Assessing Climate Change Vulnerability of Species in Northwestern North America

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Abstract

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Climate change affects plants and animals in myriad ways. However, not all species respond similarly, making climate-informed management more difficult. Therefore, managing species in the face of climate change requires an understanding of which species are most susceptible and what factors will increase their vulnerability. Vulnerability can be seen as being a function of sensitivity, exposure, and adaptive capacity. Using these three components, vulnerability assessments can identify (1) which species are most vulnerable, (2) why those species are vulnerable, and (3) which factors can be potentially leveraged to reduce vulnerability. Here, I present three chapters that explore these vulnerability components and offer a methodology for assessing vulnerability to climate change. The first chapter uses a combination of scientific literature and expert knowledge to assess the relative climate-change sensitivity of 196 plant and animal species in the Pacific Northwest region of North America. I found that although there are highly sensitive species in each of the taxonomic groups analyzed, amphibians

and reptiles were, as a group, estimated to be more sensitive to climate change than the other taxa we considered. I also demonstrate how sensitivity and confidence information can be combined to prioritize management action and future research needs. Such information will increasingly enable managers to identify which species are more sensitive and identify the key aspects that can be leveraged to increase resilience in the face of climate change. The second chapter focuses on a novel approach of modeling species distributions. Here, I demonstrate an approach to projecting climate impacts on species distributions that draws on information from both empirical and mechanistic models. These mechanistically-informed models projected less suitable environmental space than our unrefined models for the majority of species analyzed. Although the two modeling approaches projected similar trends of expansion and contraction for most species, the locations of expansion and contraction differed by approach. The results of this study demonstrate that informing empirical niche models with mechanistic model output can reduce the likelihood of over predicting suitable environmental space. Future projections from these refined modeling approaches offer insight into the location of these suitable areas and which species may be better able to persist in a changing climate. The third chapter incorporates sensitivity, exposure, and adaptive capacity to assess the relative vulnerability to climate change of 11 tree species in western North America. I used a multivariate approach to quantify elements of sensitivity to climate change, exposure to climate change, and the capacity to adapt to climate change. Of the 11 species that were analyzed, Garry oak (*Quercus garryana*) was determined to be the most vulnerable, largely due to its relatively high sensitivity. By contrast, big leaf maple (*Acer macrophyllum*) was determined to be the least vulnerable of the 11 species, largely due to its adaptive capacity. Our analyses provide a framework for assessing vulnerability and for determining why some species will likely be more vulnerable than others. Such information will

be critical as natural resource managers and conservation practitioners strive to address the impacts of climate change with limited funds.

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Introduction

Conservation and natural resource practitioners are faced with the daunting task of managing species in the face of multiple challenges including climate change. Warming temperatures, changing precipitation patterns, and alterations in disturbance regimes are already affecting species across North America (Root et al. 2003, Parmesan 2006, Fischlin et al. 2007, Chen et al. 2011). Plants are flowering earlier (e.g., Cayan et al. 2001, Abu-Asab et al. 2001, Parmesan and Yohe, 2003), species distributions have changed (Parmesan 2006, Kelly and Goulden 2008, Iverson and McKenzie 2013), and species are experiencing changes in the timing of life cycle events, such as migration, breeding, and hatching (Brown et al. 1999, Crick and Sparks 1999, Parmesan and Yohe 2003). Climatic changes have also led to local extinctions of some populations of high-elevation species, such as the American pika (*Ochotona princeps*) (Beever et al. 2003). However, not all species respond similarly to climatic change (Davis and Shaw 2001), making climate-informed management more difficult.

Managing species in the face of climate change requires an understanding of which species are most susceptible and what factors will increase their vulnerability. Vulnerability to climate change has been defined as "the extent which a species or population is threatened with decline, reduced fitness, genetic loss, or extinction owing to climate change" (Dawson et al. 2011). Vulnerability can be seen as being a function of sensitivity, exposure, and adaptive capacity. The sensitivity of an individual species is generally characterized by its ability to withstand changes in climate. Such sensitivity is largely a product of a species' natural history including life history traits, interspecific relationships, physiological factors, dependencies on sensitive habitats, and relationships with disturbance regimes. Exposure can be defined as the

degree of climatic change or climate-induced change likely to be experienced by a species (Dawson et al. 2011). Exposure is determined by the character, magnitude, rate, and variability of climate change and can be derived from projected changes in climate and climate-driven fire regimes, hydrology, invasive species, and land–use. Adaptive capacity can be defined as the ability of a species to cope with climate change by persisting in situ or moving to more suitable locations (Dawson et al. 2011). This ability to respond physiologically or behaviorally to the effects of climate change is influenced by both intrinsic and extrinsic factors such as, reproductive strategy, genetic variability, phenotypic plasticity, dispersal distance and barriers, and landscape permeability.

Using sensitivity, exposure, and adaptive capacity, vulnerability assessments can identify (1) which species are most vulnerable, (2) why those species are vulnerable, and (3) which factors can be potentially leveraged to reduce vulnerability (Williams et al. 2008). Several recent studies that have assessed climate–change vulnerability for birds (Gardali et al. 2012), rare plants (Anacker et al. 2013), and trees (Devine et al. 2012, Coops and Waring 2011). Many of these vulnerability studies have largely relied on assessing one or two vulnerability components but generally do not explicitly assess all three: sensitivity, exposure, and adaptive capacity.

Here, I present three chapters that explore these vulnerability components and offer a methodology for assessing vulnerability to climate change. The first chapter uses a combination of scientific literature and expert knowledge to assess the relative climate-change sensitivity of 196 plant and animal species in the Pacific Northwest region of North America. Species sensitivity is influenced by life-history traits such as, physiology and genetics, interspecific relationships, habitat associations, dispersal abilities, and disturbance regimes. These factors can

affect a species' sensitivity through changes in temperature, precipitation (or moisture), carbon dioxide concentrations, pH, and salinity. Species with narrow tolerances are clearly more sensitive to a changing climate and climatic extremes than are species with broader tolerances (Bernardo and Spotila 2006). Therefore, I combined information on species requirements and tolerances to create a sensitivity metric, rank each species' sensitivity to climate change, and assess species and habitat factors contributing to climate sensitivity among taxonomic groups. Then, with the help of collaborators, I built a publicly available on-line database of this information to aid in managing species in changing climates (see www.climatechangesensitivity.org).

The second chapter focuses on a novel approach of modeling species distributions. Here, I demonstrate an approach to projecting climate impacts on species distributions that draws on information from both empirical and mechanistic models. Specifically, I used a multi-step process to apply projections from the Lund-Potsdam-Jena Dynamic Global Vegetation Model (LPJ-DGVM) (Sitch et al. 2003) into empirical species distribution model projections. I thus identified areas that were both climatically suitable based on empirical evidence and were ecologically suitable based on multiple physiological, ecological, and environmental mechanistic drivers. For each species, I first determined which of the biome types predicted by the DGVM were likely to be suitable for each of the seven tree species. I then built an empirical species distribution model based on species presences and absences, in which the presences that were interpolated from digital range maps were intersected with the identified suitable biomes. To project future species distributions, I first ran the DGVM with five future climate projections to project the future distribution of biomes. Then, I used the same climate projections as input to the empirical models to projected future species distributions. The final step involved intersecting

the biome projections and the species distribution projections. 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 carbon dioxide concentrations, interactions with other basic plant functional types, and fire) and where the climate is likely to be suitable for the species I compared the projections of these models to those of simple empirical species distribution models based solely on species' current distributions.

Finally, the third chapter incorporates all three vulnerability components (sensitivity, exposure, and adaptive capacity) to assess the relative vulnerability to climate change of 11 tree species in western North America. I used a multivariate approach to quantify elements of sensitivity to climate change, exposure to climate change, and the capacity to adapt to climate change. With the help of collaborators, I conducted a series of workshops throughout the Pacific Northwest region to synthesize knowledge and insight on species sensitivity and adaptive capacity from experts and groups of experts. Combining this information with climate-change projections and information gleaned from the literature, I assessed vulnerability using a four–step approach. First, I compiled expert knowledge of the 11 tree species to produce estimates of sensitivity for each. Second, I assessed potential exposure by quantifying the magnitude of climate change projected across the range of each species. Third, I assessed each species' adaptive capacity using information on a species' reproductive strategy, dispersal ability, and climate breadth derived from the literature and expert knowledge. Finally, I quantified the multivariate dissimilarity between each species and a highly vulnerable reference species to assess relative vulnerability and better inform future forest management in the region.

Chapter 1: Relative sensitivity to climate change of species in the Pacific Northwest, North America

Abstract

Climate change affects plants and animals in myriad ways. Furthermore, not all species respond in the same way to changing climatic conditions. Therefore, managing species in the face of climate change will require an understanding of which species will be most sensitive to future climate change and what factors will make them more or less sensitive. The inherent sensitivity of species to climate change is influenced by many factors, including physiology, life-history traits, interspecific relationships, habitat associations, and relationships with disturbance regimes. Using a combination of scientific literature and expert knowledge, we assessed the relative sensitivity to climate change of 196 plant and animal species in the Pacific Northwest region of North America. We found that although there are highly sensitive species in each of the taxonomic groups analyzed, amphibians and reptiles were, as a group, estimated to be more sensitive to climate change than the other taxa we considered. We also explored the relative contribution of different factors to sensitivities across taxonomic groups and found that a dependence on one or more sensitive habitats most often contributed to sensitivity for birds, mammals, and amphibians and reptiles. We demonstrate how sensitivity and confidence information can be combined to prioritize management action and future research needs. Such information will increasingly enable managers to identify which species are more sensitive and identify the key aspects that can be leveraged to increase resilience in the face of climate change.

Introduction

Conservation and natural resource practitioners are faced with the daunting challenge of managing species in the face of multiple challenges including climate change. Warming temperatures, changing precipitation patterns, and alterations in disturbance regimes are already affecting species across North America (Root et al. 2003, Parmesan 2006, Fischlin et al. 2007, Chen et al. 2011). Plants are flowering earlier (e.g., Cayan et al. 2001, Abu-Asab et al. 2001, Parmesan and Yohe, 2003), species distributions have changed (Parmesan 2006, Kelly and Goulden 2008, Iverson and McKenzie 2013), and species are experiencing changes in the timing of life cycle events, such as migration, breeding, and hatching (Brown et al. 1999, Crick and Sparks 1999, Parmesan and Yohe 2003). Climatic changes have also led to local extinctions of some populations of high-elevation species, such as the American pika (*Ochotona princeps*) (Beever et al. 2003). However, not all species respond similarly to climatic change (Davis and Shaw 2001), making climate-informed management more difficult. Managing species in the face of such changes will require an understanding of which species will be most susceptible to future climate change and what factors will increase vulnerability or resilience.

Vulnerability to climate change can be defined as the extent to which a species or population is threatened with decline, reduced fitness, genetic loss, or extinction because of climate change and is a function of sensitivity, exposure, and adaptive capacity (Dawson et al. 2011). *Sensitivity* to climate change is the degree to which a species' survival, persistence, and reproduction is dependent on particular aspects of climate that are likely to change in the future (Dawson et al. 2011). A species can be directly sensitive to climatic factors (e.g., experiencing reduced growth at higher temperatures) or indirectly sensitive (e.g., unable to reproduce when fire is frequent). In general, an individual species' sensitivity reflects its ability to withstand

changes in climate and climate-induced environmental conditions – e.g., more sensitive species will have reduced survival or fecundity with smaller changes in climate. Such sensitivity is largely a product of a species' natural history. *Exposure* is determined by the character, magnitude, rate, and variability of climate change and can be derived from climate–change projections. Exposure can also include the indirect effects of climate change as expressed through both climate–driven and non-climate-driven changes in, for example fire regimes, hydrology, invasive species, and land–use. *Adaptive capacity* is the ability of a species to cope with climate change by persisting *in situ* or moving to more suitable locations (Dawson et al. 2011). This ability to respond physiologically or behaviorally to the effects of climate change is influenced by a number of factors including, but not limited to genetic variability, phenotypic plasticity, and evolutionary rates.

The sensitivity of a species to climate change is influenced by life-history traits, physiology, genetics, interspecific relationships, habitat associations, dispersal abilities, and its relationship to disturbance regimes. These factors can affect a species' sensitivity through changes in temperature, precipitation (or moisture), carbon dioxide concentrations, pH, and salinity. Although all species have physiological tolerances to temperature and moisture, species with narrow tolerances are more sensitive to a changing climate and climatic extremes than are species with broader tolerances (Bernardo and Spotila 2006). Examples of species' narrow physiological tolerances are turtles with temperature-dependent sex ratios in their offspring (Hawkes et al. 2007), fish with low maximum water-temperature tolerances (Schindler et al. 2003), and some high-elevation species with narrow thermal tolerances, such as the American pika (Smith 1974).

Some species are also more sensitive to climate-induced changes because they depend on ecological relationships that might change with climate, such as facilitative and competitive interactions and predator-prey relationships (Parmesan 2006). For example, in Yellowstone National Park, changes in winter conditions or wolf-pack size (i.e., *Canis lupus*) affect the availability of carrion, and hence the abundance of scavengers such as grizzly bears (*Ursus arctos horribilis*) that depend on carrion (Wilmers and Getz 2005). Without these predators, this community is less resistant to the effects of climate change (Wilmers and Post 2006).

Species that require specific habitats that are known to be sensitive to climatic change are likely more sensitive than habitat generalists. For example, Cascade torrent salamanders (*Rhyacotriton cascadae*) are found only in cold-temperature streams within a limited elevation range west of the Cascade crest. These very specific habitats are sensitive to warming temperatures and will likely shrink as temperatures warm (Mantua et al. 2010). Other species that rely on vernal pools, seasonal streams, alpine areas, or coastal lowlands and estuaries should also be more sensitive to climate change.

Species that are dependent on the particular nature (i.e., frequency and intensity) of a disturbance regime or stressor, such as fire, will be more sensitive than species that can tolerate a wide range of disturbances or a lack of disturbances. For instance, subalpine larch (*Larix lyallii*) is sensitive to an increase in fire frequency and intensity because it has adapted to relatively long fire–return intervals (e.g., up to 500 years) by having thin bark and not producing large quantities of seeds until trees are at least 80 years old (Arno and Habeck 1972; Arno 1980). Because, continued warming and earlier spring snowmelt are expected to continue in the future resulting in more frequent large wildfires and longer wildfire seasons (Littell et al. 2010, Rogers et al.

2011, Westerling et al. 2011), this sensitivity to fire frequency and intensity may make the subalpine larch particularly sensitive to climate change.

Much of what defines a species' sensitivity to climate change is a product of its natural history. Two of the predominant sources of information about species' natural histories are the scientific literature and expert knowledge. Scientific literature, including descriptions of both observational studies and experiments, can provide estimates of species' sensitivities, but often only for well-studied species (Williams et al. 2008). The critical maximum temperature, above which animals cannot survive, has been identified for at least two Pacific Northwest salamanders: southern torrent salamander (*Rhyacotriton variegatus*) and coastal giant salamander (*Dicamptodon tenebrosus*) (Bury 2008). The thermal tolerances of these two salamanders are among the lowest known for amphibians, but it is recognized that these data are limited in geographic scope and are available for only few salamander species (see Brattstrom 1963, Metter 1966, de Vlaming and Bury 1970, Claussen 1973, Bury 2008).

In the absence of observational or experimental data, expert knowledge can augment published natural history information with information from the scientific literature, empirical data, and unpublished studies. Experts tend to incorporate uncertainty from multiple sources such as incomplete natural history (McBride and Burgman 2012). However, expert knowledge can also be susceptible to biases due to personal experiences and attitudes (Shrader-Frechette 1996, Camerer and Johnson 1997, Ludwig et al. 2001, Campbell 2002).

Global studies have assessed sensitivity, exposure, and adaptive capacity. For instance, nearly 36% of bird species analyzed in California were found to be vulnerable to climate change after scoring and ranking sensitivity and exposure factors (Gardali et al. 2012). Of these vulnerable species, birds that were associated with wetland habitats were the most vulnerable. Of

100 European butterfly species analyzed, those with northern distributions were generally more vulnerable to climate change than butterfly species with southern distributions (Heikkinen et al. 2006). Although there was large species-to-species variation in this analysis, the inclusion of life-history characteristics, data on species distributions, climate, land cover, and topography strengthened the overall assessment of species susceptibility to climate change. Other climate change vulnerability assessments have used index-based tools, such as the NatureServe Climate Change Vulnerability Index (available online)[1]. This tool applies information about a species' natural history, distribution, and landscape circumstances to predict whether species will likely suffer a range contraction or possible population declines due to climate change (Byers and Norris 2011, Furedi et al. 2011, Hoving et al. 2013). Although these assessments make a significant contribution to assessing the vulnerability of species, they do not explicitly assess the key components of a species' inherent sensitivity to climate change and therefore do not identify the relative contribution of different factors across taxonomic groups.

Here, we assessed the relative sensitivity to climate change of 196 plant and animal species in the Pacific Northwest region of North America. We combine information on species requirements and tolerances from literature reviews and expert knowledge to create a sensitivity metric, rank each species' sensitivity to climate change, and assess species and habitat factors contributing to climate sensitivity among taxonomic groups. We also assess the degree to which species' sensitivities are associated with their level of endangerment. We then built a publically available on-line database of this information to aid in managing species in changing climates (see www.climatechangesensitivity.org).

[1] https://connect.natureserve.org/science/climate-change/ccvi

Methods

Study Area

Our study area is the Pacific Northwest, a region in northwestern North America that includes the states of Washington, Oregon, Idaho in the U.S. and the province of British Columbia in Canada. The region is bounded by the Pacific Ocean to the west, the Rocky Mountains to the east, the Great Basin to the south, and the boreal forest to the north, and is extremely diverse in climate, geology, topography, and vegetation (Pojar and MacKinnon, 2004). The climate of the Pacific Northwest is heavily influenced by the Pacific Ocean and numerous mountain ranges. Species in the Pacific Northwest reflect the diverse habitats they inhabit, which range from wet maritime coastal forests to arid shrub steppe in the dry interior. Many species can be found within a small area due to steep elevation gradients, a richness of environments, and complex disturbance histories and regimes.

Species

We assessed the sensitivity to climate change of 196 species: 114 birds, 35 mammals, 27 plants, and 20 amphibians and reptiles. The species were chosen based on common interests and priorities of multiple conservation and natural resource management groups (U.S.D.A. Forest Service, U.S.D.I. Park Service, U.S.D.I. Fish and Wildlife Service, Washington State Department of Fish and Wildlife, Oregon State Department of Fish and Wildlife, Idaho State Department of Fish and Game, and The Nature Conservancy).

Data Acquisition

We identified species experts and invited them to participate in ten workshops or to work independently to record information about nine factors of sensitivity (described below). Experts had a diversity of backgrounds and experience but all held advanced graduate degrees in ecology, forestry, or biology. Experts were affiliated with the following agencies and organizations: U.S. Forest Service, U.S. National Park Service, U.S. Fish and Wildlife Service, U.S. Bureau of Land Management, Washington Department of Natural Resources, Washington Department of Fish and Wildlife, Oregon Department of Fish and Wildlife, Idaho Department of Fish and Game, University of Washington, University of Idaho, Idaho Cooperative Fish and Wildlife Research Unit, Washington Natural Heritage Program, Canadian Forest Service, Parks Canada, The Nature Conservancy, Defenders of Wildlife, and a number of Tribes and First Nations. All species accounts were completed between 2009 and 2012.

The goal of the expert workshops was to identify the sensitivities of species to climate change by answering a series of questions related to each of the sensitivity factors described below, details of which can be found online[2]. To counter some of the inherent biases of expert judgment, we formalized our workshop procedure by first having the group work methodically through one of the species on the list. This process demonstrated the use of the database and calibrated the experts' scoring systems. The procedure of working through an example species as a group provided the experts some training on assessing sensitivity, provided them an opportunity to ask questions and get clarification, and ensured that participants were interpreting

[2] www.climatechangesensitivity.org

the questions in a similar way. After the example species was completed, experts either broke into groups or worked independently to assess the sensitivity of additional species. Experts had access to relevant literature to help their sensitivity assessment, but many did not finish all their species during the workshops and completed them at a later date. In some cases, individual experts worked independently to assess the sensitivity of species and relied heavily on the scientific literature. Nonetheless, these individuals were also trained to assess sensitivity by working through an example species.

For each of the sensitivity factors below, experts provided both a sensitivity score ranging from one (low sensitivity) to seven (high sensitivity) and a confidence score ranging from one (low confidence) to five (high confidence). Confidence scores represent how certain experts were about their sensitivity score. Individual scores were averaged when more than one expert assessed the sensitivity of a species. Experts also provided more detailed comments and citations when they were available. For the majority of species, sensitivities were assessed across their entire range, but there are some for which the experts identified a smaller geographic region (e.g., Idaho). Hereafter, we identify these smaller geographic extents only for those relevant species.

Sensitivity Factors

Individual species' sensitivities were assessed based on nine factors. These included: 1) whether the species is generalist or specialist, 2) aspects of physiology, 3) life-history characteristics, 4) whether the species depends on sensitive habitats, 5) dispersal distances and the presence of barriers, 6) dependence on disturbance regimes, 7) climate-dependent ecological relationships, 8) interacting non-climatic stressors, and 9) other aspects of sensitivity not

previously captured. These factors were chosen because they were identified as important in defining the sensitivity of species to climate change by experts.

Generalist/Specialist. Species that are specialists or that have relationships that are dependent on a relatively small number of other species are generally more likely to be sensitive to climate change than are generalists (Gilman et al. 2010). Experts were asked to rank the degree to which a species is a generalist or a specialist. They then identified which, if any, of the following factors make the species more of a specialist: predator-prey relationships, foraging dependencies, seed-dispersal dependencies, host plant dependencies, phenological dependencies, pollinator dependencies, or other dependencies.

Physiology. The ability of a species to tolerate changes in climate directly contributes to its sensitivity. Experts were asked to rank the species physiological sensitivity from low to high and to identify which of the following climate, and climate-change related, factors contribute to its physiological sensitivity: temperature, precipitation, salinity, pH, carbon dioxide, and dissolved oxygen.

Life-History. Experts were asked to rank species as being more r-selected—species with many offspring and a short generation time—or more k-selected—species with few offspring and high parental investment.

Sensitive Habitats. Species that depend on specific habitats that are known to be sensitive to climate change are likely to be more sensitive than species that do not rely on these habitats.

Experts were asked to determine upon which of the following sensitive habitats species are dependent: coastal lowlands, marshes, estuaries, and beaches, seasonal streams, wetlands and vernal pools, seeps and springs, alpine and subalpine areas, grasslands and balds, rocky intertidal zones, ecotones, or other habitats not already listed. This list was a product of expert input and was refined during the first two or three workshops. The scoring for sensitive habitats was either 7 (one or more sensitive habitats were identified) or 0 (no sensitive habitats were identified).

Dispersal Ability. The capability of a species to move across the landscape will likely affect its ability to respond to climate change and thus will contribute to its overall sensitivity. Experts were asked to identify the maximum annual dispersal distance—the maximum distance it would be feasible for a species to move within one year to establish a new population in a more suitable habitat. Experts ranked dispersal ability on a scale of over 100 km (low sensitivity, "1") to less than 1 km (high sensitivity, "7"). Experts were also asked to identify and quantify the presence of dispersal barriers on a scale from none to many (7).

Disturbance Regimes. Changes in the intensity and frequency of disturbances will likely affect some species more than others. Experts were asked to rank how sensitive species are to one or more disturbance regimes, from not sensitive to the nature of any disturbance regime to highly sensitive to the nature of one or more disturbance regimes. Experts were then asked to identify to which of the following disturbance regimes the species is sensitive: fire, flooding, wind, disease, drought, pollution, urbanization, pathogens, pests, or other.

Ecological Relationships. Species that have ecological relationships that are likely to be altered in the face of climate change will likely be more sensitive than those species that do not. Experts were asked to identify which of the following relationships are sensitive to climate change: forage, predator-prey, habitat, hydrological, competition, or "other". They were then asked to identify which types of the following climate and climate-driven changes in the environment affect these relationships: temperature, precipitation, salinity, pH, carbon dioxide, or other. Finally, the experts ranked how sensitive the species' ecological relationships are to the effects of climate change.

Interacting Non-Climatic Stressors. The sensitivity of species can be greatly affected by the degree to which other non-climate-related threats, such as habitat loss, already affect the species. Species that are greatly affected by other stressors may be more sensitive to climate change. Experts were asked to identify non-climate-related threats from the following: habitat loss or degradation, invasive species, other interspecific interactions, direct human conflict (including harvesting), pollution, and other. Experts were then asked to rank the degree to which those threats make the species more sensitive to climate change.

Other Sensitivities. We found that the majority of the time experts were able to assess a species' sensitivity using the aforementioned factors. For species with unique natural histories, there were other aspects of sensitivity that could not be captured with the above set of criteria; therefore, we asked the experts to identify and rank these other factors that make the species more sensitive to climate change. Experts then assigned a relative weight to "other" sensitivity factors, for each species, ranging from 0.2 to 5. For example, a weight of 1.5 meant that the "other sensitivity"

factor was 1.5 times the weight of any previous factor in influencing a species' sensitivity to climate change.

