distributions are present but future potential distributions are absent. This is important for managers wishing to assess broad patterns in species distributions related to projected climate changes.

GCM outputs may differ widely, leading to variation in output among different climate envelope projections (Beaumont et al., 2008). Using three GCMs that spanned much of the range of possible futures, from wetter to drier and from faster warming to slower warming, allowed us to assess the level of disagreement among model output as an indirect measure of model uncertainty for managers wishing to plan for future distribution shifts. Importantly, we were able to assess climate envelope model outputs regarding model uncertainty inherent in climatic projections: uncertainty being lowest in areas where future potential distributions of all model projections showed a full consensus (spatial agreement) and highest in cases where they completely differed (Araújo and New, 2007). Obviously, model uncertainty is still inherent based on the complexity of climate and ecological systems, the potential for unexpected events related to climate change, and human behavior concerning greenhouse gas emissions abatement. Nonetheless, we propose that projections with relatively high agreement among models are useful in predicting broad trends important in robust reserve design and forest management decisions.

We calculated Cohen's kappa coefficients (K) (R Development Core Team, 2013 v. 2.1.12), indicating the degree of agreement (Fielding and Bell, 1997) between baseline and future potential distribution for all modeled species in order to quantify possible divergences in potential distributions over time as a proxy for expected shifts in species distribution (online appendix).

Outputs of climate envelope models can also be used to compile richness maps based on aggregated potential species distributions (McKenney et al., 2007). We used binary, aggregated potential distributions of focal tree species as an index of broad potential changes in species richness patterns across the entire study area.

Future Vegetation Stability, Intact Late-Seral Forests, and Current Protection Schemes

In addition to potential species shifts, we used the MC1 dynamic vegetation model outputs, biogeography module (Bachelet et al., 2001) to assess potential stability of dominant types of vegetation under a changing climate. The MC1 model was derived from physiologically based biogeographic rules derived from the MAPSS model (Neilson, 1995) adapted to dynamic environmental gradients using site production information (Bachelet et al., 2001). While the Maxent climate envelope analysis (above) focused on individual rainforest species and species richness, the MC1 output provided information on overall functional types of potential vegetation (temperate coastal needleleaf forest, for example) but not individual species. We compiled MC1 outputs produced under current and future climatic conditions using three GCMs (third assessment models): Hadley (HadCM3; Johns et al., 2003), MIROC (Hasumi and Emori, 2004), and CSIRO (Gordon et al., 2002) under the A2 emissions scenario. MC1 explicitly simulates vegetation dynamics, nutrient cycles and dynamic impacts of disturbance due to fire and has been used in analyses of vegetation responses to climate change (Lenihan et al., 2008). However, MC1 does not incorporate anthropogenic disturbances such as timber harvest, agriculture, urbanization, invasive species introductions, and human-wildfire ignition sources.

All applied MC1 model outputs have a 1/12°, unprojected, grid-cell resolution that is nominally 8-km (Daly et al., 2008). We assessed vegetation stability by comparing the dominant type of vegetation predicted to be supported under modeled baseline conditions (1961–1990) to that predicted to be supported for two future time periods (2035–45 and 2075–85). We identified areas as 'stable' or 'unstable' based on whether the future climate is expected to continue to support the same dominant vegetation type through late-century based on agreement across the three GCMs.

Notably, Pacific coastal temperate rainforests are highly fragmented in southern locales, which may be more vulnerable to large-scale changes in precipitation and temperature if magnified by local edge effects. Therefore, we accessed the most current intact late-seral rainforest datasets to identify areas that overlap with stable vegetation areas as potential refugia (Keppel et al., 2012; Olson et al., 2012; Watson et al., 2013). For intactness, we downloaded the only seamless forest fragmentation dataset available for the entire Pacific coastal temperate rainforest region and published in 1995 (http://databasin.org/datasets/7f72a68ac6c343bda3ffff4bef3926de; accessed October 28, 2014).

We also intersected protected area feature classes with the MC1 stability areas to determine areas that are currently protected and projected to support climatically stable vegetation types overtime. In the USA, we used GAP status codes 1 ('strict') and 2 ('relaxed') obtained from the Protected Area Database (PAD-US CBI edition v1.1). In most cases, this database does not include administrative protections such as late-successional reserves of the Northwest Forest Plan (USFS and BLM, 1994) unless they overlapped with more stringent protections such as Wilderness and Congressionally Withdrawn Areas. The protected area data in British Columbia were obtained from Global Forest Watch Canada. Thus, we were able to show how areas of future stable vegetation, current late-seral forests and protected areas coincide in order to assess if the current conservation scheme across the entire region is well adapted to climate change or not.