After the sensitivity factors were identified and scored, we then calculated an overall climate-change sensitivity score using a weighted, additive algorithm (equation 1) and an overall confidence score by averaging the individual confidence scores for each sensitivity factor, for each of the 196 species. Our weighting of the sensitivity index is, in part, the result of many discussions that we had with experts about the relative importance of each sensitivity factor and the weights are based on collective expert input. However, we recognize that others might weight these factors differently and that other approaches of quantifying sensitivity could result in different rankings. We explored two alternative approaches including: a multiplicative algorithm (see equation 2) and a multivariate distance metric calculated between the sensitivity scores for each species and a hypothetical low sensitivity reference score (Smith et al. 2003) (detailed below).

(*equation 1*)

[(1/2 * Generalist/Specialist) + Physiology + (1/2 * Life-History) + Sensitive Habitats + Dispersal Ability + Disturbance Regimes + Ecological Relationships + Interacting Non-Climatic Stressors + (Other * Weight)] / (49 + (7 * Weight (if present))) * 100.

(*equation 2*)

[(1/2 * Generalist/Specialist) * Physiology * (1/2 * Life-History) * Sensitive Habitats * Disturbance Regimes * Ecological Relationships * Interacting Non-Climatic Stressors * (Other * Weight (if present))] / [3.5^2 * 7^6 * (7 * Weight (if present))].

For the multiplicative algorithm, we converted all zero scores to 0.1 before calculating the sensitivity score. Although the additive index was normally distributed, the multiplicative algorithm was log normally distributed and therefore we log-transformed the scores before comparing with the other metrics. The multivariate distance metric has been previously applied to assessing vulnerability by calculating the Euclidean distance between a vector of variable values representing current conditions of each watershed and a vector representing a hypothetical "natural" state (Smith et al. 2003). Applying the same method, we created a hypothetical reference species that had all extremely low sensitivity scores (Smith et al. 2003). We then calculated Pearson's correlation coefficients between each of the three sensitivity approaches.

In addition to the nine factors above, we also asked experts for their overall opinion of how sensitive the species is to climate change. Although this overall ranking was not used in the calculation of the sensitivity score, it was used as a qualitative-control metric. For instance, if the ranking of all nine sensitivity factors resulted in a low sensitivity score but the expert's overall opinion was that the species was highly sensitive to climate change, we either missed an important factor in our assessment or the expert may have interpreted one of our questions differently than we did. Therefore, when there was a large discrepancy between the sensitivity score and the overall expert opinion, we followed up with the experts to identify what was missed or misinterpreted. It was discrepancies such as these that led us to add the "other sensitivities" category described above. The addition of this category greatly reduced the number of discrepancies between the index score and the overall opinions of the experts.

Relationship between sensitivity and conservation status

We explored the relationship between current conservation status and sensitivity to climate change for the 196 species by comparing sensitivity scores among species using a 2-sample *t*-test when groups were normally distributed and a Mann-Whitney *U* test ($\alpha = 0.10$ in both cases) when groups were not normally distributed. However, some of the species that we assessed were chosen precisely because they are currently at-risk, that is they are listed as endangered, threatened, candidate, sensitive, species of concern, or species to monitor for federal or state-level listings. Therefore, we evaluated whether listed species were predisposed to having higher sensitivity scores than non-listed species by quantifying differences in a) overall sensitivity scores among listed and non-listed species b) non-climatic stressor scores among listed and non-listed species, and c) removing the non-climatic stressors factor from the overall sensitivity scores and evaluating differences among listed and non-listed species.

Results

The amphibians and reptiles that were analyzed for this study were determined to be more sensitive to climate change (median score of 76) than were birds (median score of 52), mammals (median score of 54), and plants (median score of 48) (Fig. 1, $P < 0.001$). Interestingly, the taxonomic group with the largest number of species, birds, also had the smallest range of scores: 21 to 71, compared to 36 to 90 (amphibians and reptiles), 19 to 80 (mammals) and 21 to 83 (plants). The overall confidence for each species also varied by

taxonomic group; plants and amphibians and reptiles had a median confidence score of four (out of five), whereas birds and mammals had a median score of three (out of five). These results show that some species are clearly more sensitive to climate change than others and that experts had relatively high confidence in their scores (Fig. 2).

Drivers of Sensitivity

Of the nine sensitivity factors that were assessed, a dependency on one or more sensitive habitats was the factor that was most often ranked highly for birds, mammals, and amphibians and reptiles—although physiology had almost as many high rankings for amphibians (Fig. 3). Notably, 69% of the bird species, 61% of the mammals, and 90% of the amphibians and reptiles had one or more sensitive habitats identified. For the plant species in our dataset, dispersal ability was most often highly ranked. Most of these relatively high scores were 5's (out of 7), which represented a dispersal ability of 5 to 25 km.

Not surprisingly, the sensitive habitats that were identified for the four taxonomic groups differed greatly. For birds, the most frequently identified sensitive habitats included coastal lowlands, marshes, estuaries, beaches, and intact grassland and balds (Fig. 4a). For mammals and amphibians and reptiles, "other" habitats were most often listed as sensitive habitats. These other habitats included sagebrush steppe, salt desert, peat lands, sphagnum moss bogs, mature forests or late-successional forests, and ponderosa pine woodlands. The second most often identified sensitive habitat for mammals was "alpine/subalpine" (Fig. 4b). For amphibians and reptiles, seasonal streams and "other" were most often identified as sensitive habitats (Fig. 4c). The "other" category for amphibians and reptiles included microclimates within forests and forested

talus, headwater streams, springs, and seeps of temperate, forested areas. The sensitive habitats most often identified for plants included alpine/subalpine and grasslands and balds (Fig. 4d).

The taxonomic groups also differed greatly with respect to proportional sensitivity to the other eight factors (Fig. 4). For example, many amphibian species were determined to be physiologically sensitive to climate change but relatively few bird and plant species were. Similarly, life-history played a large role in the sensitivity of many mammal species, but did so for far fewer of the species in the other taxonomic groups. Finally, non-climatic factors were more important for a higher percentage of bird species than for any of the other groups.

The Most Sensitive Species

Birds

The marbled murrelet (*Brachyramphus marmoratus*), great gray owl (*Strix nebulosa*), and the northern spotted owl (*Strix occidentalis caurina*) were the most sensitive to climate change of the bird species analyzed (Appendix A). However, the reasons for their relatively high sensitivity scores were different. For example, marbled murrelets are highly sensitive to changes in their breeding habitat, primarily late-successional forests that are within 50 to 75 km of the coast (Ralph et al. 1995). Marbled murrelets are also tightly linked to their forage habitat – near-shore waters within 5 km of the coast and at depths of up to 40 m (Raphael et al 1995) and the availability of suitable prey (i.e., offshore forage fish).

Great gray owls depend on cold high-elevation habitats in the Pacific Northwest and are also relatively sensitive to climate change. They have thick plumage that makes them intolerant of summer heat. The availability of nest sites in areas with relatively cold temperatures is an important limiting factor in the dispersal of these birds. The availability of prey also greatly

affects great gray owl populations because they feed almost exclusively on voles (*Microtus spp*.), pocket gophers (*Thomomys spp*.), and other small mammals (Bull and Duncan 1993). During years with low prey numbers, great gray owls often unsuccessfully compete with other owl species for food (e.g., great horned owl (*Bubo virginianus*), long-eared owl (*Asio otus*), and boreal owl (*Aegolius funereus*)).

The northern spotted owl is sensitive to climate change in part because it only has one brood per season and is sensitive to changes in its preferred habitat and prey. For example, the northern spotted owl predominately forages on northern flying squirrels (*Glaucomys sabrinus*) in the northern portion of its range and dusky-footed woodrats (*Neotoma fuscipes*) in the southern portion (Gutiérrez et al. 1995). Because of this, the distribution of the northern spotted owl corresponds with the prey's range. Indirect effects of climate change such as changes in disturbances (i.e., fire and insect infestations) can greatly affect northern spotted owl habitat. The owl is also highly sensitive to the presence of the larger, more aggressive barred owl (*Strix varia*), whose range is expanding. Barred owls can interbreed with the northern spotted owl, compete for similar food resources, and are known to displace northern spotted owls from their territories (Hamer 1988, Hamer et al. 1994).

There were 64 bird species that were listed as endangered, threatened, candidate, sensitive, species of concern, or species to monitor for federal or state-level listings. However, the sensitivity scores for bird species with these designations were not significantly different than sensitivity scores for bird species without the designations ($P > 0.1$). There was also no difference between 1) interacting non-climatic stressor scores for bird species that had federal or state designations and bird species with no designations ($P > 0.1$) and 2) sensitivity scores

without the interacting non-climatic factors for birds with and without listing designations ($P > 0.1$).

Mammals

Woodland caribou (*Rangifer tarandus caribou*) (northern Idaho and northeast Washington), Keen's bat (*Myotis keenii*) (Olympic Peninsula, WA), and little brown bat (*Myotis lucifugus*) (Olympic Peninsula, WA) were deemed to be the most sensitive to climate change of the mammal species analyzed (Appendix B). The woodland caribou is relatively sensitive due in large part to its specialized winter diet of arboreal lichens and its limited reproductive capacity. Woodland caribou are also dependent on high-elevation habitats and are particularly sensitive to fire. By contrast, both Keen's bat and little brown bat are not sensitive to changes in disturbances but are very sensitive to changes in microclimate, especially during periods of torpor or winter hibernation. This is especially relevant for these two species of bats on the Olympic Peninsula because they do not migrate. Both Keen's bat and little brown bat are also tightly linked to the timing and availability of insect prey, and therefore warmer temperatures could alter the timing or length of winter hibernation. Changes such as these could make these bats metabolically active at a time when insect prey is not available.

One third of the mammal species that were analyzed were listed as endangered, threatened, candidate, sensitive, species of concern, or species to monitor for federal or state-level listings. The sensitivity scores for mammal species with these designations were significantly higher than sensitivity scores for mammal species without the designations ($P < 0.05$). The species that were listed also had higher non-climatic stressor scores ($P < 0.05$) and

higher sensitivity scores without the interacting non-climatic stressors ($P < 0.05$) compared to species with no designations.

Plants

Coastal sand verbena (*Abronia latifolia*) and slickspot peppergrass (*Lepidium papilliferum*) were determined to be the most sensitive to climate change of the plant species analyzed (Appendix C). Both species are considered to be specialists because of the habitat on which they grow. Coastal sand verbena grows on sand dunes along the Pacific Northwest coast and slickspot peppergrass grows on a specific substrate in the shrub-steppe ecosystem in southern Idaho. Slickspot substrate is generally composed of small depositional patches of soil covered in a cryptogamic crust of cyanobacteria and algae with high sodium content and distinct clay layers. Both species are also highly sensitive to disturbances. Coastal sand verbena is sensitive to wind because coastal winds maintain and shift sand dunes, whereas slickspot peppergrass is highly sensitive to anthropogenic disturbances such as livestock trampling and off-road vehicle use, fire, flooding, and drought (USFWS 2009). Slickspot peppergrass is also physiologically sensitive to changes in temperature, precipitation, soil salinity, soil pH, and atmospheric carbon dioxide concentrations.

Only two plant species, slickspot peppergrass and whitebark pine (*Pinus albicaulis*), were considered to be at-risk species (listed as threatened and candidate species for Idaho, respectively). Both species had relatively high sensitivity scores and non-climatic stressors scores compared to the rest of the plant species without listing designations.

Amphibians and Reptiles

Western toad (*Anaxyrus boreas*) (North Cascade Mountains) and coastal tailed frog (*Ascaphus truei*) were determined to be the most sensitive of the amphibian and reptile species analyzed (Appendix D). Both species are sensitive to temperature changes, dependent on sensitive habitats such as seasonal streams, and highly sensitive to hydrological changes and to interacting non-climatic stressors such as habitat loss and degradation. However, the western toad is relatively more sensitive to disturbances regimes, such as flooding, drought, and disease. The western toad has also been experiencing a rapid and unexplained decline across its range, which could be attributed in part to infectious diseases, such as *Batrachochytrium dendrobatidis* and ranavirus (Schock et al. 2010).

The majority of amphibian and reptile species analyzed (64%) are listed as endangered, threatened, candidate, sensitive, species of concern, or species to monitor for federal or state-level listings. The sensitivity scores for these species were significantly higher than sensitivity scores for amphibian and reptile species without the designations ($P < 0.05$), even after the non-climatic stressors factor was removed ($P < 0.05$). Amphibian and reptile species that were listed also had higher non-climatic stressors scores compared to species with no listing designations ($P < 0.05$).

Robustness of the index

The sensitivity index is relatively robust to minor changes in its formulation. We found that removing any one of the nine sensitivity factors produced relatively little change in the sensitivity rankings (see Appendix E). Although the rankings did change somewhat when

calculating sensitivity with the multiplicative algorithm, for the most part, the most sensitive and least sensitive species generally remained in their respective rankings.

Discussion

Our results indicate that species vary in their degree of sensitivity to climate change and in the key factors influencing their sensitivities. Within taxonomic groups, the drivers of climate sensitivities were more similar than among taxa. With the exception of the birds, the spread of sensitivity scores is relatively similar across all taxonomic groups (Fig. 1), indicating that experts identified a relatively wide range of individual species sensitivities. The drivers of these sensitivities also varied by species, but were more consistent within taxonomic groups. Although sensitive habitats were most often indicated as impacting a species' sensitivity, each taxonomic group had unique combinations of factors that led to high sensitivity scores (Fig. 4).

For instance, some amphibians were identified as being relatively sensitive because of their physiological sensitivity, limited dispersal abilities, dependence on seasonal streams and the associated terrestrial forest habitats, and for being susceptible to climate-influenced diseases—consistent with previous studies (Blaustein et al. 1994, Pounds et al. 2006). Earlier spring snow melt due to warming temperatures or a transition from snow melt-dominated to transient rain-snow watersheds may shorten the hydro-period and cause some seasonal streams to dry up earlier in the year (Elsner et al. 2010). Therefore, changes in forest management, such as restricting clear-cut logging along seasonal streams, may be warranted in some places to retain canopy cover. Full canopy cover will help maintain cooler stream and stream-habitat temperatures and minimize overall temperature and moisture stress for amphibians (Bury and Corn 1988). Buffer zones that provide shade and reduce sedimentation may be required to ensure

suitable habitat for coldwater amphibian species (Vesely and McComb, 2002, Bury, 2004, Sarr et al., 2005, Olson et al., 2007).

Habitats that are recognized as being sensitive to climate change were routinely identified as contributing to a species' overall sensitivity score. The selection of this factor was important in identifying the most sensitive species for birds, mammals, and amphibians and reptiles. For birds, grasslands and balds were most frequently identified in this study, indicating that protection and restoration of these habitats in the Pacific Northwest may be warranted in light of climate change. Experts identified that four of the six most sensitive bird species depend on grasslands or balds at least once during their life cycle and that some of these systems are already threatened by invasive species such as cheatgrass (*Bromus tectorum*) (Bradley 2009), land-use change, and climatic and climate-induced changes such as changes in precipitation and fire (Bachelet et al. 2001, Rogers et al. 2011, Raymond and McKenzie 2012).

Species that rely on climatically sensitive habitats, such as alpine areas, are threatened with diminishing area and ever more isolated populations as temperature warms (Sekercioglu et al. 2008, Villers-Ruiz and Castañeda-Aguado 2013). Therefore, to ensure that these species persist, managers may want to focus on removing non-native species, preventing future establishment of undesired competitors and diseases, and facilitating reintroductions and assisted migration of desired species. Other management options in alpine areas may include tree removal and prescribed fire, but fire risk and air quality should be considered (Raymond et al. 2013).

For plants, sensitive habitats were significant in determining sensitivity but they were not as frequently identified as dispersal ability. Few plant species assessed for this study are able to move more than 1 km per year and most were believed to have a moderate number of dispersal

barriers. Furthermore, nearly 80% of the plants assessed in this study were tree species. Some have suggested that with a projected rate of temperature change of 300 to 500 m per year (Loarie et al. 2009), the rate of tree migration will likely be surpassed (Nathan et al. 2011, Zhu et al. 2012). Although there is evidence of rapid migration of some tree species (see Clark et al. 1998), many plant species have more anthropogenic barriers now than in the early Holocene when species last underwent a major climate-driven migration in response to rapidly warming temperatures. Therefore, to promote more resistant and resilient plant communities, managers may consider identifying suitable genotypes through provenance trials (Schmidtling 1994) and then planting the appropriate genotypes in new locations of their future climatic optima (Rehfeldt et al. 2006, Aitken et al. 2008). Silvicultural tools, such as thinning, can also be applied to target the release or recruitment of species that are more adapted to projected climate (i.e., warmer, drier summers).

Our results also indicate that mammals, plants, and amphibians and reptiles that already have federal or state-level listing designations are likely to be more sensitive to climate change than those that do not. Although these species tend to have more non-climatic stressors that will make them more sensitive to climate change, these indirect effects of climate change are not necessarily what makes them more sensitive to climate change than non-listed species. After removing the non-climatic stressors score from the sensitivity index, listed mammals, plants, and amphibians and reptiles still had significantly higher sensitivity scores than non-listed species. Interestingly, listed bird species do not appear to be more sensitive to climate change than non-listed bird species.

Species that already have federal or state-level listing designations and that were found to be sensitive to climate change may be even more threatened in the future. Whitebark pine and

Canada lynx may be examples of such species. Whitebark pine is currently listed as "Candidate Species for Endangered Species Protection" by the U.S. Fish and Wildlife Service, and was determined to have relatively high sensitivity to climate change in this study due to its high-elevation habitat and threats from interacting non-climatic stressors, such as the mountain pine beetle (*Dendroctonus ponderosae*) and the non–native fungus, white pine blister rust (*Cronartium ribicola*). Canada lynx (*Lynx canadensis*), which lives within North America boreal forest, was listed as "Threatened" by the U.S. Fish and Wildlife Service in 2000. This listing was designated largely due to the inadequacy of existing regulatory mechanisms to protect the species across its range. However, this listing has not considered the impacts of climate change, which may also shrink the available habitat considerably. Therefore, whitebark pine, Canada lynx, and other species may be more threatened by climate change than previously identified.

Our results also demonstrate that climate change may lead to more "at-risk" species that will require federal or state-level listing. For example, only 2 of the 27 plant species had listing designations. Although these two species were found to be relatively sensitive to climate change, there were other species with higher or similarly high sensitivity scores that are not currently listed. There were also a number of birds (e.g., Clark's nutcracker, *Nucifraga columbiana*), mammals (little brown bat), and amphibians and reptiles (black salamander, *Aneides flavipunctatus*) that are also relatively sensitive but not currently listed. Some of these un-listed species are sensitive to climate change and may require federal or state protection in the future.

We focused on 196 species that are of interest to regional wildlife management agencies and organizations and demonstrated that some species are more sensitive to climate change than others. However, sensitivity information alone cannot be used to assess vulnerability. For instance, species with high sensitivity, high adaptive capacity, and low exposure may not be very

vulnerable to climate change compared to a species with high sensitivity, low adaptive capacity, and high exposure. The vulnerability of species can also vary throughout their range, with some locations having higher exposure than other areas. Future research could combine the results of this study with assessments of species-specific exposure and adaptive capacity to quantify vulnerability. Our results also highlight a lack of basic life-history information for many of the species analyzed. This lack of information is evident when examining the average confidence scores across all species – 60% – with birds and mammals having lower average confidence scores than plants and amphibians and reptiles (see Appendices A-D).

Although sensitivity information alone cannot be used to assess vulnerability, it is evident that experts are relatively certain that many of the analyzed species in this study are sensitive to climate change (Fig. 2). This finding indicates that appropriate adaptation may be needed for these species. By contrast, only a small portion of the species that were assessed had low certainty. Therefore, it may be prudent for conservation managers to monitor these species, giving preference to the individuals with higher sensitivities, and continually assess future changes. Species with low sensitivity and a high confidence score may be less of a concern and require less monitoring and adaptation. This type of assessing and prioritizing could help conservation and natural resource practitioners better understand how climate change might impact species across our region.

Although we considered nine climate change sensitivity factors in this study, some of these factors could be considered to represent adaptive capacity and could be used to identify the most adaptable species. For example, population growth rates can be an aspect of adaptive capacity because species that can recover from low numbers rapidly are more likely to withstand rapidly changing climates and colonize new locations following climate disruption (Pianka

1970). Rapid population growth can also help maintain genetic variability. Dispersal ability could also be a factor of adaptive capacity because species that are poor dispersers will be less likely to be able to move from areas that climate change renders unsuitable into areas that become newly climatically suitable.

We demonstrated a single technique – an additive algorithm – for combining elements of sensitivity into one measure in this study, however we recognize that others may quantify sensitivity differently. Although our index was robust to minor changes in formulation, the alternative approaches to calculating sensitivity that we explored were only marginally different from one another and other techniques may result in different results. Furthermore, our sensitivity index averages the scores of individual sensitivity factors and thus may obscure extreme and outlying individual scores. A rule–based index that automatically assigns a high score when certain conditions are met may avoid this. Given the important role that sensitivity has in estimating how species might respond to climate change, future research could also examine alternative methods of calculating sensitivity metrics, such as incorporating confidence measures in assigning relative weights of factors.

Conclusion

Species are uniquely sensitive to climate change and respond individually. The factors driving climate sensitivity are more similar within than among taxa and therefore species sensitivity to climate change is expected to be largely based on species and context-specific conditions. This presents challenges for conservation practitioners, particularly given limited time and funds. Our results can aid in identifying relatively sensitive species and prioritizing management, monitoring, and future research. For instance, species for which there was high

confidence and were determined to be highly sensitive will likely require more adaptation. By contrast, species that had high confidence but were determined to be least sensitive may be a lower priority for action. And for species for which there was low confidence, they should be identified as research priorities and ought to be continually monitored, with more preference given to those with higher sensitivity scores.

In addition to prioritizing management actions, we identified which sensitivity factors contribute the most to the overall sensitivity ranking and compared those factors across taxonomic groups. One factor, sensitive habitats, had the largest total number of high sensitivity scores for three taxonomic groups (birds, mammals, and amphibians and reptiles). These habitats are critical for many sensitive species and their protection and restoration are needed. Although there are still other species that could be assessed, we believe that this publically available information will enable managers to identify which species are more sensitive and identify the key aspects that can be leveraged to increase their resilience to climate change. By focusing on the inherent sensitivity of species, our results provide a foundation for anticipating how climate change will affect biodiversity.

Figures

Figure 1. Boxplot of the median relative sensitivity scores (represented by heavy lines) and ranges (represented by whiskers) for four taxonomic groups. Boxes represent 25% - 75% of the distribution and sample sizes vary by taxonomic group; birds = 114, mammals = 35, plants = 27, and amphibian and reptile = 20.

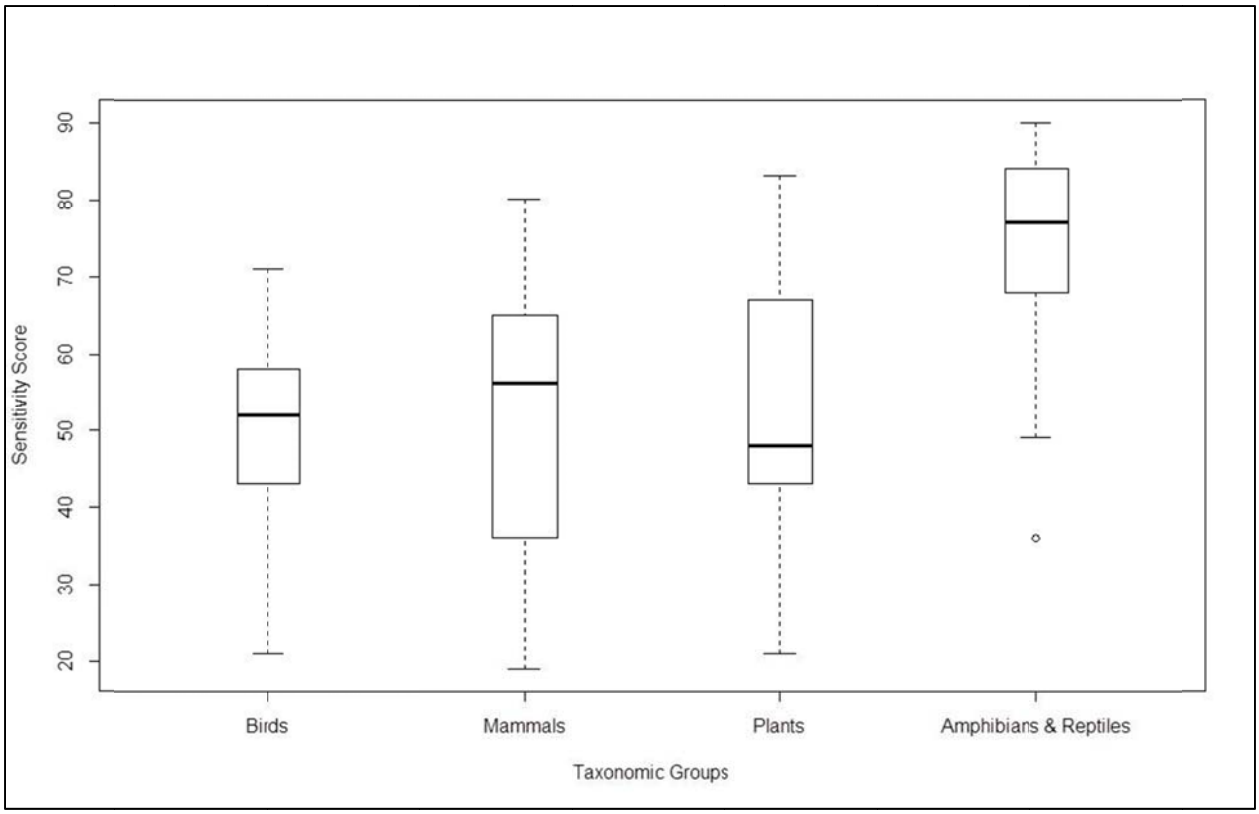


Figure 2. Relative climate change sensitivity scores and confidence scores for 196 species.

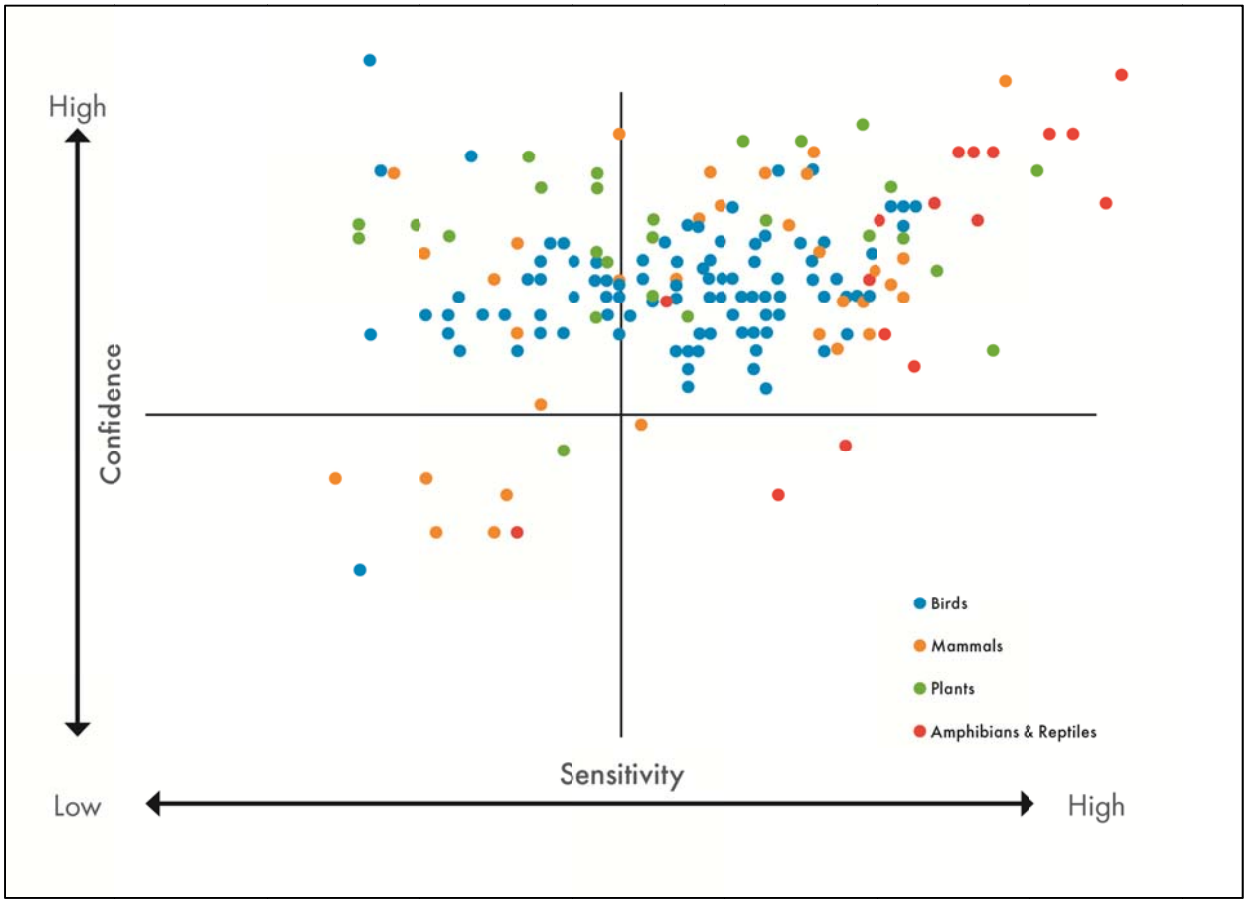


Figure 3. The total number of high sensitivity scores (i.e., scores of 5, 6, and 7) for each of the nine sensitivity factors for bird species (a), mammal species (b), plant species (c), and amphibians and reptiles (d).

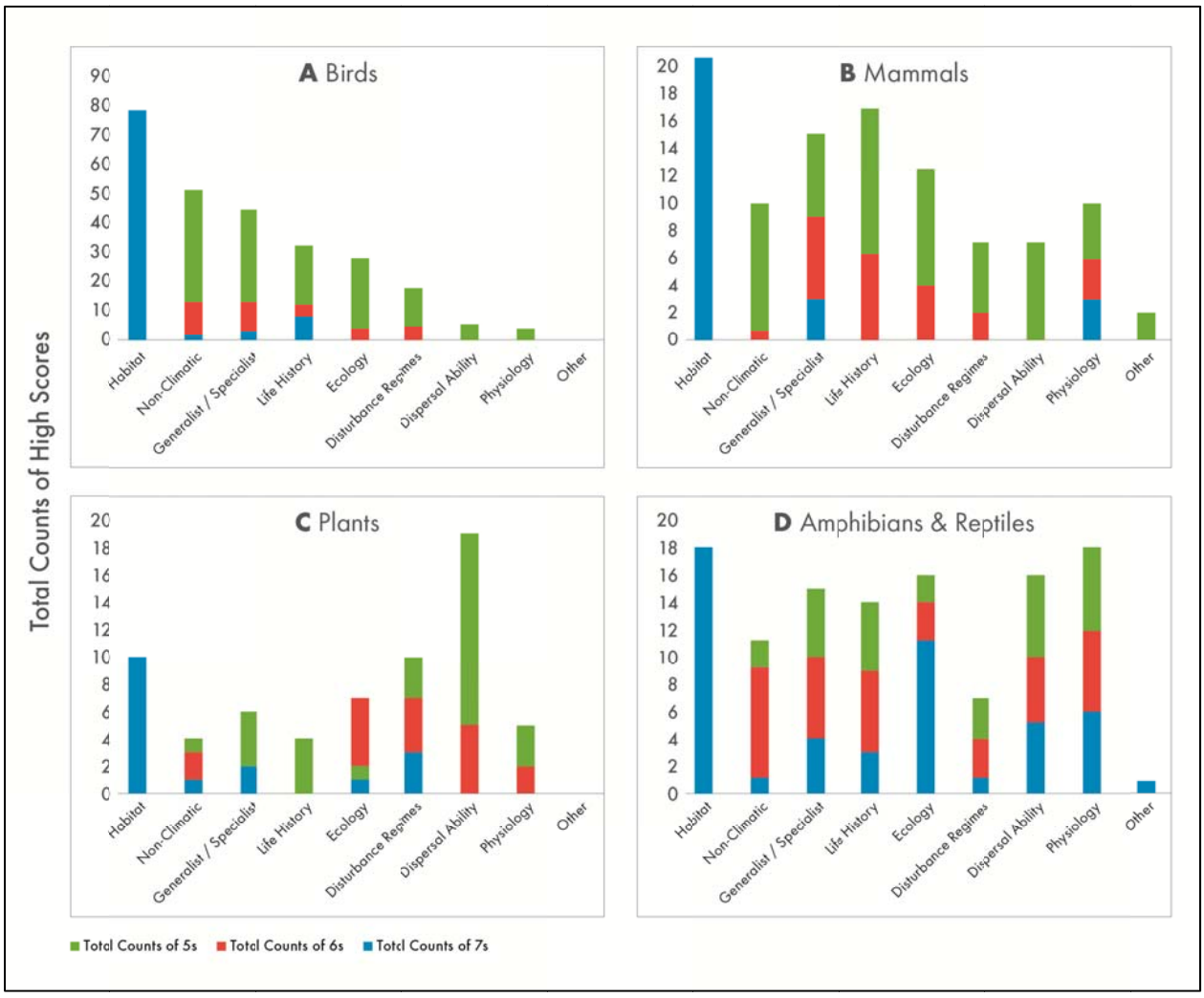
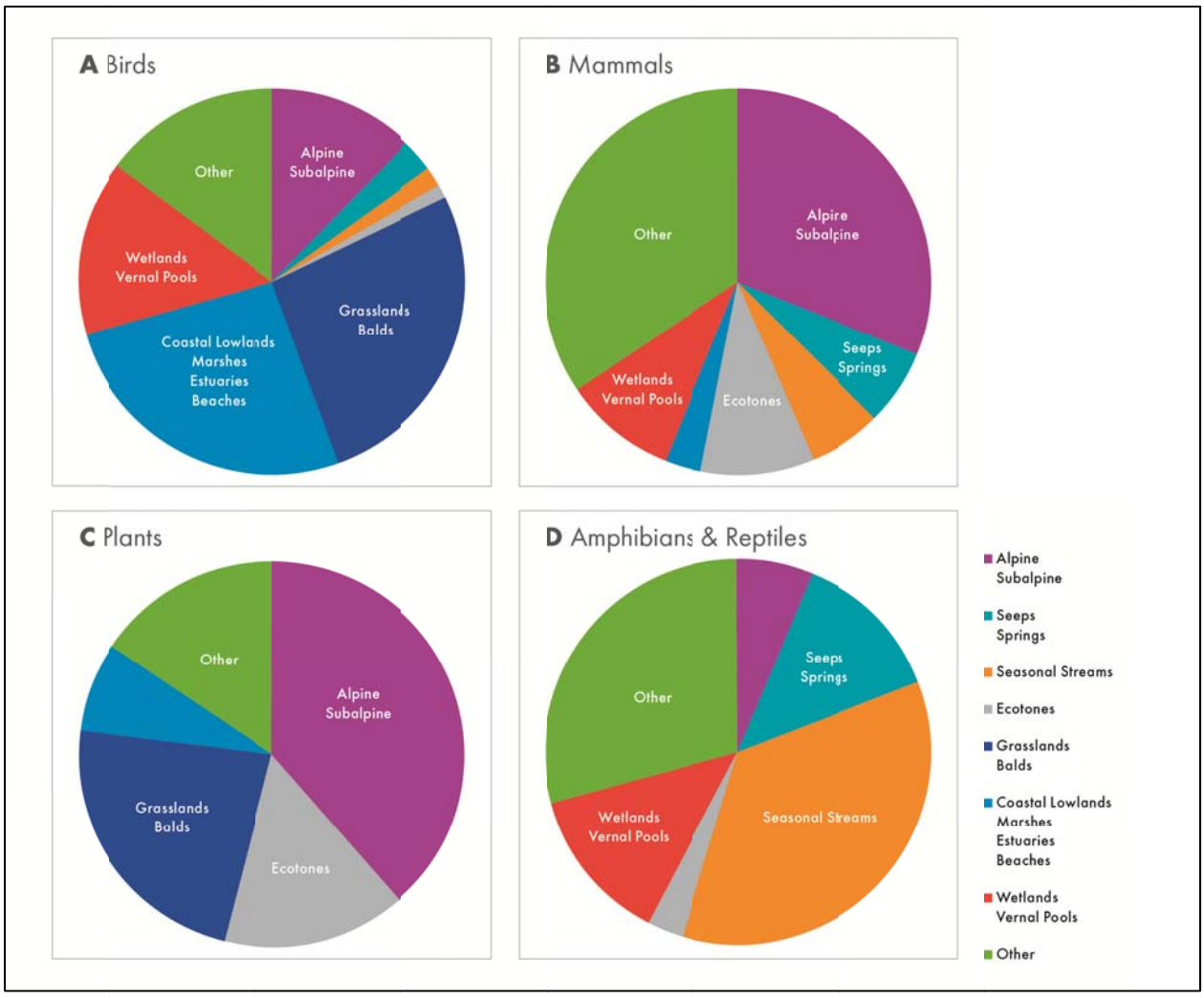


Figure 4. The total number of times each sensitive habitat was identified as contributing to climate sensitivity for bird species (a), mammal species (b), plant species (c), and amphibians and reptiles (d).



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Appendix A. Climate change sensitivity and average confidence scores for 114 bird species. Higher scores represent higher sensitivities and greater confidence.

Scientific name	Common name	Geography	Sensitivity Score	Average Confidence Score
Brachyramphus marmoratus	Marbled murrelet	Range-wide	71	4
Strix nebulosa	Great gray owl	Range-wide	70	4
Strix occidentalis caurina	Northern spotted owl	Range-wide	70	4
Sialia mexicana	Western bluebird	Range-wide	69	4
Egretta thula	Snowy egret	Range-wide	68	4
Picoides dorsalis	American three-toed woodpecker	Range-wide	67	3
Charadrius montanus	Mountain plover	Range-wide	66	3
Falcipennis canadensis	Spruce grouse	Range-wide	65	3
Loxia sinesciuris	South hills crossbill	Range-wide	65	3
Eremophila alpestris strigata	Streaked horned lark	Range-wide	65	3
Nucifraga columbiana	Clark's nutcracker	Range-wide	64	3
Aegolius funereus	Boreal owl	Range-wide	63	3
Histrionicus histrionicus	Harlequin duck	Range-wide	63	3
Bonasa umbellus	Ruffed grouse	Range-wide	63	4
Cerorhinca monocerata	Rhinoceros auklet	Range-wide	63	3
Haemorhous cassinii	Cassin's finch	Range-wide	62	4
Ammodramus savannarum	Grasshopper sparrow	Range-wide	62	4
Accipiter gentilis	Northern goshawk	Range-wide	62	4
Phoebastria albatrus	Short-tailed albatross	Range-wide	62	3
Aechmophorus occidentalis	Western grebe	Range-wide	61	4
Bucephala islandica	Barrow's goldeneye	Range-wide	59	3
Chaetura vauxi	Vaux's swift	Range-wide	59	3
Leucosticte atrata	Black rosy-finch	Range-wide	59	3
Numenius americanus	Long-billed curlew	Range-wide	59	4
Bucephala albeola	Bufflehead	Range-wide	58	4
Gavia pacifica	Pacific loon	Range-wide	58	3
Melanitta perspicillata	Surf scoter	Range-wide	58	3
Centrocercus urophasianus	Greater sage grouse	Range-wide	58	4
Anthus rubescens	American pipit	Range-wide	58	3
Cypseloides niger	Black swift	Range-wide	58	3
Myadestes townsendi	Townsend's solitaire	Range-wide	57	3
Lagopus leucura	White tailed ptarmigan	Range-wide	57	4
Pipilo chlorurus	Green-tailed towhee	Range-wide	57	4
Anas acuta	Northern pintail	Range-wide	57	3

Amphispiza belli	Sage sparrow	Range-wide	57	3
Tympanuchus phasianellus	Sharp-tailed grouse	Range-wide	57	3
Otus flammeolus	Flammulated owl	Range-wide	57	3
Cygnus buccinator	Trumpeter swan	Range-wide	57	3
Oreortyx pictus	Mountain quail	Range-wide	56	3
Contopus cooperi	Olive-sided flycatcher	Range-wide	56	3
Mycteria americana	Wood stork	Range-wide	56	3
Branta bernicla	Brant	Range-wide	55	3
Spizella breweri	Brewer's sparrow	Range-wide	55	3
Dendragapus fuliginosus	Sooty grouse	Range-wide	55	3
Charadrius alexandrinus	Snowy plover	Range-wide	55	4
Poecile hudsonica	Boreal chickadee	Range-wide	54	3
Melanerpes formicivorus	Acorn woodpecker	Range-wide	54	3
Phalacrocorax pelagicus	Pelagic cormorant	Range-wide	54	3
Dryocopus pileatus	Pileated woodpecker	Range-wide	54	4
Phoebastria nigripes	Black-footed albatross	Range-wide	54	4
Sphyrapicus thyroideus	Williamson's sapsucker	Range-wide	53	3
Dendragapus obscurus	Dusky grouse	Range-wide	53	3
Seiurus noveboracensis	Northern waterthrush	Range-wide	53	3
Agelaius tricolor	Tricolored blackbird	Range-wide	53	4
Nycticorax nycticorax	Black-crowned night-heron	Range-wide	52	3
Empidonax occidentalis	Cordilleran flycatcher	Range-wide	52	3
Asio flammeus	Short-eared owl	Range-wide	52	4
Bartramia longicauda	Upland sandpiper	Range-wide	52	3
Chlidonias niger	Black tern	Range-wide	52	3
Botaurus lentiginosus	American bittern	Range-wide	52	3
Leucosticte tephrocotis tephrocotis	Gray-crowned rosy-finch	Range-wide	51	3
Leucosticte tephrocotis wallowa	Wallowa rosy-finch	Range-wide	51	3
Grus canadensis	Sandhill crane	Range-wide	51	3
Uria aalge	Common murre	Range-wide	51	4
Melanitta fusca	White-winged scoter	Range-wide	50	3
Icteria virens	Yellow-breasted chat	Range-wide	50	3
Oreoscoptes montanus	Sage thrasher	Range-wide	50	3
Pooecetes gramineus affinis	Oregon vesper sparrow	Range-wide	50	3
Lophodytes cucullatus	Hooded merganser	Range-wide	50	3
Pelecanus erythrorhynchos	American white pelican	Range-wide	50	4
Ptychoramphus aleuticus	Cassin's auklet	Range-wide	50	3
Poecile gambeli	Mountain chickadee	Range-wide	49	4
Sitta pygmaea	Pygmy nuthatch	Range-wide	49	4
Calidris mauri	Western sandpiper	Range-wide	48	3
Dendroica chrysoparia	Golden-cheeked warbler	Texas	48	3

Gavia immer	Common loon	Range-wide	47	3
Sphyrapicus nuchalis	Red-naped sapsucker	Range-wide	47	4
Vireo olivaceus	Red-eyed vireo	Range-wide	46	3
Haematopus bachmani	Black oystercatcher	Range-wide	45	3
Cinclus mexicanus	American dipper	Range-wide	45	3
Melanerpes lewis	Lewis's woodpecker	Range-wide	45	3
Picoides arcticus	Black-backed woodpecker	Range-wide	45	3
Melanitta americana	American scoter	Range-wide	44	3
Ardea herodias	Great blue heron	Range-wide	44	3
Ixobrychus exilis hesperis	Western least bittern	Range-wide	44	3
Perisoreus canadensis	Gray jay	Range-wide	43	3
Loxia leucoptera	White-winged crossbill	Range-wide	43	4
Charadrius alexandrinus nivosus	Western snowy plover	Range-wide	41	3
Gymnorhinus cyanocephalus	Pinyon jay	Range-wide	41	3
Aquila chrysaetos	Golden eagle	Range-wide	41	4
Pelecanus occidentalis	Brown pelican	Range-wide	40	4
Regulus calendula	Ruby-crowned kinglet	Range-wide	40	3
Plegadis chihi	White-faced ibis	Western North America	39	4
Ardea alba	Great egret	Range-wide	38	3
Branta canadensis occidentalis	Dusky Canada goose	Range-wide	38	3
Accipiter striatus	Sharp-shinned hawk	Range-wide	38	4
Phalacrocorax penicillatus	Brandt's cormorant	Range-wide	38	3
Sitta carolinensis aculeata	White-breasted nuthatch	Range-wide	38	3
Picoides albolarvatus	White-headed woodpecker	Range-wide	37	3
Coccyzus americanus	Yellow-billed cuckoo	North America	36	3
Coturnicops noveboracensis	Yellow rail	Canada	36	3
Empidonax traillii brewsteri	Willow flycathcer	Range-wide	35	3
Fratercula cirrhata	Tufted puffin	Range-wide	34	3
Progne subis	Purple martin	Range-wide	33	3
Buteo swainsoni	Swainson's hawk	Range-wide	32	4
Falco columbarius	Merlin	Range-wide	31	3
Patagioenas fasciata	Band-tailed pigeon	Range-wide	31	3
Lanius ludovicianus	Loggerhead shrike	Range-wide	30	3
Buteo regalis	Ferruginous hawk	Range-wide	30	3
Athene cunicularia hypugaea	Western burrowing owl	Range-wide	28	3
Strix varia	Barred owl	Range-wide	23	4
Corvus brachyrhynchos	American crow	Range-wide	22	5
Falco peregrinus	Peregrine falcon	Range-wide	22	3
Carduelis psaltia	Lesser goldfinch	Range-wide	21	1

Appendix B. Climate change sensitivity and average confidence scores for 35 mammal species. Higher scores represent higher sensitivities and greater confidence.

Scientific name	Common name	Geography	Sensitivity Score	Average Confidence Score
Rangifer tarandus caribou	Woodland caribou	Northern Idaho and Northeast Washington	80	5
Myotis keenii	Keen's bat	Olympic Peninsula	70	4
Myotis lucifugus	Little brown bat	Olympic Peninsula	70	3
Perognathus longimembris	Little pocket mouse	Idaho	69	3
Corynorhinus townsendii	Townsend's big-eared bat	Pacific Northwest	68	3
Synaptomys borealis	Northern bog lemming	Idaho	67	3
Lynx canadensis	Canada lynx	Idaho	67	3
Vulpes vulpes cascadensis	Cascade red fox	Washington	65	3
Antrozous pallidus	Pallid bat	Pacific Northwest	64	3
Marmota caligota	Hoary marmot	North Cascades	63	4
Brachylagus idahoensis	Pygmy rabbit	Range excluding Columbia Basin	63	4
Martes pennanti	Fisher	Western North America	63	3
Gulo gulo	Wolverine	Range-wide	62	4
Ochotona princeps	American pika	Western North America	62	4
Marmota olympus	Olympic marmot	Olympic Peninsula	60	4
Martes americana	American marten	Olympic Peninsula	58	4
Neotamias amoenus celeris	Yellow-pine chipmunk	Eastern Cascades	54	4
Oreamnos americanus	Mountain goat	Range-wide	53	4
Vulpes macrotis	Kit fox	Great Basin	52	4
Peromyscus truei	Pinyon mouse	Idaho	50	3
Spermophilus elegans	Wyoming ground squirrel	Range-wide	47	2
Bassariscus astutus	Ringtail	Range-wide	45	3
Castor canadensis	American beaver	Oregon	45	4
Baeolophus ridgwayi	Juniper titmouse	Idaho	38	3
Lepus americanus	Snowshoe hare	Olympic Peninsula	36	3
Ovis canadensis	Bighorn sheep	Range-wide	36	4
Spermophilus canus	Merriam's ground squirrel	Idaho	35	2
Neotamias dorsalis	Cliff chipmunk	Idaho	34	3
Thomomys townsendii	Townsend's pocket gopher	Idaho	34	2
Tamias umbrinus	Uinta chipmunk	Idaho	29	2
Tamian ruficaudus	Red-tailed chipmunk	Washington	28	2
Cervus elaphus	Elk	Range-wide	28	4
Lasionycteris noctivagans	Silver-haired bat	Western North America	27	4
Canis lupus	Gray wolf	North America	24	4

Spermophilus variegatus	Rock squirrel	Idaho	19	2

Appendix C. Climate change sensitivity and average confidence scores for 27 plant species. Higher scores represent higher sensitivities and greater confidence.

Scientific name	**Common name**	**Geography**	**Sensitivity Score**	**Average Confidence Score**
Abronia latifolia	Coastal sand verbena	Pacific Northwest	83	4
Lepidium papilliferum	Slickspot peppergrass	Range-wide	79	3
Quercus garryana var. garryana	Garry oak	Range-wide	73	3
Pinus albicaulis	Whitebark pine	Range-wide	70	4
Larix lyallii	Subalpine larch	Range-wide	69	4
Picea sitchensis	Sitka spruce	Pacific Northwest	67	4
Abies lasiocarpa	Subalpine fir	Pacific Northwest	67	4
Picea engelmannii	Engelmann spruce	Pacific Northwest	61	4
Artemisia tridentata	Big sagebrush	Pacific Northwest	58	4
Tsuga mertensiana	Mountain hemlock	Pacific Northwest	56	4
Pinus monticola	Western white pine	Range-wide	52	3
Taxus brevifolia	Pacific yew	Range-wide	51	3
Abies procera	Nobel fir	Range-wide	48	4
Pinus contorta var. latifolia	Lodgepole pine	Range-wide	48	4
Populus tremuloides	Quaking aspen	Pacific Northwest	48	3
Chrysolepis chrysophylla	Golden chinquapin	Pacific Northwest	44	4
Pinus ponderosa	Ponderosa pine	Pacific Northwest	43	4
Pseudotsuga menziesii	Douglas-fir	Pacific Northwest	43	4
Abies grandis	Grand Fir	Range-wide	43	4
Thuja plicata	Western redcedar	Range-wide	43	4
Larix occidentalis	Western larch	Range-wide	43	3
Abies amabilis	Pacific silver fir	Range-wide	38	4
Tsuga heterophylla	Western hemlock	Pacific Northwest	37	4
Bromus tectorum	Cheatgrass	Range-wide	30	4
Gaultheria shallon	Salal	Pacific Northwest	27	4
Acer macrophylla	Big leaf maple	Pacific Northwest	21	4
Alnus rubra	Red alder	Pacific Northwest	21	4

Appendix D. Climate change sensitivity and average confidence scores for 20 amphibian and reptile species. Higher scores represent higher sensitivities and greater confidence.