Climate Envelope Model Evaluation and Most Important Climate Parameters

For the focal species, the AUC values based on the test data averaged across Maxent model runs ranged from 0.82 (western hemlock) to 0.93 (coast redwood), indicating that the models satisfactorily discriminated between presence and background information (online appendix).

The two most influential variables from the Worldclim dataset that most frequently show highest prediction power among the predictive Maxent models for focal species were 'Precipitation of Coldest Quarter' and 'Precipitation of Driest Quarter' (online appendix).

Key Findings for Focal Species and Rainforest Assemblages

Shifts of Potential Species Distributions

Aggregated potential distributions of focal conifer tree species predicted a shift for all applied GCMs by 2080s (**Figure 1**). More detailed species by species analysis are available in the online appendix. Although the intensity of shifts differed slightly among GCMs, the overall pattern showed a substantial reduction of aggregated potential species distributions for large parts of the seasonal and warm rainforest zones (south) and a broadly stable richness pattern of aggregated potential species distributions along the perhumid zone (north) – except for some northerly, island parts, and rain shadow areas (e.g., Olympic Peninsula). Quantitative comparisons of potential species distributions through time periods indicated that future distributions, in part, differ substantially compared to their baseline counterparts (**Table 1**). Averaged Cohen's kappa coefficients across all species and applied GCMs per time period revealed that differences are more pronounced by 2050s ($K=0.71$) compared to 2080s ($K=0.57$) in relation to baseline distributions.

By 2080s, potential distributions of western red cedar, Sitka spruce, and western hemlock show marked persistence (55–82%) mainly in northern portions of their range with minor contractions (2–7%) in the south (**Table 1**, **Figure 1**). Pacific silver fir, grand fir, Alaska yellow-cedar, and mountain hemlock had more substantial reductions (15–39%) in potential distributions throughout their range by 2080s. Coast redwood is expected to experience reduction of nearly one-fourth of its modeled climate envelope by 2080 (**Figure 2**, inset). Small (3%) climate related potential distribution gains were possible to the north; however, these are gone by 2080.

Table 1 Percent of baseline (1950–2000) potential distribution loss, persistence, and gain for focal species in the Pacific Coastal temperate rainforest by two time periods (2050s, 2080s), the A2A ensemble-emissions scenario, and full agreement among three General Circulation Models (CCCMA-CGCM2; CSIRO-MK2; and HADCM3)

Species	*Period*	*Loss (%)*	*Persistence (%)*	*Gain (%)*
Western red cedar	2050s	4	65	18
	2080s	6	59	28
Sitka spruce	2050s	0	83	9
	2080s	2	82	15
Western hemlock	2050s	4	74	8
	2080s	7	55	12
Pacific silver fir	2050s	24	35	3
	2080s	39	21	5
Grand fir	2050s	20	35	6
	2080s	36	17	10
Alaska yellow-cedar	2050s	8	66	4
	2080s	21	34	4
Moutain hemlock	2050s	7	59	7
	2080s	15	33	4
Coast redwood	2050s	21	16	3
	2080s	23	1	0

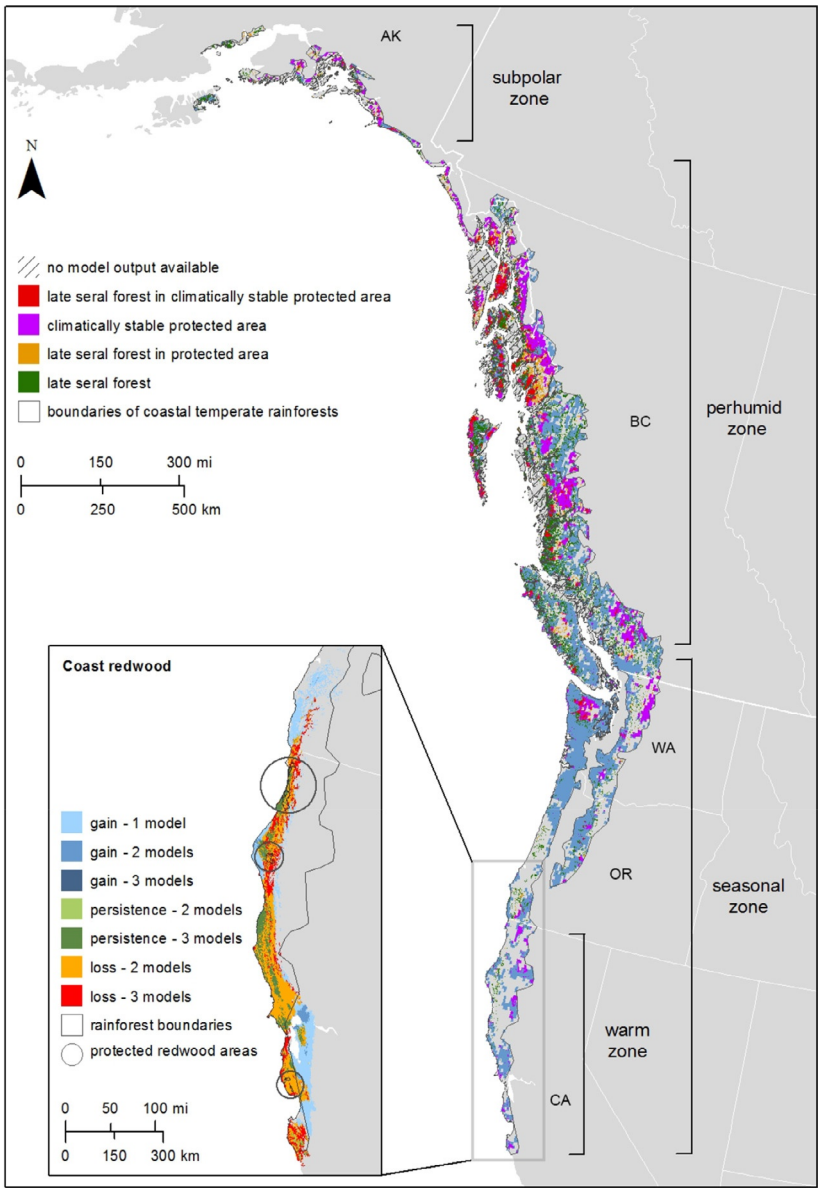

Figure 2 Predicted areas of vegetation stability (scenario A2, 2080s), protected areas, and late-seral forests in the Pacific coastal rainforests. Inset map shows potential distribution gain, persistence, and loss of coast redwood based on three GCMs (CSIRO, CCCMA, and HADCM3). The three circled areas in the redwood insert indicate protected areas where redwoods are currently found. Only the upper circled area has parks that coincide with projected redwood persistence in green.

Future State of the Ecosystem and Conservation Areas

Results from the MC1 dynamic vegetation model largely resembled the pattern obtained from climate envelope models on a broader scale (Figure 3 vs. Figure 1). Areas with potentially stable dominant vegetation communities were most densely spread across the perhumid zone and the coastal regions of the northern seasonal zone while southern areas changed more dramatically as also depicted in the species distribution models. In general, northern regions are expected to retain climate suitable for the baseline dominant vegetation types through 2080s, mostly the maritime evergreen needleleaf (e.g., western hemlock, Sitka spruce) type. Unstable areas also occur in the North, including portions of the Queen Charlotte and Haida Gwaii island and much of the mid and southern British Columbia coastline where temperate deciduous broadleaf woodland (e.g., red alder, *Alnus rubra*) is expected to expand, and the Kenai Peninsula of Alaska where the climate is expected to be more suited to temperate cool mixed forest rather than the baseline needleleaf forest. The climate currently supporting baseline subalpine forest in many areas is expected to shift toward conditions more suitable for patches of maritime evergreen needleleaf forest, temperate evergreen needleleaf forest, and temperate deciduous broadleaf forest.