Scientific name	Common name	Geography	Sensitivity Score	Average Confidence Score
Anaxyrus boreas	Western toad	North Cascades	90	5
Ascaphus truei	Coastal tailed frog	Range-wide	89	4
Rhyacotriton cascadae	Cascade torrent salamander	Range-wide	86	4
Batrachoseps wrighti	Oregon slender salamander	Range-wide	84	4
Plethodon larselli	Larch mountain salamander	Range-wide	84	4
Rhyacotriton kezeri	Columbia torrent salamander	Range-wide	84	4
Rhyacotriton variegatus	Southern torrent salamander	Range-wide	84	4
Plethodon stormi	Siskiyou Mountains salamander	Range-wide	79	4
Rana cascadae	Cascades frog	Range-wide	77	4
Aneides flavipunctatus	Black salamander	Pacific Northwest	77	4
Rana boylii	Foothill yellow-legged frog	Pacific Northwest	76	4
Rana luteiventris	Columbia spotted frog	Pacific Northwest	73	4
Plethodon idahoensis	Coeur d' Alene salamander	Range-wide	71	3
Dicamptodon aterrimus	Idaho giant salamander	Range-wide	69	3
Plethodon vandykei	Van Dyke's salamander	Range-wide	68	4
Rhyacotriton olympicus	Olympic torrent salamander	Range-wide	67	3
Rana sylvatica	Wood frog	Idaho	65	2
Elgaria coerulea principis	Northern alligator lizard	Range-wide	59	2
Crotaphytus bicinctores	Great Basin collared lizard	Range-wide	49	3
Diadophis punctatus	Ringneck snake	Pacific Northwest	36	2

Appendix E. Sensitivity analysis of the nine climate change sensitivity factors.

Scientific name	Original Sensitivity Score	Original ranking	No Generalist/Specialist Score	No Generalist/Specialist ranking	No Physiology	No Physiology ranking	No Life History	No Life History ranking	No Habitat	No Habitat ranking	No Dispersal Ability	No Dispersal Ability ranking	No Disturbance Regimes	No Disturbance Regimes ranking	No Ecology	No Ecology ranking	No Non-Climatic Stressors	No Non-Climatic Stressors ranking	No Other	No Other ranking
Anaxyrus boreas	90	1	92	1	90	1	93	1	89	1	92	1	89	8	89	1	89	2	100	2
Ascaphus truei	89	2	88	2	87	3	89	2	87	2	89	2	91	6	87	2	89	1	106	1
Rhyacotriton cascadae	86	3	85	3	83	4	85	4	83	3	83	6	98	1	83	3	86	3	100	3
Rhyacotriton kezeri	84	6	84	4	81	7	84	5	81	4	81	7	95	2	81	4	83	4	98	4
Rhyacotriton variegatus	84	7	84	5	81	8	84	6	81	5	81	8	95	3	81	5	83	5	98	5
Batrachoseps wrighti	84	4	82	6	83	5	82	7	81	6	81	9	95	4	81	6	83	6	98	6
Plethodon larselli	84	5	82	7	83	6	82	8	81	7	81	10	95	5	81	7	83	7	98	7
Abronia latifolia	83	8	81	8	87	2	85	3	80	8	87	4	80	11	80	8	82	8	96	8
Rangifer tarandus caribou	80	9	79	9	79	9	79	11	76	9	88	3	79	14	79	10	79	10	93	9
Lepidium papilliferum	79	10	77	11	77	13	82	9	75	10	85	5	75	18	80	9	77	12	92	11
Plethodon stormi	79	11	79	10	77	12	78	12	75	11	77	13	89	7	75	12	77	13	92	12
Rana cascadae	77	12	77	14	78	11	80	10	74	12	78	12	76	17	76	11	78	11	92	10
Aneides flavipunctatus	77	13	77	12	75	16	76	13	73	13	75	16	87	9	73	14	77	14	89	14
Rana boylii	76	14	77	13	76	14	75	15	71	14	74	21	86	10	71	15	74	19	88	15
Quercus garryana	73	15	76	15	79	10	74	16	69	16	71	25	71	24	74	13	74	18	86	16
Rana luteiventris	73	16	73	16	71	20	75	14	69	15	73	22	71	23	71	16	76	16	90	13
Plethodon idahoensis	71	18	70	18	71	21	73	17	67	17	69	30	71	26	69	20	81	9	83	18
Brachyramphus marmoratus	71	17	69	19	76	15	69	24	67	18	81	11	71	22	69	19	69	28	83	19
Strix nebulosa	70	19	69	20	70	29	70	21	65	20	75	17	73	20	70	17	70	25	82	20
Myotis keenii	70	21	69	21	65	46	70	22	65	21	75	18	80	12	68	25	70	26	82	21
Myotis lucifugus	70	22	69	22	65	47	70	23	65	22	75	19	80	13	68	26	70	27	82	22
Strix occidentalis caurina	70	20	68	27	75	18	69	25	65	23	77	14	73	19	68	27	68	31	82	23
Pinus albicaulis	70	23	71	17	75	17	70	20	65	19	73	23	73	21	70	18	65	39	82	24
Larix lyallii	69	26	69	25	67	38	69	28	64	26	71	27	71	25	67	32	76	15	81	25
Perognathus longimembris	69	25	69	24	69	32	71	19	64	25	69	31	71	27	69	21	71	22	81	27
Sialia mexicana	69	24	69	23	71	22	71	18	64	24	71	26	69	29	69	22	69	29	81	28
Dicamptodon aterrimus	69	27	68	29	68	36	69	30	64	27	68	36	68	32	68	24	72	21	85	17
Plethodon vandykei	68	28	68	28	63	55	68	33	63	29	68	40	77	15	63	52	75	17	81	26
Corynorhinus townsendii	68	29	67	36	67	37	67	37	63	28	71	28	67	34	67	30	73	20	79	30
Egretta thula	68	30	68	26	71	27	68	32	62	30	76	15	65	45	65	42	65	42	79	36
Picea sitchensis	67	33	67	33	67	39	69	29	62	33	67	43	67	40	69	23	71	23	79	31
Rhyacotriton olympicus	67	34	67	34	62	61	67	36	62	34	69	33	76	16	67	31	69	30	79	33
Synaptomys borealis	67	32	67	32	71	23	69	27	62	32	69	32	67	37	67	33	67	34	79	34
Picoides dorsalis	67	31	67	31	74	19	69	26	62	31	67	42	67	39	67	34	67	35	79	35
Abies lasiocarpa	67	35	66	37	66	45	68	31	61	36	66	50	68	33	66	40	71	24	79	32
Lynx canadensis	67	36	65	41	70	28	66	39	62	35	75	20	64	48	64	49	66	38	80	29
Charadrius montanus	66	37	66	38	65	48	67	35	61	38	73	24	63	49	68	28	68	32	77	37
Bucephala albeola	66	38	66	39	58	93	60	64	52	85	60	71	60	66	58	78	58	69	68	70
Falcipennis canadensis	65	39	65	42	71	25	67	34	60	42	64	53	64	46	67	35	64	43	76	40
Loxia sinesciuris	65	40	64	46	71	26	66	41	60	44	69	34	67	38	64	45	62	51	76	41
Eremophila alpestris strigata	65	41	66	40	71	24	66	40	60	43	67	44	69	30	64	43	60	60	76	43
Rana sylvatica	65	42	68	30	66	42	67	38	60	41	64	52	62	55	66	38	66	37	77	38
Vulpes vulpes cascadensis	65	43	67	35	69	33	65	43	61	37	66	51	66	42	64	46	64	47	73	53
Antrozous pallidus	64	45	65	45	63	54	63	49	59	47	67	41	67	35	63	51	65	40	76	39
Nucifraga columbiana	64	44	63	48	70	31	64	44	58	48	68	37	63	50	68	29	61	55	75	45
Marmota caligota	63	50	63	51	64	51	63	50	57	53	67	45	62	56	64	47	67	36	74	46
Aegolius funereus	63	46	62	53	67	41	64	45	57	52	64	54	62	57	67	36	64	44	74	48
Bonasa umbellus	63	48	63	49	67	40	65	42	57	51	62	63	62	58	67	37	64	45	74	49
Histrionicus histrionicus	63	47	62	54	62	62	62	55	57	55	67	46	69	31	64	44	64	46	74	50
Cerorhinca monocerata	63	49	63	50	69	34	60	56	57	56	67	47	67	41	62	55	62	52	74	51
Brachylagus idahoensis	63	51	60	60	66	43	63	47	57	59	62	67	64	47	66	39	64	49	75	44
Martes pennanti	63	52	62	52	66	44	62	53	57	54	66	49	62	63	64	50	62	54	76	42
Carpodacus cassinii	62	53	64	47	61	69	63	52	56	62	63	57	63	53	61	62	68	33	73	52
Gulo gulo	62	57	59	61	58	85	60	63	56	64	70	29	70	28	63	53	61	56	73	54
Ammodramus savannarum	62	54	62	55	63	57	63	51	56	61	68	38	63	51	63	54	61	57	73	55
Accipiter gentilis	62	55	65	43	63	56	62	54	56	63	68	39	63	52	61	61	61	58	73	56
Phoebastria albatrus	62	56	65	44	70	30	59	65	56	65	63	58	65	43	61	60	58	63	73	57
Ochotona princeps	62	58	59	65	56	105	63	48	56	70	63	62	67	36	65	41	65	41	74	47
Picea engelmannii	61	60	62	56	60	77	64	46	55	71	60	72	62	60	64	48	64	48	71	58

Aechmophorus occidentalis	61	59	60	57	69	35	60	57	55	72	69	35	57	84	60	68	60	61	71	59
Marmota olympus	60	61	60	58	61	70	59	67	54	74	63	59	63	54	58	71	63	50	70	60
Elgaria coerulea principis	59	66	59	62	57	94	59	69	52	79	60	73	62	61	62	56	62	53	69	61
Leucosticte atrata	59	64	58	68	60	78	60	62	52	78	64	55	60	67	62	57	57	70	69	62
Chaetura vauxi	59	63	58	67	62	64	60	59	52	77	62	65	60	69	62	58	57	71	69	63
Bucephala islandica	59	62	58	66	62	63	60	58	52	76	62	64	62	59	60	65	57	72	69	64
Numenius americanus	59	65	58	69	64	52	58	70	52	80	67	48	57	85	60	69	57	74	69	65
Artemisia tridentata	58	73	59	64	61	72	60	61	51	87	56	90	58	80	58	75	61	59	68	66
Centrocercus urophasianus-2	58	69	56	82	65	50	59	66	51	88	61	68	54	98	61	63	58	64	68	67
Melanitta perspicillata	58	68	60	59	58	84	59	68	51	89	61	69	58	77	58	74	58	65	68	68
Gavia pacifica	58	67	58	70	65	49	57	79	51	90	61	70	58	78	56	83	58	67	68	69
Martes americana - Olympics	58	72	57	76	63	58	56	82	51	91	63	60	61	64	58	72	56	78	68	71
Anthus rubescens	58	70	59	63	61	71	60	60	51	86	58	77	61	65	58	73	56	79	68	72
Cypseloides niger	58	71	56	83	63	60	55	86	51	92	63	61	65	44	56	82	56	80	68	73
Tympanuchus phasianellus	57	79	57	78	62	68	58	78	51	94	55	95	59	76	62	59	53	98	68	74
Myadestes townsendi	57	74	56	84	60	81	58	74	50	98	57	86	57	86	60	70	60	62	67	75
Pipilo chlorurus	57	76	58	71	57	95	58	76	50	99	57	87	60	74	60	67	57	73	67	76
Lagopus leucura	57	75	57	77	62	66	57	80	50	100	60	75	60	72	55	89	57	75	67	77
Anas acuta	57	77	58	72	60	79	58	72	50	96	60	74	60	71	57	79	55	84	67	78
Amphispiza belli	57	78	58	73	62	65	58	71	50	95	57	85	60	73	57	80	55	85	67	79
Otus flammeolus	57	80	56	85	64	53	56	81	50	101	57	88	62	62	60	66	52	99	67	80
Cygnus buccinator	57	81	58	74	60	80	58	73	50	97	64	56	60	68	55	87	52	101	67	81
Tsuga mertensiana	56	85	57	81	56	100	58	77	49	109	54	105	58	82	58	76	58	66	65	82
Contopus cooperi	56	83	57	80	63	59	56	83	49	110	58	79	54	99	56	85	56	82	65	83
Oreortyx pictus	56	82	57	79	58	86	58	75	49	108	58	78	58	79	54	96	56	83	65	84
Mycteria americana	56	84	58	75	61	73	55	87	49	111	58	80	54	100	61	64	54	93	65	85
Branta bernicla	55	86	56	86	57	96	56	85	48	113	55	97	60	75	52	103	57	77	64	86
Spizella breweri	55	87	56	87	60	82	54	92	48	115	57	89	57	87	55	90	55	86	64	87
Dendragapus fuliginosus	55	88	56	88	60	83	56	84	48	112	55	96	57	88	57	81	52	100	64	88
Charadrius alexandrinus	55	89	54	93	62	67	54	90	48	114	62	66	60	70	55	88	48	124	64	89
Neotamias amoenus celeris	54	95	55	91	58	88	54	94	46	122	51	112	54	103	56	86	58	68	63	90
Poecile hudsonica	54	90	54	94	56	101	55	89	46	119	54	106	56	94	56	84	56	81	63	91
Melanerpes formicivorus	54	91	52	103	61	76	55	88	46	118	56	91	56	92	54	99	54	94	63	92
Dryocopus pileatus	54	93	53	98	61	75	54	91	46	120	56	92	58	81	54	97	51	104	63	93
Phalacrocorax pelagicus	54	92	55	90	58	87	54	93	46	121	58	81	56	91	54	98	51	105	63	94
Phoebastria nigripes	54	94	56	89	61	74	51	108	46	123	56	93	56	93	58	77	49	113	63	95
Oreamnos americanus	53	100	51	112	55	108	51	112	45	130	55	100	57	90	55	91	57	76	62	96
Sphyrapicus thyroideus	53	96	52	104	57	98	54	96	45	127	55	98	52	106	55	94	55	87	62	97
Seiurus noveboracensis	53	98	54	96	57	97	54	95	45	126	52	110	55	97	55	93	52	102	62	99
Dendragapus obscurus	53	97	54	95	55	106	54	97	45	128	55	99	57	89	52	104	52	103	62	100
Agelaius tricolor	53	99	53	99	55	107	53	100	45	129	60	76	55	95	55	92	50	108	62	101
Nycticorax nycticorax	52	101	54	92	54	109	52	101	45	132	54	104	52	111	54	95	54	91	62	98
Vulpes macrotis	52	102	53	97	51	118	52	102	61	40	51	111	51	112	49	116	49	112	61	102
Empidonax occidentalis	52	103	53	100	54	110	52	105	44	136	54	109	54	102	54	100	54	95	61	103
Asio flammeus	52	104	52	105	58	90	51	109	44	137	58	83	49	126	51	111	54	96	61	104
Pinus monticola	52	108	53	102	54	111	54	98	61	39	46	129	46	132	49	120	54	97	61	105
Bartramia longicauda	52	105	52	106	58	91	53	99	44	133	54	107	54	101	51	107	51	106	61	106
Chlidonias niger	52	106	51	113	58	92	52	104	44	135	54	108	58	83	51	106	49	115	61	107
Botaurus lentiginosus	52	107	53	101	58	89	52	103	44	134	58	82	51	113	51	109	49	117	61	108
Taxus brevifolia	51	113	49	117	50	124	49	119	60	45	48	125	45	134	52	105	55	88	60	109
Leucosticte tephrocotis tephrocotis	51	109	49	115	52	115	52	106	43	143	55	101	52	107	50	112	55	89	60	110
Leucosticte tephrocotis wallowa	51	110	49	116	52	116	52	107	43	144	55	102	52	108	50	113	55	90	60	111
Grus canadensis	51	111	52	107	57	99	49	117	43	145	55	103	55	96	48	124	50	110	60	112
Uria aalge	51	112	52	108	52	114	47	128	60	46	50	117	52	109	48	125	48	126	60	113
Peromyscus truei	50	114	49	122	47	136	50	116	58	49	49	120	49	125	47	127	54	92	59	114
Melanitta fusca	50	115	52	109	54	112	51	113	42	150	51	114	51	116	49	118	51	107	58	115
Oreoscoptes montanus	50	117	47	126	56	104	51	111	42	149	51	113	51	115	54	102	49	114	58	116
Icteria virens	50	116	52	110	51	119	51	114	42	151	51	115	54	104	51	108	49	116	58	117
Pooecetes gramineus affinis	50	118	51	114	56	102	49	118	42	152	51	116	51	117	51	110	49	118	58	118
Lophodytes cucullatus	50	119	49	118	56	103	51	110	42	148	58	84	49	127	46	128	49	121	58	119
Pelecanus erythrorhynchos	50	120	52	111	51	120	48	123	42	153	56	94	51	114	54	101	46	127	58	120
Ptychoramphus aleuticus	50	121	49	119	51	121	46	130	58	50	49	121	51	118	49	119	46	128	58	121
Crotaphytus bicinctores	49	122	47	130	46	142	48	126	56	60	48	124	50	121	50	114	50	109	56	124
Poecile gambeli	49	123	49	120	48	133	49	120	57	57	45	132	48	130	45	134	50	111	57	122

Sitta pygmaea	49	124	47	127	48	134	49	121	57	58	48	126	50	122	48	126	45	131	57	123
Populus tremuloides	48	129	48	123	46	137	49	122	56	67	42	148	44	141	49	121	49	119	56	125
Pinus contorta var. latifolia	48	128	47	129	51	123	51	115	56	66	42	147	39	155	49	122	49	120	56	126
Abies procera	48	127	47	128	46	138	48	125	56	68	44	139	46	133	46	130	49	122	56	127
Calidris mauri	48	125	49	121	51	122	48	124	39	160	49	122	54	105	49	117	44	135	56	128
Dendroica chrysoparia	48	126	44	136	54	113	47	127	56	69	46	130	49	128	46	129	42	144	56	129
Spermophilus elegans	47	132	48	125	50	125	46	131	38	164	45	137	50	124	50	115	48	125	55	130
Gavia immer	47	130	48	124	52	117	44	135	38	165	50	118	52	110	45	132	45	132	55	131
Sphyrapicus nuchalis	47	131	45	132	50	126	47	129	55	73	45	133	43	142	45	136	45	133	55	132
Vireo olivaceus	46	133	46	131	46	139	45	133	54	75	44	140	44	139	44	137	44	137	54	133
Bassariscus astutus	45	134	44	135	38	162	42	148	52	84	43	143	50	119	43	138	48	123	53	134
Castor canadensis	45	139	44	137	50	128	44	136	36	168	48	128	50	123	45	133	43	139	52	135
Haematopus bachmani	45	135	45	133	50	127	43	141	36	169	50	119	50	120	43	141	43	141	52	136
Picoides arcticus	45	138	43	146	50	130	43	142	52	83	48	127	40	150	43	142	40	147	52	137
Cinclus mexicanus	45	136	42	149	50	131	44	137	52	82	45	134	45	135	40	148	40	148	52	138
Melanerpes lewis	45	137	43	145	50	129	45	132	52	81	43	144	45	137	40	150	40	149	52	139
Melanitta americana	44	140	44	138	46	140	45	134	35	172	44	142	44	140	46	131	46	129	51	140
Ardea herodias	44	141	44	139	46	141	43	143	35	174	49	123	46	131	42	146	46	130	51	141
Chrysolepis chrysophylla	44	143	44	140	44	146	43	145	51	93	37	160	39	156	49	123	44	136	51	142
Ixobrychus exilis hesperis	44	142	45	134	49	132	44	138	35	173	46	131	49	129	42	145	42	145	51	143
Pinus ponderosa	43	144	43	143	41	153	43	140	50	107	38	156	41	149	43	140	45	134	50	144
Pseudotsuga menziesii	43	145	43	144	43	147	43	139	50	106	38	155	41	148	43	139	43	138	50	145
Perisoreus canadensis	43	146	44	141	48	135	42	149	33	178	43	146	45	138	45	135	43	140	50	146
Abies grandis	43	148	43	147	43	148	43	146	50	103	38	157	40	152	43	143	43	142	50	147
Thuja plicata	43	149	43	148	43	149	43	147	50	104	38	158	40	153	43	144	43	143	50	148
Larix occidentalis	43	150	44	142	45	143	42	150	50	105	38	159	43	145	40	151	40	150	50	149
Loxia leucoptera	43	147	41	150	45	144	43	144	50	102	45	135	43	143	38	157	38	153	50	150
Charadrius alexandrinus nivosus	41	151	41	151	45	145	41	151	31	184	45	138	45	136	40	149	38	152	48	151
Gymnorhinus cyanocephalus	41	152	38	155	43	150	41	152	48	116	40	151	43	144	36	164	38	154	48	152
Aquila chrysaetos	41	153	40	152	40	154	37	158	48	117	45	136	40	151	40	152	36	162	48	153
Regulus calendula	40	155	40	154	39	157	41	153	46	124	37	161	39	157	39	154	37	159	46	154
Pelecanus occidentalis	40	154	40	153	37	169	38	156	46	125	44	141	37	162	39	155	37	160	46	155
Plegadis chihi	39	156	38	156	38	163	38	155	45	131	43	145	36	168	38	158	33	168	45	156
Baeolophus ridgwayi	38	157	36	164	40	156	35	165	44	141	35	166	40	154	37	159	37	156	44	157
Ardea alba	38	158	38	157	39	158	35	166	27	188	42	150	42	146	39	153	39	151	44	158
Branta canadensis occidentalis	38	159	38	158	42	151	37	157	27	187	42	149	37	163	42	147	37	158	44	159
Accipiter striatus	38	160	38	159	37	170	35	167	44	142	37	163	37	166	37	162	37	161	44	160
Abies amabilis	38	163	38	161	37	171	37	160	44	139	32	171	42	147	37	160	35	165	44	161
Phalacrocorax penicillatus	38	161	38	160	35	174	37	161	44	140	39	153	37	164	37	161	35	166	44	162
Sitta carolinensis aculeata	38	162	35	168	42	152	38	154	44	138	37	162	39	158	35	167	32	170	44	163
Tsuga heterophylla	37	165	37	162	38	164	37	159	43	146	31	174	33	175	36	165	38	155	43	164
Picoides albolarvatus	37	164	34	170	40	155	36	163	43	147	40	152	36	169	33	171	31	173	43	165
Lepus americanus	36	166	35	166	37	166	36	162	42	154	35	167	30	179	35	166	37	157	42	166
Diadophis punctatus	36	170	36	165	32	179	33	173	42	157	32	173	35	173	35	169	42	146	42	167
Ovis canadensis	36	169	37	163	39	159	34	169	25	192	39	154	37	165	39	156	35	164	42	168
Coccyzus americanus	36	167	35	169	39	160	34	170	42	156	35	168	39	159	30	178	32	171	42	169
Coturnicops noveboracensis	36	168	33	175	39	161	36	164	42	155	32	172	39	160	35	168	30	176	42	170
Spermophilus canus	35	171	35	167	36	173	33	172	40	159	29	179	36	167	36	163	34	167	41	171
Empidonax traillii brewsteri	35	172	34	171	38	165	34	171	40	158	33	170	38	161	31	175	29	180	40	172
Neotamias dorsalis	34	173	33	173	37	167	32	174	39	162	28	182	35	171	32	173	35	163	40	173
Thomomys townsendii	34	174	33	174	37	168	34	168	39	161	28	181	35	170	32	172	32	169	40	174
Fratercula cirrhata	34	175	34	172	37	172	29	178	39	163	37	164	35	172	30	179	30	178	39	175
Progne subis	33	176	30	177	33	176	32	175	38	166	36	165	33	174	29	182	31	174	38	176
Buteo swainsoni	32	177	32	176	35	175	29	179	37	167	35	169	23	191	35	170	30	177	37	177
Patagioenas fasciata	31	179	29	181	33	178	29	180	36	171	31	175	31	178	31	176	26	183	36	178
Falco columbarius	31	178	30	178	33	177	30	177	36	170	29	180	33	176	29	183	26	184	36	179
Bromus tectorum	30	182	30	179	30	184	31	176	35	175	30	176	20	194	30	181	32	172	35	180
Lanius ludovicianus	30	180	27	185	32	181	29	181	35	176	27	184	30	180	30	180	27	182	35	181
Buteo regalis	30	181	29	182	32	180	27	183	35	177	30	177	32	177	27	185	25	186	35	182
Tamias umbrinus	29	183	28	183	31	182	28	182	33	179	24	188	26	184	31	174	29	179	34	183
Tamian ruficaudus	28	185	29	180	30	183	25	184	32	180	20	192	28	183	28	184	30	175	32	184
Cervus elaphus	28	184	28	184	28	187	24	186	32	182	28	183	25	185	30	177	28	181	32	185
Athene cunicularia hypugaea	28	186	26	187	30	185	25	185	32	181	25	186	30	181	27	186	25	187	32	187
Lasionycteris noctivagans	27	187	27	186	29	186	24	188	32	183	29	178	25	187	27	187	25	188	32	186

Gaultheria shallon	27	188	26	188	26	189	24	187	31	185	24	189	29	182	26	188	26	185	31	188
Canis lupus	25	189	25	189	26	188	21	191	29	186	26	185	24	188	24	189	22	192	29	189
Strix varia	23	190	23	190	25	190	20	192	27	189	25	187	25	186	23	190	20	195	27	190
Corvus brachyrhynchos	22	191	23	191	24	191	19	194	26	190	24	190	24	189	17	196	24	189	26	191
Falco peregrinus	22	192	21	192	24	192	19	195	26	191	24	191	24	190	21	191	21	193	26	192
Acer macrophylla	21	194	21	194	23	194	22	189	25	193	18	194	20	195	20	194	23	190	25	193
Alnus rubra	21	195	21	195	23	195	22	190	25	194	18	195	20	196	20	195	23	191	25	194
Carduelis psaltia	21	193	21	193	23	193	20	193	25	195	20	193	23	192	20	193	20	196	25	195
Spermophilus variegatus	20	196	19	196	20	196	18	196	23	196	16	196	20	193	20	192	20	194	23	196

Chapter 2: Informing empirical niche models with mechanistic model projections to assess climate impacts on tree species distributions in northwestern North America.