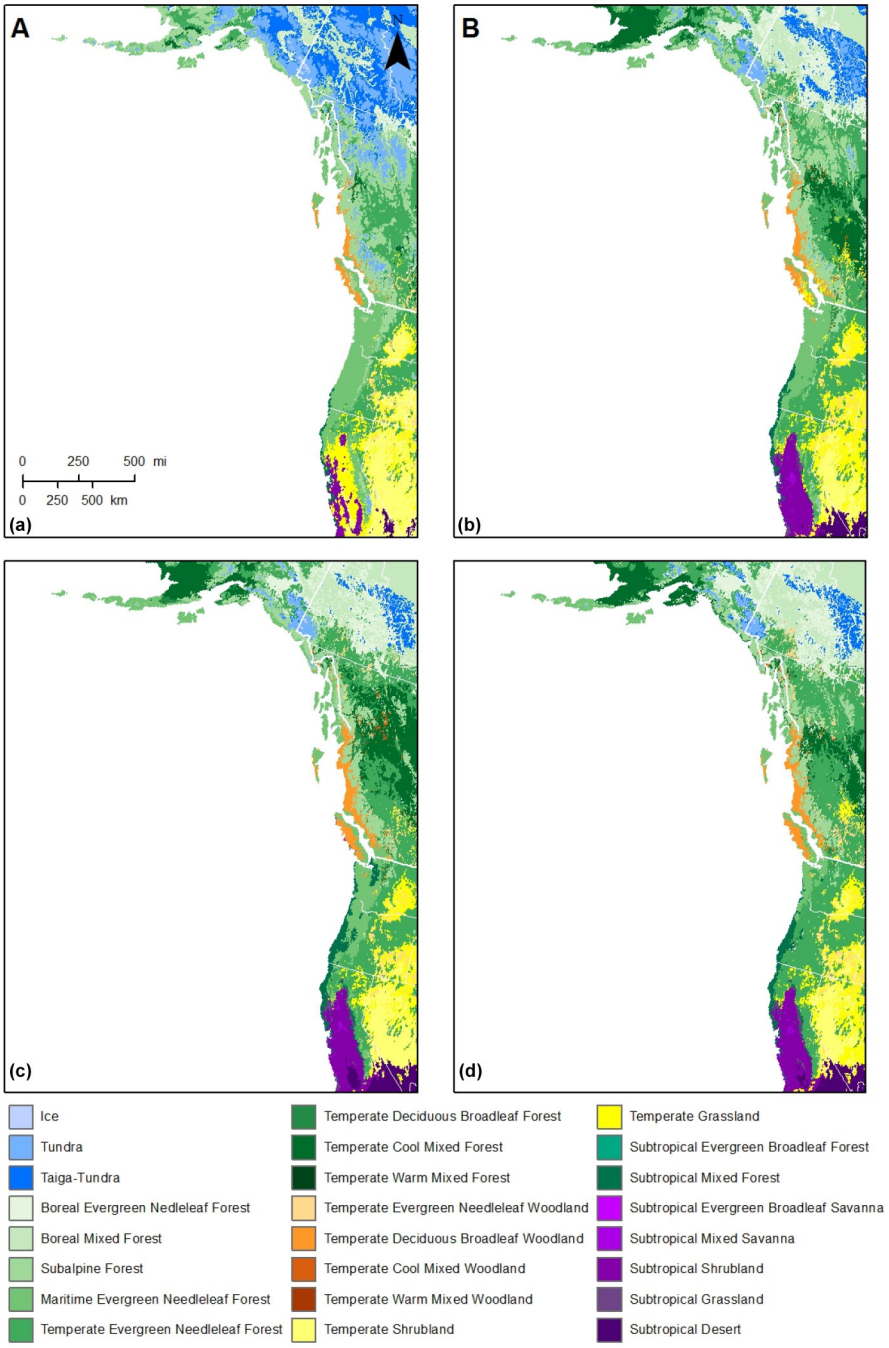

Figure 3 Outputs from MC1 functional vegetation model show baseline (a) and future dominant types of vegetation for 2080s (2075–85) based on three GCMs: CSIRO (b), MIROC (c), and HADCM3 (d).

In southern areas, shifts in dominant vegetation types were well dispersed throughout the warm zone and within the seasonal zone, especially the Cascades and southern coastal areas. For instance, starting just north of the Oregon/California border, the climate niche supporting maritime evergreen needleleaf (redwood, Douglas-fir zone) is expected to contract.

There was often a mismatch between current protected areas of coastal temperate rainforests with areas of future potential stability in dominant vegetation types, or with larger extents of late-seral forests, in particular, within the perhumid zone where older forests are especially concentrated and relatively intact (see Figure 2). This pattern was also shown when the proportion of vegetation stability for all protected areas that are completely located within the study area is plotted per state or province that intersects the coastal temperate rainforests (Figure 4). For instance, Washington and Oregon show the lowest vegetation stability, British Columbia the highest.

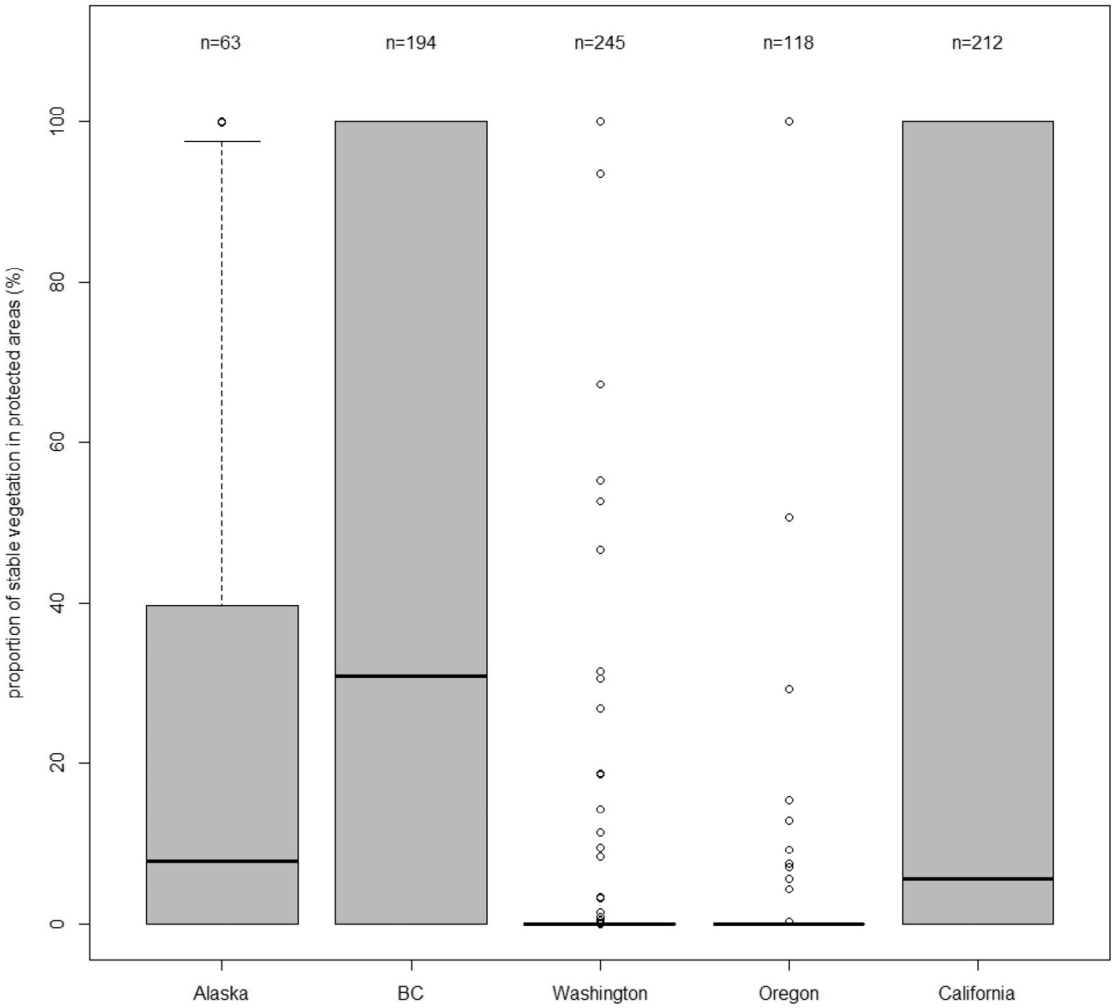

Figure 4 Predicted vegetation stability in protected areas per state or province derived from outputs of the MC1 model based on the agreement of three GCMs under the A2 scenario for 2080s (2075–85) (BC = British Columbia).