Abstract

Both empirical and mechanistic models have been used to assess the potential impacts of climate change on species distributions. These two general modeling approaches have their strengths and their weaknesses. Empirical models require little data on the mechanistic links between species and their environments and thus allow for modeling of poorly studied species across large spatial extents. However, empirical models do not directly incorporate important biotic factors, such as competition and growth. Mechanistic approaches can explicitly model processes and relationships that determine a species' range and have the potential to better predict how a species will respond to a novel environmental state than do empirical models. However, mechanistic models require large amounts of specific information on growth, physiology, and competitive interactions, which is generally not available for most species. Here, we demonstrate an approach to projecting climate impacts on species distributions that draws on information from both empirical and mechanistic models. More specifically, we refined projections from empirical niche models for seven tree species with projections from a dynamic global vegetation model (DGVM) that simulates the distributions of biomes in northwestern North America. First, we intersected digital tree species range maps with suitable biomes and built our empirical niche models. Then, we used five future climates to project future distributions of both biomes and species niches. The third step involved intersecting the biome projections and the niche projections. These areas of intersection are places where both models predict suitable habitat. We then compared our refined model output with projections from

conventional empirical models and found that the two approaches provided substantially different results. These mechanistically-informed models incorporate important biological processes, such as species competition, physiological responses of plants to changes in atmospheric CO_2 concentrations, and disturbances (from the DGVM) as well as what are likely to be species-specific climatic constraints (from the niche models). The refined models projected less suitable environmental space than our unrefined models for the majority of these species. The two modeling approaches also projected similar trends of expansion and contraction for most species, but the locations of expansion and contraction differed by modeling approach. Nevertheless, the ranges of noble fir and western larch were projected to contract the most of the species analyzed and there was no suitable environmental space that was projected for subalpine larch. The results of this study demonstrate that informing empirical niche models with mechanistic model output can reduce the likelihood of over predicting suitable environmental space. Future projections from these refined modeling approaches offer insight into the location of these suitable areas and which species may be better able to persist in a changing climate. There is a clear need to improve the understanding of the current drivers of species' distributions, growth, reproduction, and survival. Future projections from refined modeling approaches that incorporate important biological factors, such as competition and the effects of increased carbon dioxide concentrations offer insight into species' potential future distributions and which species may be better able to persist in a changing climate.

Introduction

Plant species have moved and are moving in response to historical and present-day climate change (Kullman 2002; Beckage et al. 2008; Holzinger et al. 2008; Zhu et al. 2012). Changes in temperature and precipitation, carbon dioxide concentrations, competition among species, and disturbance regimes will all affect where plants will be able to grow in the future (Brubaker 1986, McKenzie et al. 2004, Hicke et al. 2006, Littell et al. 2010). In general, some of the largest changes will likely occur at the climatic limits of species distributions (Brubaker 1986, Allen and Breshears 1998, Thuiller et al. 2008, Williams et al. 2010).

Predictive models are one of the most commonly used tools to assess the potential impacts of climate change on species distributions. These predictive models can generally be classified as either mechanistic (process-based) or empirical (correlative) (Gusian and Zimmermann, 2000). Empirical modeling approaches that identify correlative relationships between species distributions and biophysical and climatic factors are often referred to as bioclimatic models, climate envelope models, species distribution models, or niche models. These models use fitted statistical relationships between a species distribution and historical or present-day climate. They then use these same relationships to project the species niche in the future under different climates. Although these models are correlative and do not necessarily represent causality between predictor and response variables, they can include limiting factors, (i.e., temperature, water, nutrition), disturbance factors (both natural and anthropogenic), and resource factors (i.e., energy and water) (Guisan and Thuiller, 2005).

A key strength of empirical niche models is the simplicity of input data; they require little data on the mechanistic links between species and their environments and thus allow for modeling of poorly studied species across large spatial extents. However, empirical modeling is

informed by knowledge of the underlying mechanisms and thus predictor variables should be selected based on this information. Nevertheless, the strength of empirical models is also their greatest weakness. Empirical niche models assume equilibrium between the current distribution of organisms and predictor variables, such as climate, and project these static relationships into the future (Guisan and Zimmermann, 2000; Wiens et al., 2009). There are a number of issues associated with this assumption. For example, species may have established under very different environmental conditions and are likely adapted to historical combinations of temperature and precipitation that may not exist today or into the future, and empirical models may incorrectly classify these non-analog conditions as unsuitable in the future (Hijmans and Graham, 2006). In addition, empirical niche models do not directly incorporate biotic factors, such as competition, establishment, dispersal, migration, growth, mortality, and evolutionary change (Pearson and Dawson, 2003; Pearson, 2006; Davis et al., 1998; Hampe, 2004).

Although empirical models have multiple weaknesses, they nonetheless are an important tool for conservation planning. A number of studies have assessed potential future habitat for tree species in western North America using empirical approaches. For example, Rehfeldt et al. (2006) and Crookston et al. (2010) projected the future climate space for 83 tree species in the Pacific Northwest and showed some loss of suitable habitat and extensive shifts in distributions by the end of the century. The loss of suitable habitat was also projected for some boreal species in British Columbia, in a study that used bioclimatic envelope models to track the habitat of individual tree populations (Gray and Hamann 2012).

In contrast to empirical niche models, mechanistic approaches explicitly model processes and relationships that determine a species range. These models attempt to predict 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. Mechanistic models generally require more detailed information on processes and an in-depth understanding of the associated response of species to environmental factors and dynamics. These models have the potential to better predict how a species will respond to a novel environmental state than do empirical models (Strasburg et al., 2007).

One of the greatest strengths of mechanistic models is that their predictions are based on causal relationships for a given species or group of species (Guisan and Zimmermann, 2000). This can be beneficial when interpreting why a species range has changed and allows for further extrapolation. Although mechanistic models have been used to simulate the distribution of individual tree species (e.g., Coops and Waring, 2011), they require large amounts of 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. An example of these models is a dynamic global vegetation model (DGVM), which can simulate the spatial and temporal patterns of vegetation distribution, classified as plant functional types (Sitch et al., 2003). Plant functional types can be combined with other mechanistic model output such as foliar projective cover and plant height to define biomes (e.g., Shafer et al., 2012); however, this coarse classification is somewhat limited for conservation planning.

Given some of the inherent weaknesses of both empirical and mechanistic models, recent studies have begun to integrate the two modeling approaches (e.g., Kearney and Porter, 2009; Buckley et al., 2010; Higgins et al., 2012; Dormann et al., 2012; Booth et al., 2012). For trees in North America, some have combined statistical habitat suitability models with 1) dispersal

models to examine the possible colonization of new suitable habitat (Iverson et al. 2004, McKenney et al. 2007, Meier et al. 2012), 2) modification factors that incorporate known species attributes to assess potential response under new climatic and disturbance regimes (Iverson et al. 2011), and 3) physiologically based growth models (Coops et al. 2009). For example, tree species distributions in the Pacific Northwest are generally projected to contract and shift northward (by 330 km under a no-dispersal scenario and 700 km under a full-dispersal scenario) (McKenney et al. 2007), suggesting that there will be major redistributions. However, these regional modeling approaches do not address the processes of competition between species or the direct and indirect effects of CO_2 enrichment.

Here, we combine the strengths of both empirical and mechanistic models by informing empirical niche model projections with output from a DGVM that simulates the distribution of biomes for seven tree species in northwestern North America. Our approach applies known mechanisms affecting vegetation and incorporates species-specific climatic constraints not addressed by the mechanistic model. We build these refined models first with historical climate and biome data and then make projections of potential changes in suitable environmental space based on five future climate projections.

Methods

Study Area

The study encompasses the western states of the U.S.A. and provinces of Canada in northwestern North America (Figure 1). The 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. The region is extremely diverse in climate, geology, topography, and vegetation. The climate of the region is heavily influenced by the Pacific Ocean to the west and the numerous mountain ranges found throughout the region. Forests range from wet, maritime coastal forests to dry, continental pine forests in the interior.

General Modeling Approach

We used a multi-step process to inform empirical niche models with DGVM projections (Figure 2a). This process involved projecting areas that were both climatically suitable and were likely to support the basic type of vegetation (i.e., biome) in which the species would exist. First, we determined which of the biome types predicted by the DGVM were likely to be suitable for each of the seven tree species (Table 1). This selection of relevant biomes was generally intuitive and was based on habitat associations and associated forest cover (Burns and Honkala, 1990). We then intersected digital tree species range maps with the identified suitable biomes and built our empirical niche models. To project future niches, we ran the DGVM with five future climates to project the future distributions of biomes. Then, we used the same climate projections as input to the empirical models and projected future niches. The final step involved intersecting the biome projections and the niche projections. 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 carbon dioxide concentrations, interactions with other basic plant functional types, and fire) and where the climate is likely to be suitable for the species. We compared the projections of these models to those of conventional empirical niche models based solely on species current distributions (Figure 2b).

For each species, modeling approach, and future projected climate, we then calculated the percentage of each species distribution that was stable, projected to expand, and projected to contract by comparing the future projections with the current predicted distribution. Stable is defined as predicted future areas that are in the same locations as the current predicted distribution, in other words the future distribution occupies the same locations as the current distribution. Expansion is defined as predicted future areas that are in new locations, not previously occupied in the current distribution. And contraction is defined as the loss of areas previously occupied by the current distribution. We then calculated the overall percent net change in projected species distributions.

Data

Tree Species & Distribution Maps

We modeled the environmental niche of seven tree species: Pacific silver fir (*Abies amabilis*), grand fir (*Abies grandis*), noble fir (*Abies procera*), subalpine larch (*Larix lyallii*), western larch (*Larix occidentalis*), Pacific yew (*Taxus brevifolia*), and western redcedar (*Thuja plicata*). These tree species represent a wide range of climatic tolerances and their distributions were fully contained within the study area. After downloading the digital range maps from the U.S. Geological Survey "Atlas of United States Trees" (Little, 1971), we converted them from polygons into 1-km^2 resolution grid cells. We used this relatively fine resolution to strike a balance between the ability to detect large-scale, continental climate patterns across the study area and providing high resolution projections of niche change. Other studies have found this resolution useful for land management (e.g., Rehfeldt et al., 2006) and resolutions finer than 1-km^2 may give a false impression of accuracy that does not currently exist in climate predictions.

Climate data

Historical climate data were derived from the Climatic Research Unit (CRU), University of East Anglia, CL 2.0 (New et al. 2002) and CRU TS 2.1 (Mitchell and 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, which were then downscaled to a 10‘ latitude by 10‘ longitude global grid. The CRU CL 2.0 and CRU TS 2.1 data sets were then limited to an envelope encompassing the study area, and downscaled further to a 30 arc-second resolution grid using a geographic distance-weighted bilinear interpolation method (Shafer and Bartlein, 2011). We identified 36 climate and bioclimatic variables (Table 2) that are biologically important controls to tree growth (Prentice et al. 1992, McKenzie et al. 2003, Williams et al. 2007) and we used these to model current tree niches.

We then used future climate projections from the IPCC Fourth Assessment Report run for the SRES A2 greenhouse–gas emissions scenario to model future tree niches. The A2 emissions scenario represents a world with increasing population growth, regionally oriented economic development, slower development, and implementation of new technologies (Nakicenovic and Swart 2000). We used projections from each of the five following general circulation models (GCMs) for the time period 2070 – 2099: BCCR BCM 2.0 (BCCR 2005), CCCma CGCM 3.1 (Flato 2005), CSIRO MK 3.0 (Collier 2005), INM-CM 3.0 (Volodin 2005), MIROC 3.2 MEDRES (Nozawa 2005).

Dynamic Global Vegetation Model Data

Biomes were projected using the Lund-Potsdam-Jena Dynamic Global Vegetation Model (LPJ) (Sitch et al. 2003, Shafer, 2013). LPJ is a process-based model that uses monthly temperature, precipitation, sunshine, annual atmospheric CO_2 concentrations, and soil data to simulate composition and structure of dominant vegetation in the form of plant functional types (PFTs). LPJ then combines PFTs with multiple mechanistic processes, such as photosynthesis, growth, resource competition, population dynamics (establishment and mortality), and disturbances, such as fire. Each PFT is also constrained by bioclimatic limits which determine whether it can survive or regenerate within a given grid cell (Stich et al. 2003). LPJ also incorporates changes in atmospheric CO_2 concentrations, an important feature for accurately simulating vegetation responses to future climate change. LPJ was run with the same climate data and projections described above. LPJ output was not used as predictor variables in the empirical niche models.

Niche Modeling

To model climate suitability, we first converted digitized range maps to binary grids (Figure 2). We then used the statistical program, R (R Development Core Team, 2013), and a random forests package "randomForest" (Liaw and Wiener, 2002) to build and evaluate tree distribution models. Random forests is an ensemble classifier that builds multiple classification trees using an iterative process that randomly selects 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. Each tree was generated with a subset of the observations and each split in each model was made with a subset of the

predictor variables. This resampling of predictors and observations reduces the impact of collinearity among predictor variables, allows the model to explore the full range of data space, and tends to improve model fit (Elith and Graham, 2009).

We split our dataset 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, the package "randomForest" resampled the training dataset 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 dataset and thus we used that ratio of absences to presences when building our models. The random forest models produce probability estimates ranging from 0 to 1. Therefore, we converted this range of values to a binary format representing "suitable" or "not suitable" niche predictions by determining an optimal threshold value for each species model. This threshold value was identified using the "PresenceAbsence" package, 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 towards the lower right until it first touches the ROC curve (Figure 3) (Freeman and Moisen, 2008a). 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 and Bell, 1997). Prevalence is defined as the overall proportion of locations where the variable is 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 dataset. We used the mean decrease in the Gini index to identify the most important variables and selected

the least correlated variables for the final model. Most models had two to three predictor variables. Having fewer climate variables in these final models also simplified our inferences as to the climatic controls for each species. We then used the final model to predict potential climatic suitability for each species across the study area and visually compared these results with (a) distribution maps (Little, 1971) and (b) other studies (e.g., Rehfeldt et al., 2006; Crookston et al. 2010; Hamann and Wang 2006).

Results

Future projections produced by our refined modeling approach were considerably different than those produced by our unrefined niche models for six of the seven species (Figures 4 and 5). Furthermore, our refined models projected less suitable environmental space than our unrefined models for the majority of these species, including, Pacific silver fir, noble fir, western larch, and western redcedar. The largest differences in net change between the unrefined and refined modeling approaches were for noble fir (-85%) and western larch (-66%) (Figure 4). For these two species, the areas projected as potentially contracting increased moderately between the unrefined and refined models but the largest changes were due to a substantial decrease in areas of potential expansion, with a -57% change for noble fir and a -36% change for western larch. Neither of our modeling approaches predicted any future presences for subalpine larch after applying the threshold value.

Our results also show that although the two modeling approaches forecast similar trends of expansion and contraction for most species (i.e., Pacific silver fir, noble fir, western larch, and western redcedar), the geographic locations of potential expansion and contraction differ

significantly. These differences are most evident when examining the similar direction of change for pacific silver fir and western redcedar (Figure 4), and the substantial differences of where the ranges of each species is projected to contract and expand (Figure 5). For instance, both the refined and unrefined models project large areas of potential expansion of Pacific silver fir's environmental space, however, the unrefined model projects some of these areas along the Pacific coast and the western slopes of the Cascades which is not found with the refined model projections. For noble fir, the pattern of different locations of projections between modeling approaches is even more pronounced, with large areas of potential expansion to the west of its current range for the unrefined model and no expansion in these areas for the refined model (Figure 5).

Our refined models projected more suitable environmental space in the future for two species, Pacific yew and grand fir (Figure 4). This increase in suitable environmental space occurred even though the refined models had smaller initial environmental spaces than the unrefined models. This pattern of more suitable space being projected by the refined model is similar among the two species. However, Pacific yew had larger increases in areas projected to be stable and to potentially expand from the unrefined to the refined models, 10% and 17%, respectively. Furthermore, grand fir had more moderate increases of stable areas (3%) and potential expansion (14%), but was the only species to switch from a negative net change for the unrefined model (-16%) to a positive net change for the refined model (5%).

The close visual match between the predicted presences for each species and their original distribution maps suggests that both our refined and unrefined models were able to adequately predict the current distribution for the seven tree species. The out of bag errors averaged 2.3% for the empirical niche models and 1.8% for refined niche models, whereas the

commission errors (i.e., predicting a presence when there is none) averaged 14.1% for the unrefined models and 11.1% for refined models. The omission errors –predicting no presence when one is there – averaged 1.3% for the unrefined models and 1.2% for refined models (Table 3). Interestingly, the out of bag error is negatively correlated with the size of the tree species range, with species that have the largest range also having the largest out of bag error. This is likely a result of our models generally misclassifying presences more often than absences. Although we controlled the ratio of absences to presences to 10 to 1, tree species with larger distributions had more opportunities to have their presences misclassified. Our final models also contained fewer predictor variables for each species except for subalpine larch, which required more climate variables to successfully predict at least 70% of the presences and 90% of the absences in the evaluation datasets (see Tables 4 and 5).

Refining tree species distributions with their relevant biomes resulted in, on average, about a 70% overlap of their current distributions with the relevant biomes (Table 1, Figure 6). However, this overlap varied substantially among species with only 38% overlap between the original distribution of noble fir and the cool forest biome and 90% overlap between the original distribution of subalpine larch and the cold forest, cool forest, cold open forest/ woodland, and cool open forest/ woodland biomes (see Table 1). This wide range of values is due, in part, to the selection of which biomes were most appropriate for each species and the relatively general classifications of biomes produced by the DGVM. Nevertheless, the match between species and their relevant biomes is justified for the level of detail specified by mechanistic model and therefore illustrates a more realistic portray of actual distribution of species. For example, Figure 6 shows a map of the distribution of Pacific silver fir and the combined distributions of both the

cool and cold forest biomes. In this incidence, 61% of the distribution of Pacific silver fir remained after refining it with these two biomes.

The climate variables that were most important in all models generally represent precipitation and temperature limits for each species (see Tables 4 and 5). Overall, potential evapotranspiration during December-February was most often identified as being important across the seven species. Intuitively, snow water equivalent was important for predicting the presence of higher elevation species, such as subalpine larch and Pacific silver fir. Annual temperature range (i.e., mean temperature during the warmest month minus the mean temperature of the coldest month) was an important predictor for some lower elevation species, such as Pacific yew.

However, some of the climate variables differed between modeling approaches for the same species. For instance, both Pacific yew and western redcedar had moisture indices as their second most important predictor variable in their unrefined models, but then had temperature-related variables in their refined models (see Tables 4 and 5). This change in the nature of predictor variables resulted in somewhat different future projections. Furthermore, the two modeling approaches differed in the northeast portion of western redcedar's future niche, with the refined model showing expansion in portions of the Canadian Rockies and the unrefined model projecting a large area of contraction. For Pacific yew, areas of expansion were projected in the eastern Sierra Nevada, central and eastern Oregon, and northern Vancouver Island for the refined model whereas for the unrefined model these areas were projected to contract.

Discussion

Informing empirical model projections with mechanistic model output provided substantially different and arguably more realistic projections of potential future niches than conventional empirical models. Specifically, using available data from mechanistic models that simulate important biological processes, such as species competition, physiological responses of plants to changes in atmospheric CO_2 concentrations, and disturbances likely allowed us to provided more realistic projections of future species' distributions (Kearney and Porter, 2009). We have improved our empirical niche models by including these known processes and thus our refined models likely offer a better estimate of the true realized niche of species (Hutchinson, 1957). Empirical models that are based purely on correlations run the risk of not fully reflecting the actual processes controlling a species distribution (Guisan & Zimmermann, 2000) and potentially over predicting future areas of suitability. For instance, our refined models projected much less suitable environmental space than our unrefined models for the majority of species. This finding also highlights that our refined models project that some species may be more climatically sensitive than what our unrefined models project.

The mechanistically-informed modeling approach we used takes an important step towards assessing suitable environmental space of tree species in the future. For instance, mechanistic model output was used to identify and refine areas that are not suitable for some species because of inappropriate soils, competition with other species, or fire. This is important for conservation planning because detailed information on where species are located, such as plot data, can be difficult to acquire, challenging to crosswalk across international boundaries, and is not available in some areas (Elith et al., 2006). The process of refining species' distributions with relevant biomes also removed areas that are known to be too dry and too cold for some species,

such as deserts and very high elevations. For instance, the process of refining grand fir's distribution removed unsuitable areas at very high elevations in the Cascade and southern Canadian Rocky Mountains. These areas were well outside the range of elevations at which trees are able to grow at.

Our modeling results showed large areas of potential range contraction for noble fir and western larch and no future projections for subalpine larch, patterns supported by other studies within our study area (e.g., Hamann and Wang 2006; McKenney et al. 2007; Crookston et al. 2010). Noble fir tends to grow primarily on montane sites with high precipitation, mostly in the form of snow, and relatively cool temperatures (Franklin, 1990). Declining future snowpack and warming temperatures may be responsible for much of its shrinking environmental space in the southern portion of its distribution in the future. However, future projections also indicate some potential areas of expanded environmental space in the northern portion of its range, in the North Cascade Mountains and parts of British Columbia. However, noble fir does not begin producing seeds until 20 to 50 years of age and seeds are relatively heavily, usually fallings within one or two tree heights of the seed trees (Carkin et al., 1978). Therefore, given that some of the future suitable environmental space is more than 100 km away, assisted migration may be necessary to facilitate noble fir's migration.

Large areas of potential range contraction were also projected for western larch, a finding supported by other studies (Rehfeldt et al., 2006). This trend was driven by warming temperatures and declines in moisture index and snow water equivalent. However, 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). Therefore western larch may be able to migrate and potentially keep

pace with its optimal habitat. Low to moderate-severity fires are essential for the establishment of western larch in natural forest stands and although 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), many of these events may be too severe.

The lack of suitable future environmental space for subalpine larch may be partly explained by poorer performing models, which required more climate variables than other models in this study. Nevertheless, subalpine larch is not expected to have much suitable environmental space in the future for multiple reasons. First, subalpine larch has been found to be relatively sensitive to changes in climate occupying some of the coldest high-elevation sites that trees grow on and a change in precipitation, such as snow or the seasonal duration of snowpack, will likely influence the ability of this species to persist in some areas (Case, 2014). Second, subalpine larch has a disjunct distribution, with a portion in the Rocky Mountains and another portion in the Cascade Range (Arno and Habeck, 1972), providing a barrier to gene flow. Third, subalpine larch do not produce appreciable quantities of seeds until they are at least 80 years old and only dominant trees that are several hundred years of age, produce the largest crops (Arno 1990).

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 and McKenzie, 2013). Subsequently, both our modeling approaches show that most species 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., McKenney 2007; Rehfeldt et al., 2006; Crookston et al. 2010). Both modeling approaches indicate areas of expansion for grand fir and Pacific yew to the north of its current distribution,

largely driven by warming temperatures and an increasingly moist climate. Also, much of grand fir's overall net increase for the refined model is attributed to the projected increase in precipitation and moisture indices throughout the region. Moreover, both the refined and unrefined models for grand fir were largely driven by spring precipitation, which is projected to increase in western Washington, western British Columbia, and the Canadian Rockies (Figure 7). The mechanistic model indicates that the extent of cool forest 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. For instance, some of the most productive commercial stands of grand fir are in the Nez Perce National Forest in northern Idaho (Foiles 1965), an area projected to decline in suitable environmental space in the future. By contrast, Lewis County, Idado, which lies just east of the New Perce National Forest, is projected to have more suitable environmental space in the future.

We have presented one mechanistically-informed approach to projecting suitable environmental space, however, other studies have explored alternative modeling techniques and methods (e.g., see Iverson and McKenzie, 2013 and Kearney and Porter, 2009 for reviews). Some of these other approaches have incorporated dispersal (Iverson et al., 2004), competition (Meier et al., 2012), and the effects of disturbance regimes (Iverson et al., 2011), however, they do not explicitly incorporate the effects of CO_2 enrichment and the subsequent species interactions. Alternative modeling techniques, such as maximum entropy modelling and generalized linear models will also likely provide different future projections (Elith and Graham, 2009). The best performing models may differ by individual species (Keenan et al., 2009) and in some cases ensemble projections from multiple modeling techniques may be warranted (Araújo

and New, 2007). Low prevalence and poor model quality have also been shown to be sensitive to the choice of presence – absence thresholds (Freeman and Moisen, 2008b) and could be further explored, especially for the subalpine larch models.