Relevance to Climate Adaptation Strategies and Land Management

Shifting Potential Distributions as a Surrogate for Ecosystem Change

Our focal species results correspond well with recent literature on range shifts of tree species caused by climate change (Chen et al., 2011; Hickling et al., 2006; Parmesan and Yohe, 2003; Shafer et al., 2001; Wang et al., 2012) and, while the magnitude of shifts differed, the trends were similar. For instance, using different GCMs than ours, Hamann and Wang (2006) found the distribution of western hemlock may increase by 50% over baseline area in British Columbia, shifting up in elevation and northward under the A2 emissions scenario by 2085. Coops and Waring (2011) also found a 50% gain for western hemlock and for other coastal

conifers that are likely to remain 'highly adapted' through the 2080s under the A2 emissions scenario. Others also have predicted northward shifts and shrinking baseline ranges of tree species in North America (McKenney et al., 2007; Murphy et al., 2010).

We found a core zone featuring the highest richness of potential focal species distributions in British Columbia between Vancouver Island and southeast Alaska, and areas of higher potential vegetation stability in these same areas. These regions could potentially act as refugia for temperate rainforest conifer species and assemblages and, because they have the lowest levels of forest fragmentation, may also be relatively insulated from edge-related local climate effects (Chen et al, 1995; Harper et al., 2005). Similarly, both approaches indicated greater loss and instability in the southern portion of the study area, particularly within the seasonal zone, supporting the generalized patterns of declining focal species richness southward.

What Is Driving the Projected Shifts?

A downside of our modeling approaches is that they do not provide us with definitive information on what is driving the projected shifts in communities or species. However, increases in frequencies and duration of extreme events have been documented in many regions and are expected to increase (Field et al., 2012). Extreme events are expected to be the primary drivers for many species and ecosystem impacts (Jentsch and Beierkuhnlein, 2008). Droughts have been correlated with elevated rates of forest dieback in North America due to water deficiency (Birdsey and Pan, 2011; Michaelian et al., 2011; van Mantgem et al., 2009), and might thus be crucial drivers of future distribution of temperate rainforest (DellaSala et al., 2011). For instance, water deficit may contribute to reductions of species distributions (both aggregated and species-specific) in the drier, southern parts of coastal temperate rainforests in our study area. However, declining low elevation snow and summer fog (southern rainforest distribution), not modeled in our study, might have a bigger effect on the distribution of yellow-cedar (Hennon et al., 2012) and coast redwood (Johnstone and Dawson, 2010), respectively, than the climate variables that we modeled. Further, projected increases in fires in southern rainforest areas may exacerbate climate-related changes to rainforest assemblages (Littell et al., 2009).

Model Limitations and Uncertainties

Climate envelope models are often criticized for relying on over-simplistic assumptions such as equilibria among species and their environment, omitting other predictors such as biotic interactions that might determine the fundamental niche (Araújo and Pearson, 2005), and lacking predictor quality (Soria-Auza et al., 2010). Biotic interactions and dispersal limitations are known to contribute to mismatches between model outputs and reality (Soberón and Peterson, 2005; Zimmermann et al., 2009). However, climate envelopes are known to perform best at a regional scale because they show general ecological trends and patterns (Boucher-Lalonde et al., 2012; Warren, 2012), as was the case in our study area. Moreover, the Worldclim predictor set is currently the most abundantly used set of climatic parameters, and to date the only one allowing for high resolution predictive modeling on a global scale. The applied model scale is appropriate, especially for species featuring smaller ranges or for modeling of complex terrain (Seo et al., 2009).

The MC1 dynamic vegetation model has been frequently used to investigate potential ecosystem vulnerability to climate change (Gonzalez et al., 2010). Comparing static climate envelope predictions with the dynamic MC1 vegetation model outputs revealed a more robust pattern (Kearney et al., 2010) of the bigger picture of shifting vegetation types across the Pacific coastal temperate rainforest region and also allowed us to apply our results on different data and spatial scales.

None of the models integrate human disturbances. There is no quantitative connection between Maxent and MC1 model outputs because focal tree species do not fully coincide with broad vegetation types. However, information derived from both model types complement each other on a coarse level and thus can more reliably inform management decisions by reducing uncertainty arising from any one model alone (also see Coops and Waring, 2011 for similar cross-model applications). Moreover, we propose that human impact is most likely to increase throughout the region, thus our models most likely under-estimate climate change effects exacerbated by human disturbance.