Even though our refined models produced arguably more realistic future projections, there is still room for improvement. The climate variables that were identified as being the most important were related to water and energy, which is consistent with other studies (see Field et al., 2005), however, our models did not capture all of the species' observed physiological limits. For instance, both the refined and unrefined models for Pacific silver fir project future suitable environmental space in the southern Canadian Rockies, an area with very cold temperatures during the winter. Because Pacific silver fir is generally limited by cold temperatures (Packee et al., 1983), the likelihood of it establishing and growing in such a region is low. Pacific silver fir is also dependent on adequate soil moisture during the growing season. Therefore, we explored an alternative approach that used published information on the cold temperature tolerance and adequate soil moisture tolerance of Pacific silver fir (Thompson et al., 1999; McKenney et al., 2007) to constrain its future distribution to areas that would be suitable (see Appendix). Overall, constraining the distribution of Pacific silver fir only marginally changed the future projections with some decrease in the areas of potential expansion, mostly in the southern portion of its range and in the Canadian Rockies. Furthermore, refining species' ranges with relevant biomes may not be suitable for some species for which some suitable environmental space exists outside the distribution of the relevant biomes. For these species, the process of refining their distributions with biomes may lead to poor models or significantly different predictor variables suggesting different limiting factors – that is one model may indicate energy-limitations while

the refined model may indicate water-limitations. Capturing different limitations in the models would also result in different future projections.

Future research could investigate whether our models capture the actual current presences and absences of species using detailed plot data. These data could also be used to examine the relative abundance of species across their range, which is important when determining forest species composition and the potential for new assemblages. Data on species abundances would also improve the ability to model dispersal and potential migration into new suitable environmental space. The relationships between the species analyzed in this study and the identified climate variables could be further examined to highlight constraints to tree growth and survival and could potentially be applied to other species in other areas.

Conclusion

Conventional empirical modeling approaches have a number of inherent weaknesses but can be improved by refining projections with mechanistic model outputs. These refined modeling approaches apply known mechanisms affecting vegetation, such as species competition, changes in atmospheric CO_2 concentrations, and disturbances and incorporate species-specific climatic constraints not addressed by mechanistic models. As a result, mechanistically-informed modeling approaches provide substantially different and arguably more realistic future projections of suitable environmental space. For example, informing empirical niche models with mechanistic model output can reduce the likelihood of over predicting suitable environmental space by refining current species distributions to areas that have suitable soils and by removing areas that are climatically extreme, such as mountain tops

and desserts. Although there is a clear need to improve understanding of the current drivers of species' distributions, growth, reproduction, and survival, future projections from these mechanistically-informed modeling approaches offer insight into the location of these suitable areas and which species may be better able to persist in a changing climate. An important next step will be to validate these refined empirical models with detailed plot data and explore alternative statistical models and species.

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Table 1. Tree species, their relevant biomes, and the percent of the original species distribution that is found within the biome distributions, as defined by the dynamic global vegetation model (DGVM).

Species	**Biomes**	**Percent of species distributions that are found in biomes**
Pacific silver fir *(Abies amabilis)*	cold forest, cool forest	61
Grand fir (Abies grandis)	cool forest, coastal cool forest, cool open forest/woodland, cool open forest/woodland with broadleaf evergreen component	87
Noble fir (Abies procera)	cool forest	38
Subalpine larch (Larix lyallii)	cold forest, cool forest, cold open forest/woodland, cool open forest/woodland	90
Western larch (Larix occidentalis)	cold forest, cool forest, cold open forest/woodland, cool open forest/woodland	89
Pacific yew (Taxus brevifolia)	cool forest, coastal cool forest, cool open forest/woodland with broadleaf evergreen component	71
Western hemlock (Thuja plicata)	cool forest, coastal cool forest	60

Table 2. The 36 climate variables, their abbreviations, and their corresponding units that were used in as predictor variables in model building of seven tree species.

Abbreviation	**Variable Name**	**Units**
CHILL	The number of days in the year with a mean temperature <= 5°C	number of days
FROST	The number of days in the year with a mean temperature greater than 0°C	number of days
GDD0	Growing degree days (0°C base)	number of days
GDD5	Growing degree days (5°C base)	number of days
MAT	Mean annual temperature	degrees Celsius
MI_ANN	Moisture index (annual) (annual actual evapotranspiration/annual potential evapotranspiration)	millimeters
MI_DECIDOUS	Moisture index (deciduous)	millimeters
MI_DJF	Moisture index (December-February)	millimeters
MI_EVERGREEN	Moisture index (evergreen)	millimeters
MI_JJA	Moisture index (June-August)	millimeters
MI_MAM	Moisture index (March-May)	millimeters
MI_SON	Moisture index (September - November)	millimeters

MTCO	Mean temperature during the coldest month	degrees Celsius
MTWA	Mean temperature during the warmest month	degrees Celsius
PET_ANN	Potential evapotranspiration (annual)	millimeters
PET_DECIDOUS	Potential evapotranspiration (deciduous)	millimeters
PET_DJF	Potential evapotranspiration (December-February)	millimeters
PET_EVERGREEN	Potential evapotranspiration (evergreen)	millimeters
PET_JJA	Potential evapotranspiration (June-August)	millimeters
PET_MAM	Potential evapotranspiration (March-May)	millimeters
PET_SON	Potential evapotranspiration (September-November)	millimeters
PRANGE	Total precipitation of the wettest month minus total precipitation of the driest month	millimeters
PREC_ANN	Total annual precipitation	millimeters
PREC_ANN_MEAN	Mean annual precipitation	millimeters
PREC_DJF	Total precipitation during December-February	millimeters
PREC_DRY	Total precipitation during the driest month	millimeters
PREC_JJA	Total precipitation during June-August	millimeters
PREC_MAM	Total precipitation during March-May	millimeters
PREC_MJJAS	Total precipitation during May-September	millimeters
PREC_SON	Total precipitation during September-November	millimeters
PREC_WET	Total precipitation during the wettest month	millimeters
SWE_ANN	Snow Water Equivalent (annual)	millimeters
TMP_DJF	Temperature during December-February	degrees Celsius
TMP_MAM	Temperature during March-May	degrees Celsius
TMP_SON	Temperature during September-November	degrees Celsius
TRANGE	Mean temperature of the warmest month minus mean temperature of the coldest month	degrees Celsius

Table 3. Classification errors from the confusion matrix, with out of bag errors (OOB), commission errors, and omission errors for both the refined and unrefined models for seven tree species. Tree species codes are: ABAM – Pacific silver fir (*Abies amabilis*), ABGR – grand fir (*Abies grandis*), ABPR – noble fir (*Abies procera*), LALY – subalpine larch (*Larix lyallii*), LAOC – western larch (*Larix occidentalis*), TABR – Pacific yew (*Taxus brevifolia*), and THPL – western redcedar (*Thuja plicata*).

Species	**Number of climate variables in final model**	**OOB (%)**	**Commission Errors (%)**	**Omission Errors (%)**
unrefined ABAM	3	1.51	10.72	1.03
refined ABAM	3	1.66	10.74	1.38
unrefined ABGR	3	2.08	17.18	1.15
refined ABGR	3	1.81	12.88	1.22
unrefined ABPR	3	0.83	3.48	0.81
refined ABPR	3	0.24	1.27	0.23
unrefined LALY	9	0.95	5.67	0.91
refined LALY	11	0.55	2.20	0.53
unrefined LAOC	3	2.14	11.02	1.77
refined LAOC	3	1.88	8.96	1.62
unrefined TABR	2	3.55	23.12	1.45
refined TABR	2	3.15	22.50	1.73
unrefined THPL	2	5	27.66	2.18
refined THPL	2	3.12	19.41	1.98

Table 4. Final random forest model results and important predictor variables for unrefined niche models. Tree species codes are the same as in Table 3.

Species Code	Number of climate variables in final model	Out of Bag Errors (OOB %)	Optimized thresholds ratio	Correctly predicted presences (%)	Correctly predicted absences (%)	Most important predictor variable	Second important predictor variable	Third important predictor variable	Additional important predictor variables
ABAM	3	1.51	0.63	83.67	99.34	PREC_AN N	PET_DJF	SWE_ANN	
ABGR	3	2.08	0.56	79.45	99.11	PREC_MA M	PET_EVER GREEN	MTCO	
ABPR	3	0.83	0.91	78.29	99.91	TRANGE	PET_SON	PREC_MJJ AS	
LALY	9	0.95	0.82	72.1	99.73	PET_DJF	SWE_ANN	MI_DJF	PREC_DRY , MI_MAM, FROST, PREC_DJF, GDD5, MTWA
LAOC	3	2.14	0.71	74.71	99.11	PET_DJF	TRANGE	MI_DJF	
TABR	2	3.55	0.47	77.54	98.49	TRANGE	PET_DJF		
THPL	2	5	0.46	75.44	97.48	PREC_SO N	PET_DJF		

Table 5. Final random forest model results and important predictor variables for refined niche models. Tree species codes are the same as in Table 3.

Species Code	Number of climate variables in final model	Out of Bag Errors (OOB %)	Optimized thresholds ratio	Correctly predicted presences (%)	Correctly predicted absences (%)	Most important predictor variable	Second important predictor variable	Third important predictor variable	Additional important predictor variables
ABAM	3	1.66	0.75	75.1	99.38	PREC_AN N	PET_DJF	SWE_ANN	
ABGR	3	1.81	0.62	80.84	99.27	PREC_MA M	PET_EVERG REEN	MTCO	
ABPR	3	0.24	0.96	77.73	99.97	PRANGE	SWE_ANN	PREC_DRY	
LALY	11	0.55	0.87	72.82	99.88	PET_SON,	PET_DJF,	PREC_MAM,	SWE_ANN , TRANGE, MI_DJF, TMP_DJF, MI_MAM, FROST, GDD5, MTWA
LAOC	3	1.88	0.74	75.91	99.21	PET_DJF	TRANGE	SWE_ANN	
TABR	2	3.15	0.7	72.6	98.67	TRANGE	FROST		
THPL	2	3.12	0.6	73.64	98.57	PREC_SON	GDD5		

Figures

Figure 1. Study area. The map denotes the combined extent of all seven tree species distributions and the extent for which climate data were downscaled.

Figure 2. Two niche modeling approaches; A) represents a mechanistically-informed approach of refining species distributions with mechanistic model output (DGVM) and then building, projecting, and refining future species distributions; B) represents the conventional approach of combining historical climate and species distributions to build the model and then applying future climate to project future species distributions.

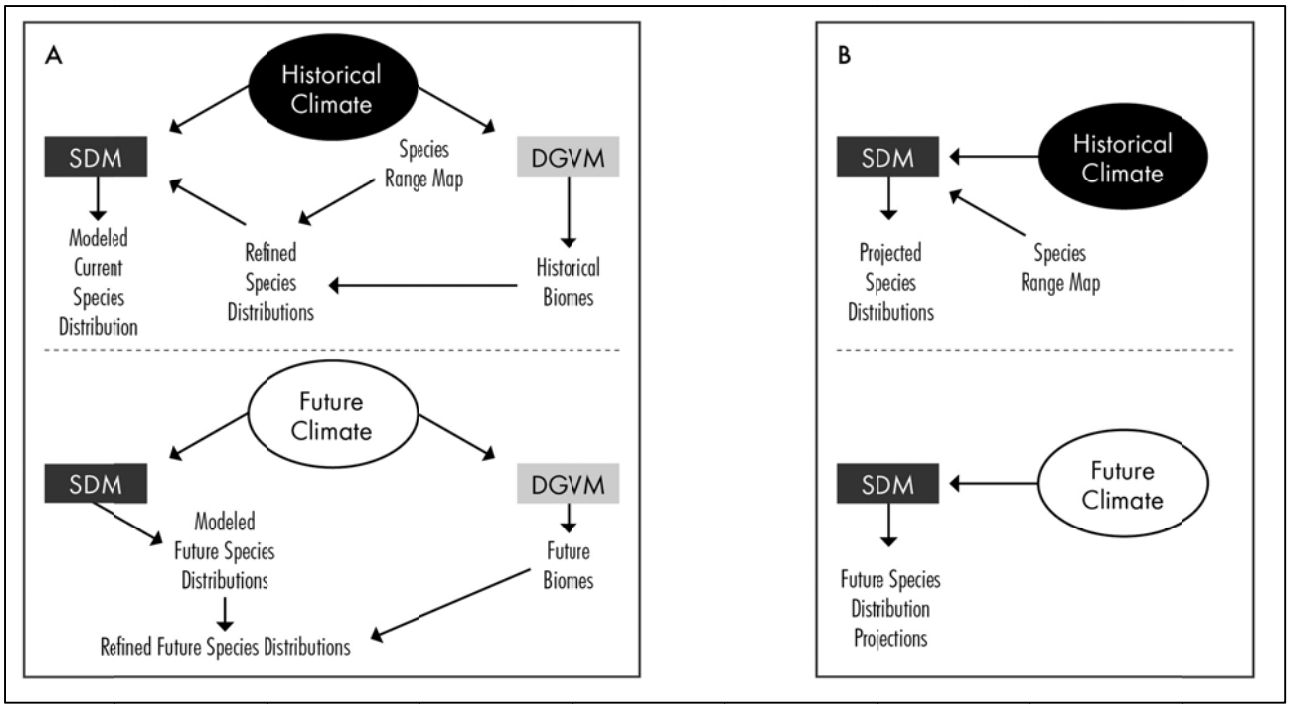
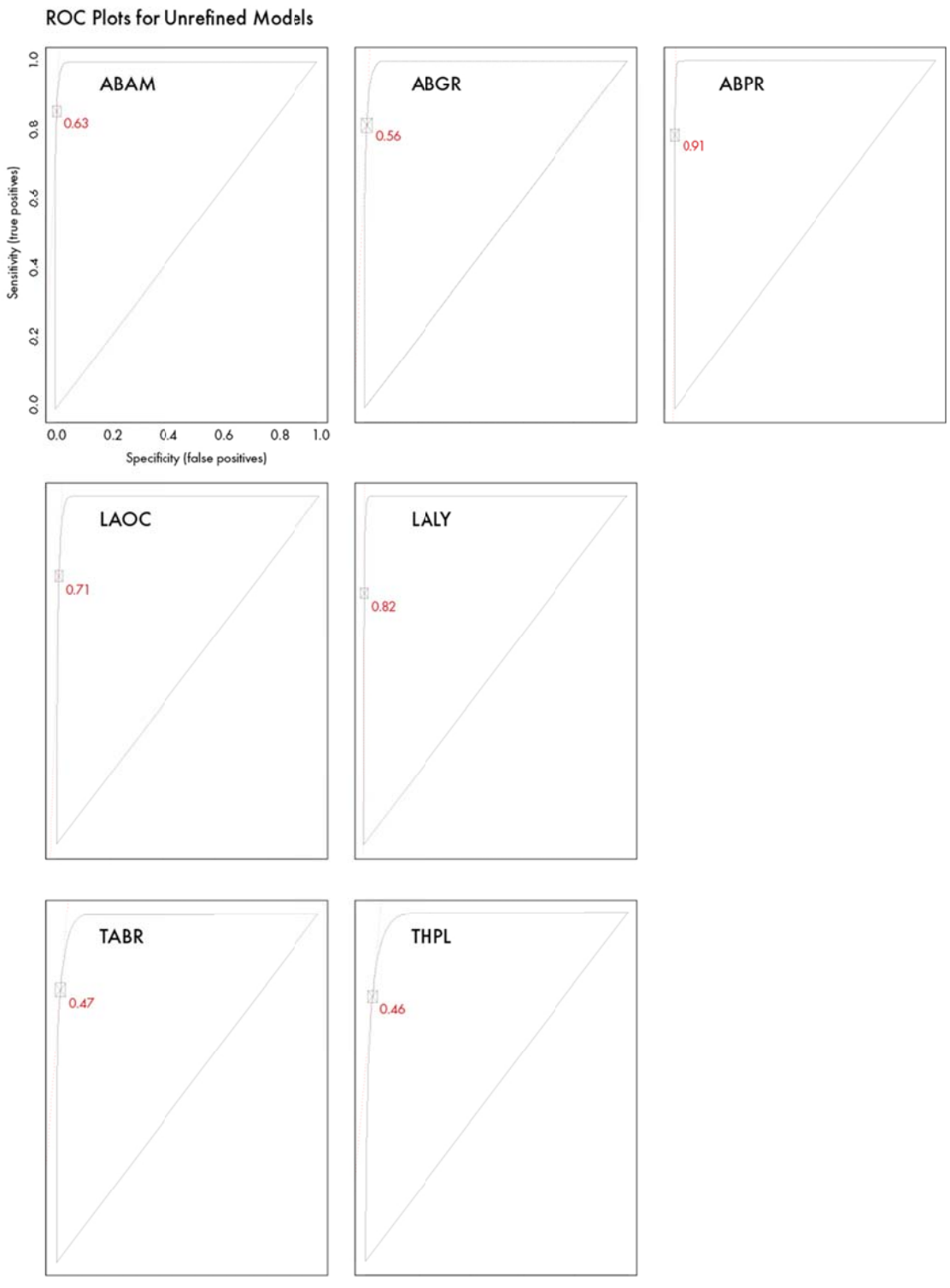


Figure 3. Receiver Operator Characteristic (ROC) plots for 1) unrefined tree species distribution models and 2) refined tree species distribution models for seven tree species showing the optimized threshold and the corresponding line with the slope based on the ratio of the relative costs of false positive predictions and false negative predictions divided by the prevalence. Tree species codes are the same as in Table 3.


ROC Plots for Unrefined Models
ABAM
0.63
ABGR
0.56
ABPR
0.91
LAOC
0.71
LALY
0.82
TABR
0.47
THPL
0.46
Sensitivity (true positives)
Specificity (false positives)
0.0
0.2
0.4
0.6
0.8
1.0

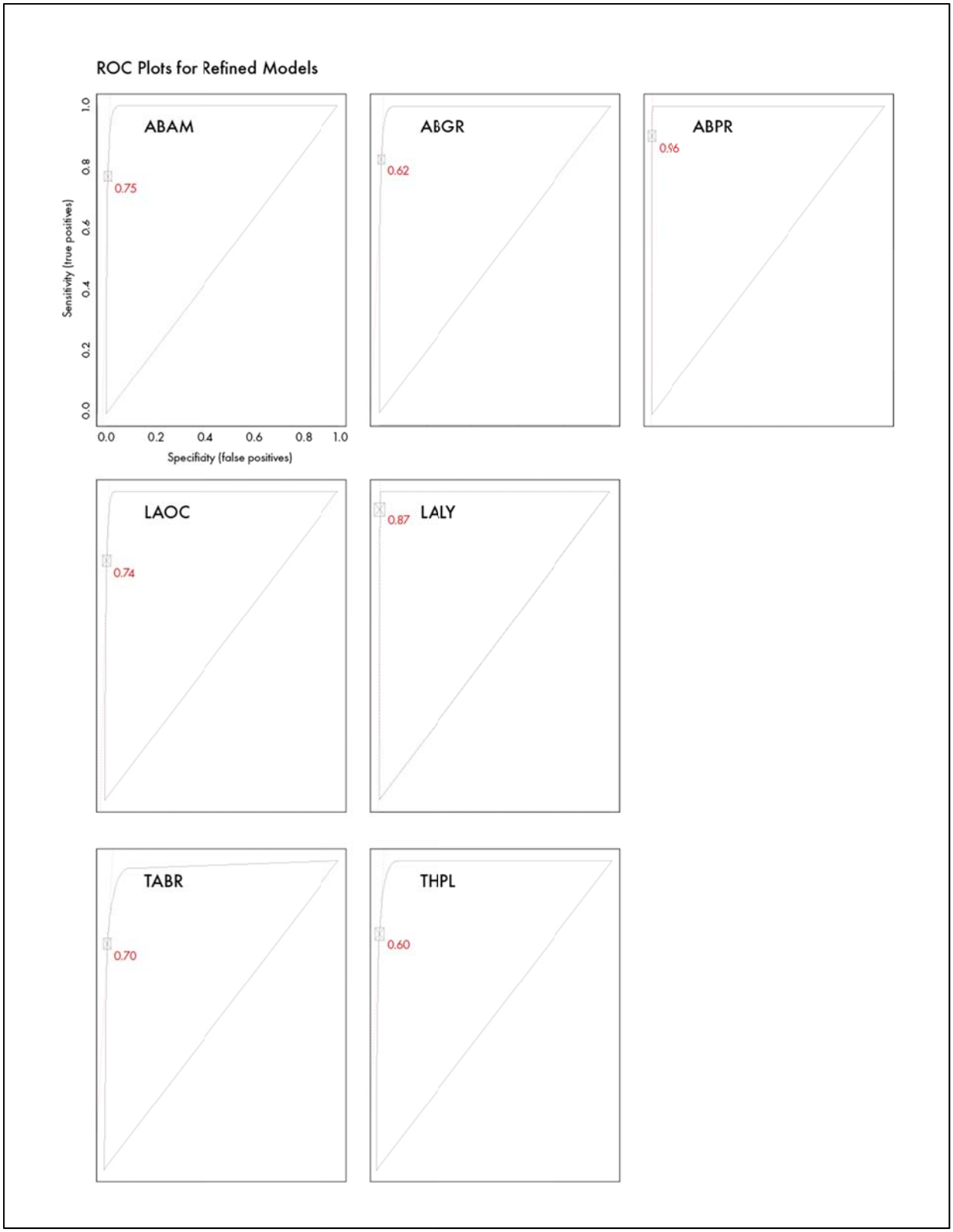

ROC Plots for Refined Models
ABAM
0.75
ABGR
0.62
ABPR
0.96
LAOC
0.74
LALY
0.87
TABR
0.70
THPL
0.60
Sensitivity (true positives)
Specificity (false positives)
0.0
0.2
0.4
0.6
0.8
1.0

Figure 4. Percent change for stable, expansion, contraction, and net change of future suitable environmental space for seven tree species for refined and unrefined models. Tree species codes are the same as in Table 3.

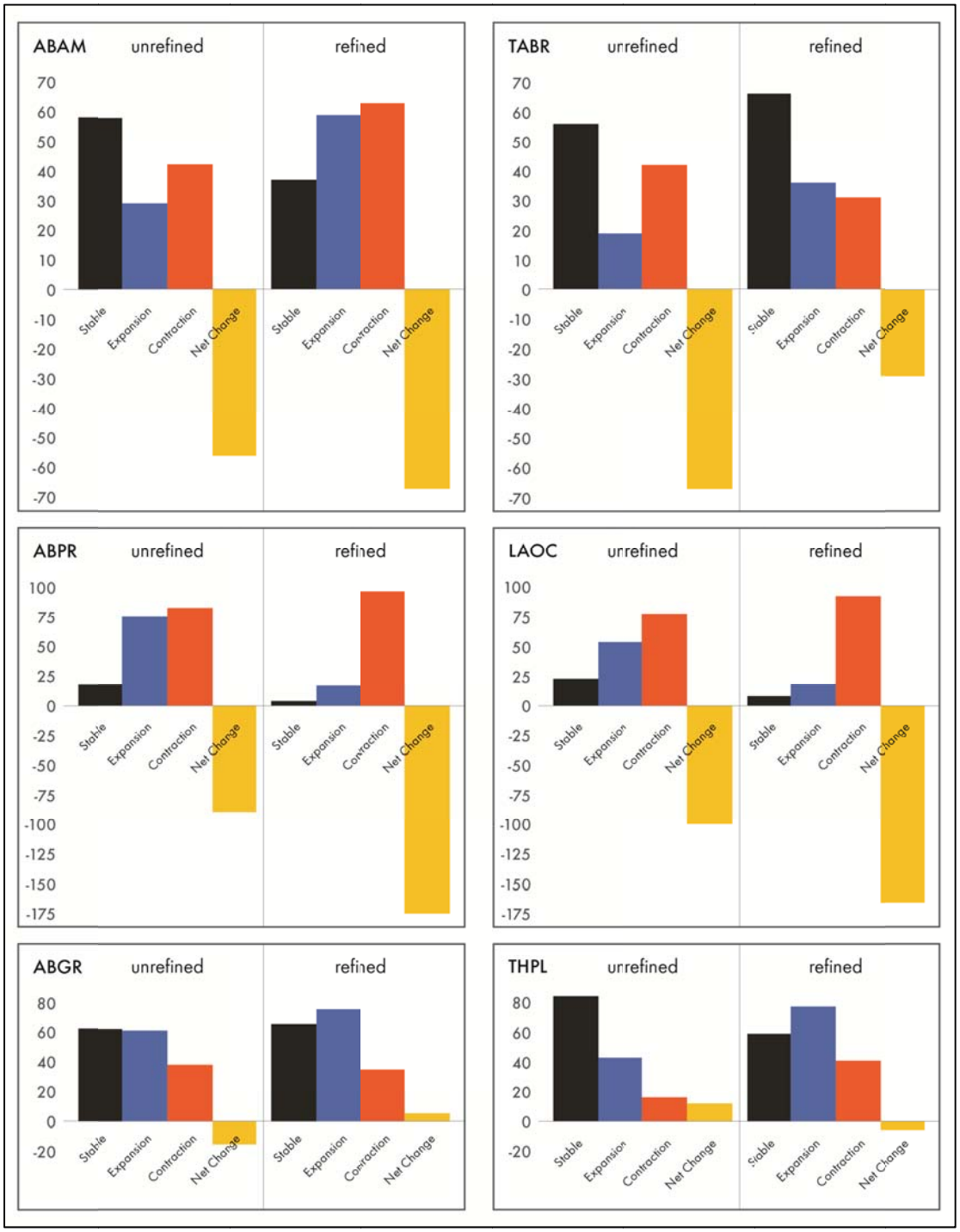


Figure 5. Future projections for both the refined and unrefined distributions of seven tree species and the ensemble of five general circulation models for the time period 2070 to 2099 for the A2 emissions scenario. Tree species codes are the same as in Table 3.

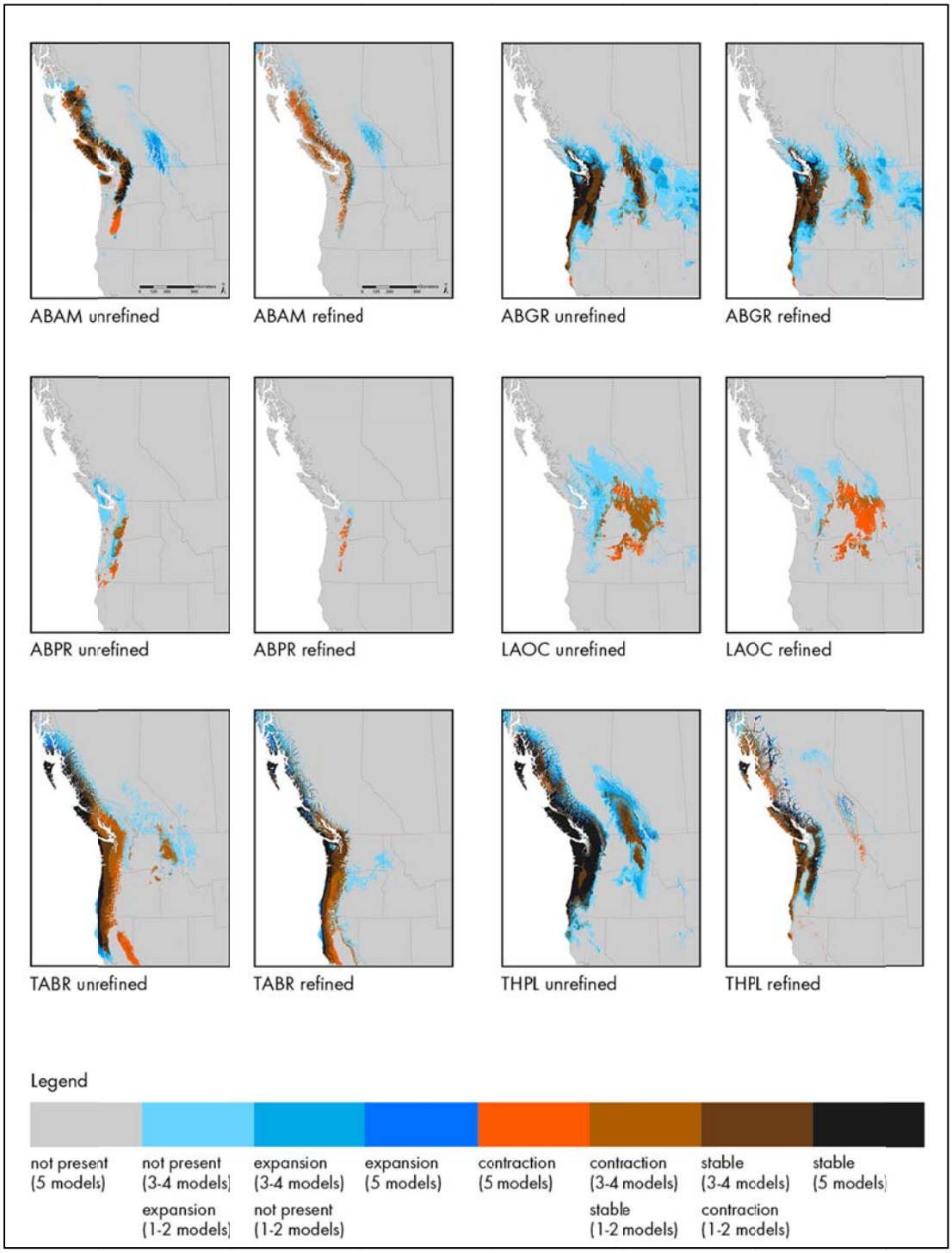


Figure 6. Geographic distributions of seven tree species and their relevant DGVM biomes. Overlap areas are represented by the dark red color. Tree species codes are the same as in Table 3.

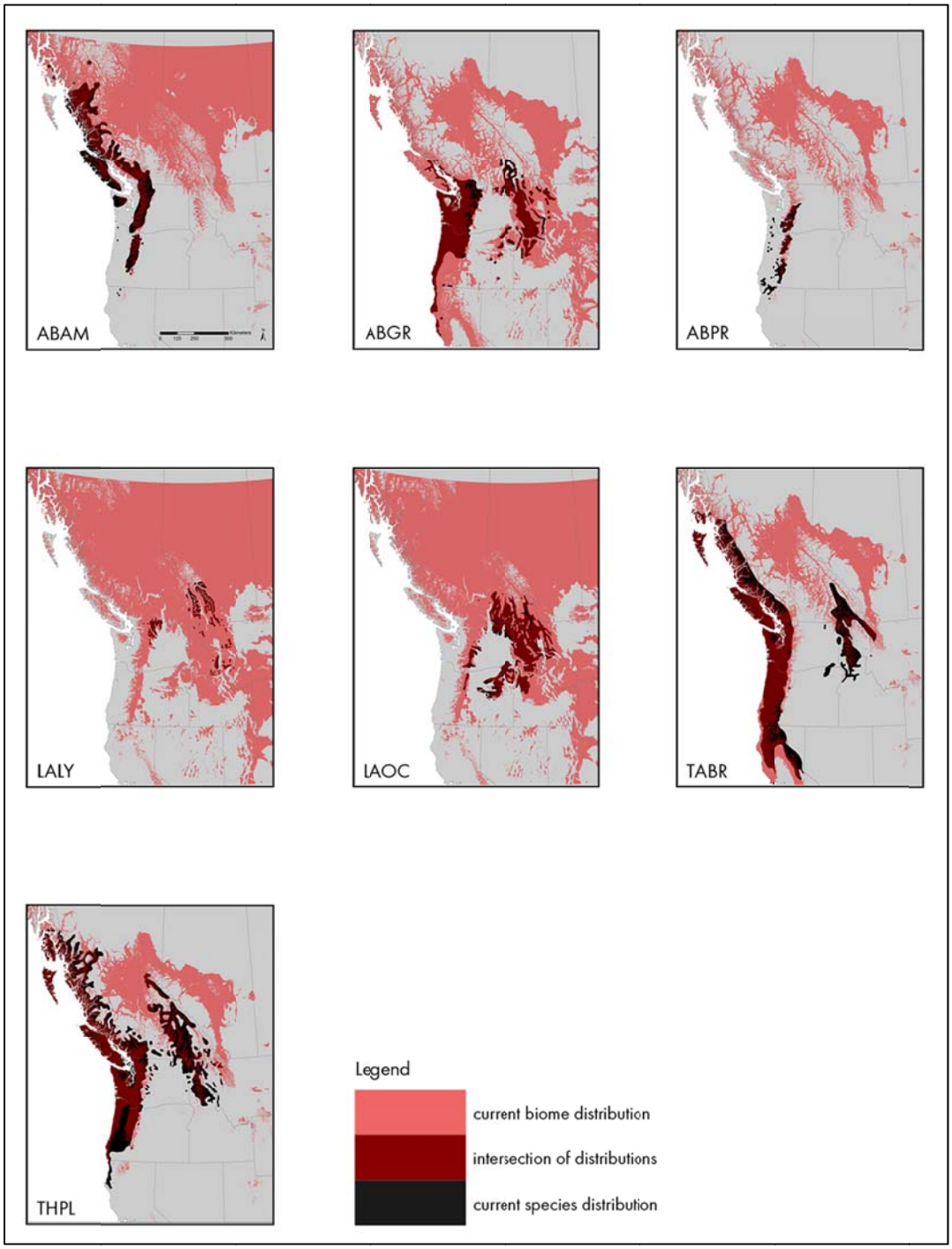
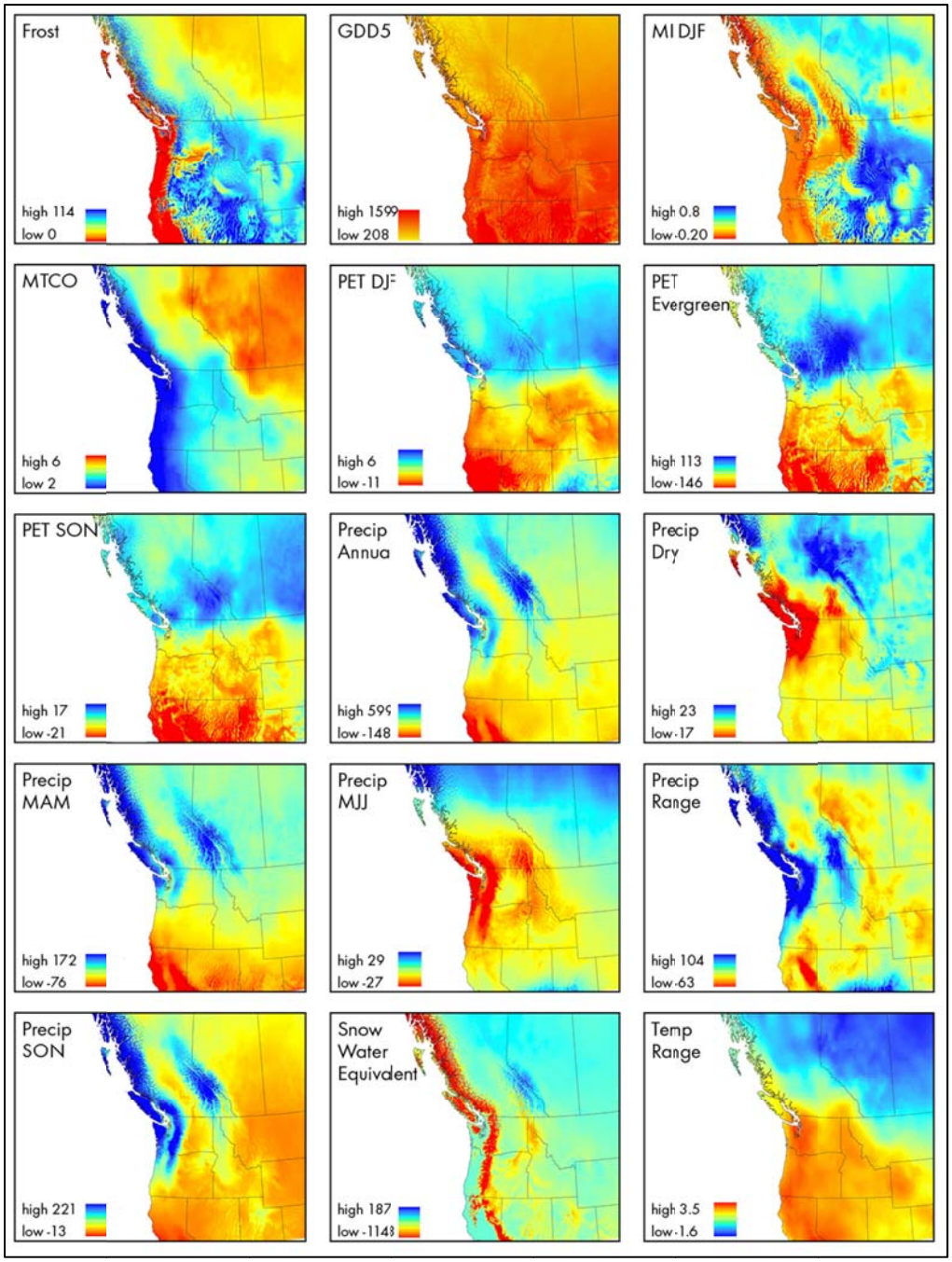


Figure 7. Difference between historical climate (1961 – 1990) and the ensemble of five general circulation models for the time period 2070 to 2099 for 15 climate variables and the A2 emissions scenario. Tree species codes are the same as in Table 3 and climate variable abbreviations are the same as in Table 2.



Appendix. Constraining future projections of Pacific silver fir (*Abies amabilis*).

Pacific silver fir (*Abies amabilis*) has historically grown in a distinctly maritime climate in the Pacific Northwest with relatively cool summers and mild winters. Winter temperatures are seldom lower than -9° C (16° F) (Packee et al., 1983). Although a summer dry season is characteristic in the Pacific Northwest, Pacific silver fir is dependent on adequate soil moisture during the growing season and therefore it is most abundant on sites where summer drought is minimal, such as areas of heavy rainfall, seepage, or prolonged snowmelt (Crawford and Oliver, 1990). Because of these known temperature and moisture limitations, we explored further refining our future species distribution projections by constraining suitable environmental space with these climatic limitations.

To accomplish this, we first averaged the future projections for mean temperature during the coldest month (i.e., January) and annual moisture index (actual evapotranspiration/ potential evapotranspiration) for the five general circulation models (GCMs) using the statistical program R (R Development Core Team, 2013). We then removed all values less than -9° C to create a new layer of cells that had suitable temperatures for Pacific silver fir during the coldest month and removed all values below 0.50 mm for areas that had suitable moisture index (Packee et al., 1983; Thompson et al., 1999). Then, we intersected suitable temperatures and moisture index with the refined future species distribution projections. These areas of intersection are places A) where the mechanistic dynamic global vegetation model (DGVM) predicts that the basic plant functional type to which the species belongs should be able to exist, B) where the climate is likely to be suitable for the species based on the species distribution models, and C) where the mean temperature during the coldest month is warmer than -9° C and the annual moisture index

is greater than 0.5 mm. We then compared the projections from this suitable cold temperature and moisture index model to those of the DGVM-refined species distribution model (Table 1).

Future Projections	DGVM - Refined Model	Suitable Cold Temperature and Moisture Index - Refined Model	Percent Difference
Expansion (1-2 models)	111,473	99,609	-10.6%
Expansion (3-4 models)	36,133	33,993	-5.9%
Expansion (5 models)	722	719	-0.4%
Contraction (5 models)	66,926	65,479	-2.2%
Contraction (3-4 models)	84,431	80,859	-4.2%
Contraction (1-2 models)	42,131	41,736	-0.9%
Stable (5 models)	5,609	5,596	-0.2%

Table 1. The number of cells occupied by the DGVM-refined model and the suitable cold temperature-refined model for Pacific silver fir.

Further refining the species distribution of Pacific silver fir only marginally changed the future projections. There was only a very slight change in the number of cells projected to be stable for Pacific silver fir, indicating that these areas were not influenced by our new approach. The largest changes (decrease) were in the number of cells projected for expansion with 1-2 models and 3-4 models, and most of this change was attributed to decreases in annual moisture index. The geographic locations where this change in suitable environmental space occurred for moisture index was in the southern portion of Pacific silver fir's range and along the eastern flank of the Cascade Mountains (Figure 1). These areas are projected to become drier and will likely not be suitable for Pacific silver fir in the future.

The geographic location of the largest decrease of expansion for temperature during the coldest month was in the Canadian Rockies. Climate models agree that this area will warm in the future, however, it still has very cold temperatures during the coldest month and therefore refining with this variable only had minor changes in suitable environmental space. Our results

illustrate that although there are some areas that will continue to be unsuitable for Pacific silver fir in the future, much of the Canadian Rockies, and especially the southern Canadian Rockies may in fact become suitable in the future.

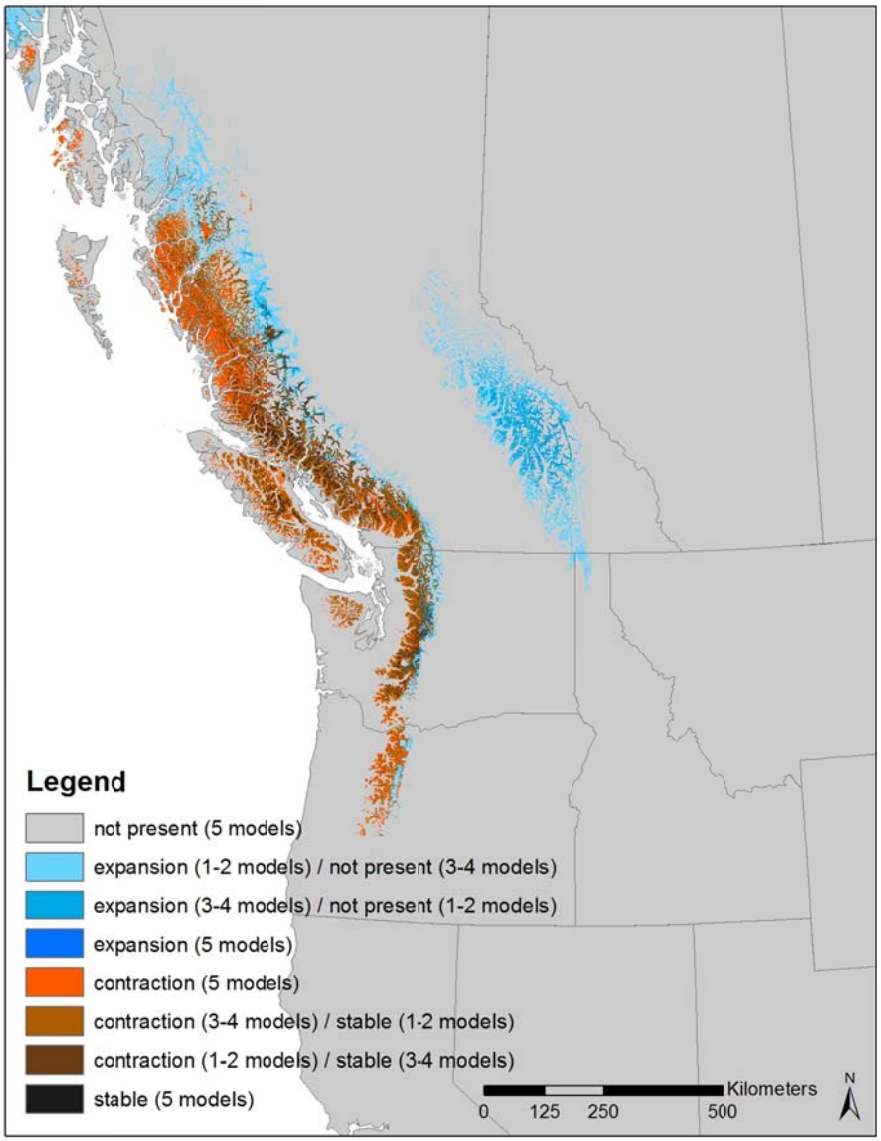


Figure 1. Refined future projections for Pacific silver fir for five general circulation models for the time period 2070 to 2099 for the A2 emissions scenario. Projections have been informed by a dynamic global vegetation model and further refined by areas of suitable cold temperature and moisture index values.

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Chapter 3: Relative vulnerability to climate change of trees in western North America

Abstract

Many recent changes in tree mortality, tree species distributions, and tree growth rates have been linked to changes in climate. Given that future climatic changes will likely surpass those experienced in the recent past, trees will likely face additional challenges as temperatures continue to rise and precipitation regimes shift. Managing forests in the face of climate change will require a basic understanding of which tree species will be most vulnerable to climate change and in what ways they will be vulnerable. We assessed the relative vulnerability to climate change of 11 tree species in western North America using a multivariate approach to quantify elements of sensitivity to climate change, exposure to climate change, and the capacity to adapt to climate change. Our assessment was based on a combination of expert knowledge, published studies, and projected changes in climate. The 11 species exhibited a range of vulnerabilities. Garry oak (*Quercus garryana*) was determined to be the most vulnerable, largely due to its relatively high sensitivity. Garry oak occupies some of the driest low woodland and savanna sites from British Columbia to California and is highly dependent on disturbances, such as periodic, low intensity fire. These low intensity and high frequency fires suppress competition and intrusion of Garry oak woodlands by conifers. Garry oak is also highly sensitive to changes in precipitation and generally only dominates dry sites. Big leaf maple (*Acer macrophyllum*) was determined to be the least vulnerable of the 11 species, largely due to its adaptive capacity. Big leaf maple can reproduce quickly after disturbances and its seeds can disperse long distances potentially allowing it to move in response to a changing climate. Our analyses provide a framework for assessing vulnerability and for determining why some species will likely be more

vulnerable than others. Such information will be critical as natural resource managers and conservation practitioners strive to address the impacts of climate change with limited funds.

Introduction

Warming temperatures, changes in precipitation patterns, and increasing atmospheric carbon dioxide concentrations are affecting vegetation across North America (Root et al. 2003; Fischlin et al. 2007; Chen et al. 2011). Plants are flowering earlier (e.g., Cayan et al. 2001, Abu–Asab et al. 2001, Parmesan and Yohe, 2003), tree growth rates are changing (McKenzie et al. 2001, Williams et al. 2010) and net primary productivity is being altered (Boisvenue and Running 2006). In addition, the distributions of some plants are shifting in response to both warming temperatures and changes in available moisture (Beckage et al. 2008, Kelly and Goulden 2008, Crimmins et al. 2011). In some systems, climatic changes have led to widespread mortality (Breshears et al. 2005, van Mantgem et al. 2009, Allen et al. 2010, Anderegg et al. 2013, Choat et al. 2012). Coupled with these direct effects of climate change, changes in disturbances, such as fire and some insects and diseases, will substantially affect where plants will be able to grow and how they interact (Brubaker 1986, McKenzie et al. 2004, Hicke et al. 2006, Littell et al. 2010).

Climate models project increases in mean annual temperature of roughly 3.0°C by the 2080's and an intensified seasonal precipitation cycle with wetter autumns and winters and drier summers in the northwestern U.S. (Mote and Salathé 2010). In response, tree species will remain in their current locations, shift in distribution, or go locally extinct. The largest changes will likely occur in areas in which trees are currently stressed and/or new colonizations are most likely, such as at treeline, forest–grassland ecotones, and more generally at the climatic limits of species distributions (Brubaker 1986, Allen and Breshears 1998, Thuiller et al. 2008, Williams et al. 2010). For example, there has been a dramatic drought–induced shift in species composition and forest structure over a 40–year period in northern New Mexico (Allen and Breshears 1998).

Specifically, there has been a substantial decline in ponderosa pine forest (*Pinus ponderosa*) and an increase in piñon–juniper woodland (*Pinus edulis* and *Juniperus monosperma*) in response to climatic change. Piñon pine and juniper out–compete ponderosa pine for available water and are better able to persist at lower elevations under drought conditions (Allen and Breshears 1998). These results highlight the different climate sensitivities and responses of individual species.

Individual responses of trees to climatic change have also been documented in other parts of western North America. For example, in Southern California, white fir (*Abies concolor*) moved upslope at a faster rate than Jeffrey pine (*Pinus jeffreyi*) in response to changes in regional climate over a 30-year period (Kelly and Goulden 2008). In western North America, as with other regions, tree growth and climate relationships vary by both species and location (Fagre et al. 2003, Ettinger et al. 2011). Managing forests in the face of such changes will require an understanding of which species will be the most vulnerable to future climate change and what factors will lead to increased vulnerability or resilience.

Vulnerability to climate change has been defined as "the extent which a species or population is threatened with decline, reduced fitness, genetic loss, or extinction owing to climate change" (Dawson et al. 2011). Furthermore, vulnerability can be seen as being a function of sensitivity, exposure, and adaptive capacity (Dawson et al. 2011). The sensitivity of an individual species is generally characterized by its ability to withstand changes in climate. Such sensitivity is largely a product of a species' natural history including life history traits, interspecific relationships, physiological factors, dependencies on sensitive habitats, and relationships with disturbance regimes. Exposure can be defined as the degree of climatic change or climate-induced change likely to be experienced by a species (Dawson et al. 2011). Exposure is determined by the character, magnitude, rate, and variability of climate change and can be

derived from projected changes in climate and climate-driven, fire regimes, hydrology, invasive species, and land–use. Adaptive capacity can be defined as the ability of a species to cope with climate change by persisting *in situ* or moving to more suitable locations (Dawson et al. 2011). This ability to respond physiologically or behaviorally to the effects of climate change is influenced by both intrinsic and extrinsic factors such as: reproductive strategy, genetic variability, phenotypic plasticity, dispersal distance and barriers, and landscape permeability.

Using sensitivity, exposure, and adaptive capacity, vulnerability assessments can identify (1) which species are most vulnerable, (2) why those species are vulnerable, and (3) which factors can be potentially leveraged to reduce vulnerability (Williams et al. 2008). Several recent studies that have assessed climate–change vulnerability for birds (Gardali et al. 2012, Foden et al. 2013), rare plants (Anacker et al. 2013), trees (Devine et al. 2012, Coops and Waring 2011) and amphibians and corals (Foden et al. 2013). Studies exploring the vulnerability of trees have largely relied on assessing one or two vulnerability components but they have not explicitly assessed all three; sensitivity, exposure, and adaptive capacity.