Rainforest Management Implications

At broad spatial scales, northern coastal regions and their protected areas (BC, Alaska) may be more resilient to climate change than southern areas that are highly fragmented and more vulnerable to edge effects (also see Thompson et al., 2009). That pattern holds true for coastal regions compared to interior drier regions (Wang et al., 2012) perhaps because of climatic buffering of maritime climates. Our results therefore are important for maintaining ecological integrity and climate resilience in high priority conservation areas from north to south such as the Tongass Rainforest of Alaska, Great Bear rainforest of BC, Olympic National Park of Washington, portions of the Western Cascades, and coast redwoods (DellaSala et al., 2011). Notably, ecological integrity and climate resilience are emphasized in the 2012 National Forest Planning Rule and climate resilience is emphasized in President Obama's Climate Action Plan (Executive Office of the President, 2013). Thus, the largely intact nature of the Tongass National Forest should provide important opportunities for meeting both policy objectives and for the northward expansion of rainforest communities in the face of climate change. Managers may also increase resilience potential by maintaining or restoring climatically stable vegetation along elevation and north-south gradients to accommodate shifting distributions. However, the slightly reduced richness of potential distributions and climatic instability in southern parts of the region show that some of the currently protected old forest stands are also vulnerable to climate change (online appendix) and may require additional actions. In particular, declines

in yellow-cedar may warrant consideration of assisted migration if this species is not able to colonize new climate spaces (Loss et al., 2011).

The Great Bear rainforest located in the perhumid zone is among the world's last remaining large extents of old-growth rainforest (DellaSala et al., 2011). Large portions of this rainforest show vegetation stability under a changing climate, including large extents of remaining old forest and high richness of focal tree species' potential distributions. Thus, we suggest that this region might also serve as broad-scale refugia if sufficiently protected from anthropogenic stressors that might exacerbate climate change impacts (Thompson et al., 2009; Watson et al., 2013).

Olympic National Park is situated in the seasonal rainforest zone and features exceptional plant richness, including many unique epiphytes (McCune and Geiser, 2009). Climate envelope richness of focal tree species is high within the core area of the park suggesting upslope shifts assuming melting glaciers. Importantly, the boundary regions of the park, including old-forest stands, show potential stability (online appendix) but are surrounded by highly fragmented private lands where conservation incentives are needed to retain stable dominant vegetation.

The Western Cascades are a secondary rainforest belt located in the northern portion of the seasonal zone that has been subjected to intensive logging. Lower resilience to climate change is indicated by unstable vegetation and decreasing climate envelope richness of focal tree species. Large proportions of remaining old forest remnants will likely be affected. While the larger protected areas, such as North Cascades National Park, Glacier National Park, and Alpine Lakes Wilderness show potential vegetation stability, some smaller areas (generally <1000 km^2) may experience climate-related stress to the dominant vegetation (online appendix).

Coast redwoods are situated in the warm zone within the most southern region of coastal temperate rainforests; the last, heavily diminished, redwoods are a conservation priority (Noss, 2000) and the apparent vulnerability of redwood to climate change in a significant portion of its range adds to conservation significance. Restorative actions within higher stability but previously logged areas may help to alleviate climate stressors for redwood. In addition, it is possible that redwood is resilient, at least initially, to shifts in its climate niche as increased growth rates measured in old-growth redwood forests are thought to be related to a lengthening of the growing season (Sillett et al., 2010). Our projections indicate that this apparent positive climate response of redwood might be short lived due to its projected shrinking climate niche.

Conclusions

Future temperate rainforest communities of the Pacific Coast of North America may persist mainly in northern latitudes and upper elevations where land-use disturbances are less likely to exacerbate changes to the focal species' climate envelope. They also may persist in pockets of relatively stable microrefugia (e.g., north-facing older forests) in the south if buffered from human disturbances (Olson et al., 2012). Projected changes in dominant vegetation types and focal species distributions, and identification of relatively stable intact patches, can aid managers in developing strategies for persistence of extant rainforest communities. Our work also provides valuable management insights into where important tree species may require assisted migration (e.g., yellow-cedar and redwood).

Finally, we note that in the time to peer review and publish this manuscript (>2 years) climate change models have been updated (IPCC, 2014). Thus, our projections need to be continuously updated (every five years or when new models come out) based on ongoing refinements to downscaled GCMs. Nevertheless, our broad-scale findings should prove useful in helping managers with comprehensive adaptation planning now for climate shifts in rainforest species and assemblages over a large region in order to avoid ecologically costly lags in conservation and management options given climate shifts are already underway.

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