Here, we assess the vulnerability to climate change of 11 tree species in western North America. We conducted a series of workshops throughout the region to synthesize knowledge and insight on species sensitivity and adaptive capacity from experts and groups of experts. Combining this information with climate-change projections and information gleaned from the literature, we assessed vulnerability using a four–step approach. First, we compiled expert knowledge of the 11 tree species to produce estimates of sensitivity of each. Second, we assessed potential exposure by quantifying the magnitude of climate change projected across the range of each species. Third, we assessed each species' adaptive capacity using information on species' reproductive strategy, dispersal ability, and climate breadth derived from the literature and expert

knowledge. Finally, we quantified the multivariate dissimilarity between each species and a highly vulnerable reference species to assess relative vulnerability and better inform future forest management in the region.

Methods

Study Area

Our study area covered 2.4 million square kilometers in western North America encompassing the western states of the U.S. and provinces of Canada. The region is roughly bounded by the Pacific Ocean to the west, the Rocky Mountains to the east, the U.S.–Mexican border to the south, and the Yukon Territory to the north (Figure 1). The region is extremely diverse in climate, geology, topography, and vegetation. The climate of western North America is heavily influenced by the Pacific Ocean to the west and the numerous mountain ranges found throughout the region. Forests range from wet, maritime coastal forests dominated by Sitka spruce (*Picea sitchensis*) to dry, continental pine forests in the interior.

Tree Species

We assessed the vulnerability to climate change of 11 tree species: Pacific silver fir (*Abies amabilis*), grand fir (*Abies grandis*), noble fir (*Abies procera*), big leaf maple (*Acer macrophyllum*), subalpine larch (*Larix lyallii*), western larch *(Larix occidentalis*), whitebark pine (*Pinus albicaulis*), western white pine (*Pinus monticola*), Garry oak (*Quercus garryana*), Pacific yew (*Taxus brevifolia*), and western redcedar (*Thuja plicata*). We chose these species based on

input and knowledge from regional natural resource managers. This diverse set of tree species represents a wide range of life–history traits, climate sensitivities, and adaptive capacities.

Experts and Working Groups

We identified a number of individuals as being experts on the 11 tree species and invited them to participate in workshops (held between 2011 and 2012) or to work independently to record information about relative sensitivity and adaptive capacity of the species. Experts had a diversity of backgrounds and experience but all held advanced graduate degrees in ecology, forestry, and/or biology.

The goal of expert workshops was to identify the sensitivity of species to climate change by going through a series of questions related to each of the sensitivity factors below, details of which can be found online (CCSD 2013). To counter some of the inherent biases of expert judgment, we formalized our workshop procedure by first having the group work methodically through one of the species on the list. This process demonstrated the use of the database and calibrated the expert scoring system. In all workshops there were a number of relevant questions that spurred further discussion and therefore this portion took about two hours to complete. The procedure of working through an example species as a group provided the experts with training on assessing sensitivity as well as an opportunity to ask questions and get clarification, and ensured that participants were interpreting the questions in the same way. After the example species was completed, experts either broke into groups or worked independently to assess the sensitivity of additional species. In some cases, individual experts were invited to work independently to assess the sensitivity of species and relied heavily on scientific literature.

However, these individuals were also trained and calibrated to assess sensitivity by working through an example species.

For each of the sensitivity factors listed below, experts provided both a sensitivity score ranging from one (low sensitivity) to seven (high sensitivity) and a confidence score ranging from one (low confidence) to five (high confidence). Experts also provided additional information, including more detailed comments and citations when they were able.

Sensitivity Factors

Individual species sensitivities were assessed with respect to six factors. These included: 1) whether the species is generalist or specialist, 2) aspects of physiology, 3) whether the species depends on sensitive habitats, 4) dependence on disturbance regimes, 5) climate-dependent ecological relationships, and 6) interacting non-climatic stressors.

Generalist/Specialist. The degree to which a tree species is a generalist or a specialist can be assessed by identifying specific requirements (e.g., substrate, nutrient, water, and climate) and known interspecific interactions and dependencies (e.g., on seed dispersers or pollinators). For example, a tree species that has specific site requirements and/or pollinator dependencies is likely to be more sensitive to changes in climate than species that do not have those specialized relationships.

Physiology. The sensitivity of a tree species can be greatly affected by a species' physiological ability to acclimatize to changes in temperature, moisture, and carbon dioxide. A tree that can

grow and reproduce within a wide range of climatic conditions will be less sensitive to changes in climate than will a species that can only function within a narrow range of climates.

Sensitive Habitats. Some species of trees exist only in specific habitats and some of these habitats are known to be sensitive to a changing climate. Some of the sensitive habitats identified by experts in our working groups include riparian areas, savannas, upper and lower treelines, and alpine/sub–alpine areas. Trees that are limited to these sensitive habitats will be more sensitive to climate change than trees that are not.

Disturbance Regimes. Species that are highly sensitive to the particular nature of a disturbance regime or stressor will likely be more sensitive to climate change than species that can tolerate a wide range of disturbances. Experts identified a number of examples of disturbance regimes that are likely to influence sensitivity including fire, wind, disease, drought, insects and pests, and pathogens.

Ecological Relationships. Climatic changes and climate–driven changes (e.g., changes in temperature, precipitation, salinity, pH, and carbon dioxide) can affect various aspects of a tree's ecology. For example, changes in precipitation and temperature may affect hydrology, the ability of seeds to establish, and the competitive interactions with other species. Changes in soil pH and/or carbon dioxide levels may favor some species over others. Trees that have ecological relationships that are greatly affected by changes in climate will, all else being equal, be more sensitive to climate change.

Interacting Non–Climatic Stressors. Non–climate–related threats, such as habitat loss or degradation and invasive or exotic species, can also affect the degree to which a tree species is sensitive to climate change.

After these sensitivity factors were assessed, we calculated an overall climate change sensitivity score based on the Bray-Curtis dissimilarity between the sensitivity scores for each species and a hypothetical high sensitivity reference species. This type of analysis – measuring the dissimilarity between something and a hypothetical reference – has been used in other regional vulnerability assessments and has been shown to provide unique results compared to other assessment techniques while also accounting for the covariance substructure of the data set (Smith et al. 2003). The hypothetical reference species had very high sensitivity scores for each of the six sensitivity factors (i.e., sevens for each sensitivity factor). This approach is relatively conservative because the Bray-Curtis dissimilarity measure is based on the sum of the minimum values and thus the maximum difference between the species with the lowest sensitivity and the reference species is emphasized. Because different approaches to combining diverse metrics into a single measure often produce different results and can be more or less sensitive to changes in the inputs, we conducted a sensitivity analysis on our multivariate measure of sensitivity. Our sensitivity analysis involved systematically removing each of the six sensitivity factors and assessing the impact on the resulting five-variable metrics. In addition to the sensitivity analysis, we explored the effects of using a simple additive algorithm (*equation 1*, also see Laidre et al. 2008) as alternative approach to combining the six sensitivity metrics into one sensitivity score.

(*equation 1*)

Sensitivity = (Generalist/Specialist (1–7) + Physiology (1–7) + Sensitive Habitats (1–7) + Disturbance Regimes (1–7) + Ecological Relationships (1–7) + Interacting Non–Climatic Stressors (1–7)) / 42 * 100.

Exposure

We assessed exposure by quantifying the magnitude of change in multivariate climate space between historical climatic conditions and an ensemble of projected future climates across a species' current geographic range. We used ClimateWNA to downscale historical data and future climate projections to a 1–km^2 grid. ClimateWNA is a program that generates both directly calculated and derived climate variables for specific locations across western North America (Wang et al. 2006, Hamann and Wang 2005, Wang et al. 2012) using Parameter–elevation Regressions on Independent Slopes Model (PRISM, Daly et al. 2002) and ANUSPLIN. ANUSPLIN is a smoothing approach that interpolates multi–point and multivariate data using thin plate smoothing splines (Hutchinson 1989). We generated mean annual, seasonal and monthly climate data for the period of 1961 to 1990.

We used climate projections from the IPCC Fourth Assessment Report run for the SRES A2 greenhouse–gas emissions scenario. The A2 emissions scenario represents a world with increasing population growth, regionally oriented economic development, slower development, and implementation of new technologies (Nakicenovic and Swart 2000). We used projections from each of the five following GCMs averaged over the years 2070 to 2099: BCCR BCM 2.0 (BCCR 2005), CCCma CGCM 3.1 (Flato 2005), CSIRO MK 3.0 (Collier 2005), INM-CM 3.0 (Volodin 2005), MIROC 3.2 MEDRES (Nozawa 2005).

We chose 11 climate variables to represent exposure: mean annual temperature, mean temperature during the warmest month, mean temperature during the coldest month, the difference in temperature between the warmest and the coldest month, mean maximum temperature during spring, mean maximum temperature during winter, precipitation as falling as

snow, mean total precipitation for the driest month, mean total precipitation during the wettest month, mean total precipitation during autumn, and Hargreaves climatic moisture deficit. These variables represent the spatial variability of climate across the study area and are biologically important controls to tree growth (Prentice et al. 1992, McKenzie et al. 2003, Williams et al. 2007). We then standardized all climate variables from both the historical and future climate datasets to ensure that all variables would be equally weighted and so that future climate–change trends would be emphasized over historical inter–annual climate variability (Williams et al. 2007).

We calculated the Euclidean distance between historical climate and each of the five future climate projections for each grid cell and all 11 climate variables. We then averaged these Euclidean distance values in each cell and calculated the mean value of all cells across an individual species' distribution. Because we did not apply sensitivity and adaptive capacity spatially across individual species' distributions, we chose to represented exposure with one number for each species (i.e., the mean of the Euclidean distance of all grid cells across the species' distribution). Species' distributions were derived from digitized range maps (USGS 2012). We calculated an overall exposure score using Bray-Curtis dissimilarity between the mean Euclidean distance scores for each species and a hypothetical high Euclidean distance reference score. We calculated the exposure score using Bray-Curtis dissimilarity to be consistent with the sensitivity score.

Adaptive Capacity

To quantify adaptive capacity, for each tree species, we assessed reproductive strategy, dispersal ability, and climate breadth. We included reproductive strategies as an aspect of

adaptive capacity because species that can recover from low numbers rapidly are more likely to be able to withstand rapidly changing climates as well as colonize new locations following climate disruption (Pianka 1970). Rapid population growth can also help maintain genetic variability. We included dispersal ability as a factor of adaptive capacity because species that are poor dispersers will be less likely to be able to move from areas that climate change renders unsuitable and into areas that become newly climatically suitable. We defined dispersal ability as a function of maximum annual dispersal distance and the relative influence of dispersal barriers. Barriers, such as mountains, arid lands, clearcuts, and agriculture, will reduce the ability of some tree species to disperse. Reproductive strategies and dispersal abilities were quantified and separately ranked on a scale of one (low reproductive strategy and dispersal ability of less than 1km) to seven (high reproductive strategy and dispersal ability greater than 100km) by experts for each of the 11 tree species. As with sensitivity, the experts entered these scores along with more detailed information, including references, into an online database (CCSD 2013).

We assessed climate breadth as the range of climates that each species occupies. Species that occupy a wider range of climates are likely to be able to better adapt to climate change as they are likely to either have relatively high levels of phenotypic plasticity or they have relatively high genetic diversity (Brown 1995). We quantified climate breadth for each of the 11 species using the USGS Climate–Vegetation Atlas of North America by calculating the minimum and maximum values for the following climate and bioclimatic variables: mean annual temperature, mean annual precipitation, July temperature, mean temperature of the coldest month, January precipitation, July precipitation, growing degree days on a 5°C base, and moisture index that incorporates the full seasonal cycle of precipitation and evapotranspiration (actual evaporation/ potential evaporation, based on Thornthwaite and Mather 1955, Willmott et al. 1985) (Thompson

et al. 1999). We then subtracted the minimum value from the maximum value to get a range for each climate variable for each species. We normalized these differences and summed them for each species. Although most of these variables are the same as was used for calculating exposure, others differ slightly due to data availability of the USGS Climate–Vegetation Atlas of North America. Nonetheless, both sets of climate variables generally represent biologically important controls to tree growth and the spatial variability of climate across the study area.

We calculated an overall adaptive capacity score using Bray-Curtis dissimilarity between the adaptive capacity scores for each species and a hypothetical low adaptive capacity reference species. This hypothetical reference species did not have the capacity for rapid population growth, was a poor disperser, and had little climatic breadth. Again, we conducted a sensitivity analysis to investigate the effects of removing each of the three adaptive capacity factors and we explored an alternative approach to combining the individual adaptive capacity factors. Our alternative method for integrating the three adaptive capacity factors involved normalizing them as a proportion of the maximum scores for each factor and then adding these values together for each species.

Calculating Vulnerability

Species that have relatively high sensitivity and exposure scores and relatively low adaptive capacity will be more vulnerable to climate change. Therefore, after assessing and quantifying sensitivity, exposure, and adaptive capacity, we calculated the Bray-Curtis dissimilarity between the scores for sensitivity, exposure, and adaptive capacity for each species and a hypothetical highly vulnerable reference species. Again, we explored the sensitivity of our

results to the factors included in our vulnerability calculation and the way we calculated vulnerability. First, we conducted a sensitivity analysis by systematically removing each of the three vulnerability components and recalculated the Bray-Curtis dissimilarity score for each species. We also explored two alternative approaches of assessing vulnerability by first normalizing the additive sensitivity scores, the mean Euclidean distance scores, and the additive adaptive capacity scores as a proportion of their maximum scores. We then 1) added the relativized sensitivity and exposure scores and subtracted the adaptive capacity scores for each species and 2) multiplied the relativized sensitivity and exposure scores and divided them by the adaptive capacity scores for each species.

Results

Relative Vulnerability

Of the 11 tree species analyzed, Garry oak, subalpine larch, and whitebark pine were determined to be the most vulnerable to climate change (Table 1). Their vulnerability stems from their relatively high sensitivity and their relatively low adaptive capacity. By contrast, big leaf maple was determined to be the least vulnerable due to a relatively low sensitivity to climate change and relatively high adaptive capacity. This relatively low vulnerability is anticipated despite the fact that big leaf maple was also found to have relatively moderate to high exposure to climate change.

Sensitivity

Whitebark pine, subalpine larch, and Garry oak were determined to be the most sensitive to climate change of the species analyzed (Figure 2). However, the reasons for their relatively high sensitivity differ. For example, Garry oak is sensitive to climate change because it occupies some of the driest low woodland and savanna sites from British Columbia to California and is highly dependent on disturbances, such as periodic, low intensity fire. Low intensity and high frequency fires suppress competition and intrusion of Garry oak woodlands by conifers, such as Douglas–fir (Voeks 1981). Garry oak will likely continue to be sensitive to changes in fire patterns in the future as more frequent and intense wildfires are projected throughout western North America (Rogers et al. 2011). Garry oak was also found to be sensitive to changes in precipitation and although it is found on sites with a wide range of mean annual precipitation (e.g., 660 to 2555mm, Thompson et al. 1999), it can usually only out-compete competitors on dry sites with high frequency, low intensity fires (Agee 1993). Garry oak is also highly sensitive to the rate and magnitude of land–use change and habitat fragmentation and thus Garry oak woodlands are some of the most threatened ecosystems in Northwest North America (MacDougall et al. 2004, Dunwiddie and Bakker 2011).

Whitebark pine and subalpine larch were determined to be highly sensitive to climate change because both species occupy high elevation sites and were identified as being sensitive to changes in precipitation and disturbances, such as fire. Whitebark pine is also sensitive to non–climatic stressors, such as the mountain pine beetle (*Dendroctonus ponderosae*) and the non–native fungus, white pine blister rust (*Cronartium ribicola*). Subalpine larch is sensitive to changes in temperature and precipitation and occupies some of the coldest, mesic, high elevation treed sites in western North America. Subalpine larch seeds require low temperatures and full sunlight for germination (Habeck 1991) and large quantities of seed are not produced until trees

are at least 80 years old and are more regularly produced when trees reach 200 years of age (Arno and Habeck 1972). By contrast, big leaf maple was found to be the least sensitive among the 11 species primarily because it is less dependent on disturbance regimes, has a lower physiological sensitivity to climate change, and does not have as many non–climatic stressors that might have synergistic relationships with climate change. However, the spread of exotic pests such as the Asian long–horned beetle (*Anoplophora glabripennis*) could negatively impact big leaf maple and thereby increase its sensitivity to climate change.

The overall ranking of sensitivity scores, as calculated by Bray-Curtis dissimilarity, is relatively resilient to minor changes in which sensitivity factors are included. We found that removing any one of the six sensitivity factors produced relatively little change in the sensitivity rankings (see Table 2). We also calculated sensitivity with an additive algorithm, which resulted in a change in the ranking of the middle species; however, the three most and three least sensitive species remained in their respective rankings (see Table 2).

Exposure

Among the 11 species, Pacific silver fir is projected to experience the most climatic change (i.e., exposure) across its distribution followed by noble fir (Figure 3). These relatively high exposure scores are largely explained by the substantial projected decrease in precipitation that falls as snow, changes in precipitation during the driest and wettest months, and an increase in the mean temperature of the warmest month (Table 3). Furthermore, Pacific silver fir has a large proportion of its distribution in the Cascade and Olympic Mountains in Washington and Oregon and in the Coast Mountains in British Columbia, areas projected to lose up to 2400 mm

of snow pack (measured as April 1 snow water equivalent) between historical (1970–1999) and future time periods (2040s) (Climate Impacts Group, 2009). Noble fir also has a large proportion of its distribution in the central and south Cascade Mountains.

Interestingly, the three species with the highest sensitivities (whitebark pine, Garry oak, and subalpine larch) have relatively low projected exposures (Figure 3). The distributions of two of these species, whitebark pine and subalpine larch are found mostly in the southern Canadian Rocky Mountains, an area that is projected to lose less precipitation falling as snow and have a smaller change in climatic moisture deficit than the Cascade Mountains. Garry oak is mainly found in the lowlands west of the Cascade Mountains, also an area with less projected climatic change.

Adaptive Capacity

Garry oak has the lowest overall adaptive capacity because it grows relatively slowly, has irregular seed crops, and its seeds are dependent on gravity and/or animals for dispersal (Stein 1990). Western larch and subalpine larch also have relatively low adaptive capacities due, in large part, to their somewhat limited climate breadth. For example, subalpine larch tends to grow on cold, mesic sites that are higher in elevation than any other tree species and does not compete well outside of its climatic optimum (Burns and Honkala 1990). However, warming temperatures may create new suitable climate space just upslope for this species. By contrast, big leaf maple has the highest adaptive capacity score due to its reproductive strategy, its ability to disperse relatively long distances, and its wide tolerance of a range of climates (Minore and Zasada 1990).

The overall ranking of adaptive capacity scores is moderately sensitive to changes in which of the three adaptive capacity factors are included. Although the rankings do change somewhat (see Table 4), big leaf maple remains the species with the most adaptive capacity and the species with the least adaptive capacity generally retain their rankings. Adaptive capacity scores calculated using an additive algorithm result in nearly the same ranking as the multivariate analysis, with only slight changes for a few middle species (Table 4).

The multivariate vulnerability analysis was also moderately sensitive to changes in which of the three vulnerability components are included. The vulnerability rankings changed only slightly without exposure and adaptive capacity scores and changed moderately without sensitivity scores (Table 5). The vulnerability rankings do not change when either an additive or a multiplicative algorithm are used instead of the multivariate analysis (Table 5).

Discussion

As climates continue to change, natural resource managers and conservation practitioners will be faced with daunting decisions about which species and ecological systems should receive the benefits of limited funding. The first step in prioritizing actions to address climate change will likely include some type of formal or informal vulnerability assessment. The analyses presented here demonstrate one such assessment by quantifying all three components of vulnerability through the application of expert knowledge, information from the literature, and projected climatic changes. In addition to resulting in a ranking, vulnerability analyses have the potential to provide information about why species are more or less vulnerable and thus to inform the development of species–specific adaptation options (Glick et al. 2011).

Garry oak was found to be more vulnerable to climate change compared to the other ten tree species because of its high sensitivity and low adaptive capacity. Specifically, Garry oak is sensitive to interacting non–climatic stressors, such as land conversion and landscape fragmentation, and these stressors predispose Garry oak to be more susceptible to the effects of climate change. Therefore, Garry oak resilience can be increased by reducing these stressors and increasing habitat connectivity and the protection of existing stands (Dunwiddie and Bakker 2011). Additionally, Garry oak is sensitive to changes in disturbance regimes, such as fire and thus using prescribed burning in combination with other restoration techniques (i.e., herbicide treatments and planting seedlings) will also increase the resilience of Garry oak (Hamman et al. 2011). Experimental treatments that simulate the effects that potential future climates may have on Garry oak and regular monitoring of existing Garry oak populations can also help determine how this species will likely respond to climate change and where it might survive. Restoration and planting of Garry oak in new areas will increase resilience and may be warranted as some unsuitable sites may become more favorable for Garry oak because of further climatic changes (Bachelet et al. 2011).

Whitebark pine and subalpine larch are both sensitive to changes in fire frequency and intensity. Subalpine larch has thin bark and is highly susceptible to fire and whitebark pine is adapted to relatively long fire–return intervals (e.g., up to 500 years) (Arno 1980, Tomback et al. 2001). However, when fires do burn, they tend to expose mineral soil for seedling establishment. Fire can also reduce competition for older, more fire-resistant cohorts by killing other competitors, such as subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) that would otherwise invade high elevation stands (Arno 2001). However, recent warming and an earlier spring snowmelt have led to more frequent large wildfires and longer wildfire seasons

(Westerling et al. 2006), a trend that is projected to continue in the future (Littell et al. 2010, Rogers et al. 2011, Westerling et al. 2011). Therefore, successful management strategies to preserve subalpine larch and whitebark pine will likely include reducing fuel loads in and around stands and facilitating regeneration by planting seedlings.

Unlike Garry oak, whitebark pine and subalpine larch have relatively higher adaptive capacities in part because their seeds are winged and wind-disseminated over larger areas. For whitebark pine, seeds can also be facilitated by other species, such as, Clark's nutcrackers (*Nucifraga columbiana*), which are able to cache seeds long distances (8 km or more) from seed sources (Tomback and Linhart 1990, Tomback et al. 2001). However, interspecific interactions such as animal–assisted dispersal could be affected by warming temperatures and a change in the timing of seed production and the synchronicity of disperses (Root et al. 2003).

Subalpine larch is generally found on high elevation sites that are very cold and moist and whitebark pine typically grows on high elevation sites that are cold and somewhat dry. Subsequently a change in precipitation, such as snow or the seasonal duration of snowpack, will likely influence the ability of these species to persist and reproduce, but in different ways. The vast majority of precipitation (about 66%) is in the form of snow at high-elevation sites and snowmelt during the summer dry period (June – September) is critically important for tree growth and seedling establishment (Burns and Honkala 1990). In addition to supplying water during the summer dry period, snow also provides protection from damaging ice particles in high winds (Tranquillini 1979), and is a limiting factor for some encroaching lower elevation tree species (Franklin et al. 1971, Harsch et al. 2009). If competition from other conifers is

controlled, these areas could be refugia for subalpine larch and whitebark pine and the species that rely on their seeds.

In addition to other climate change sensitivities, whitebark pine is also highly susceptible to outbreaks of mountain pine beetle and white pine blister rust. Current populations of whitebark pine are already being affected by these stressors and therefore warming temperatures and a change in precipitation, notably snowpack, will greatly affect where future outbreaks occur and how intense they are. To conserve healthy whitebark pine stands, managers may want to conduct detailed microsite mapping to identify locations where mountain pine beetle and white pine blister rust have not invaded or stands where there is high tolerance to white pine blister rust. Future research could also focus on whitebark pine's genetic variation, which will be critically important when assessing the adaptive capacity of this species in light of white pine blister rust (see Mahalovich and Hipkins 2011).

The tree species with the lowest relative vulnerability, big leaf maple, is comparatively insensitive to climate change and therefore is a good example of a generalist species that may be able to expand its range under climate change (Dukes and Mooney 1999, Thuiller et al. 2005, Menendez et al. 2006). Although big leaf maple seeds are somewhat large in size (up to 12 mm long), they are relatively light in weight and dispersal is primarily by wind and is estimated to be from 1 to 5 km (CCSD 2014). Big leaf maple also sprouts profusely after being cut and can produce seeds early in life – at ten years of age and every year thereafter if conditions are suitable (Olson et al. 1974). However, big leaf maple is generally not considered a pioneer species that will quickly invade disturbed areas (Minore and Zasada 1990) and like many deciduous tree species it requires relatively mesic soils. The frequency and intensity of

disturbances that create small gaps in the forest will likely determine whether big leaf maple is able to capitalize on potentially new suitable habitat.

Many invasive species are able to reproduce in large numbers and disperse long distances and will likely better adapt as competitive interactions and suitable habitat change (Dukes and Mooney 1999). Big leaf maple has traits in common with invasive species in the genus *Pinus*, such as a short juvenile period and low seed mass, which enable them to quickly disperse to suitable habitats relatively far from their current locations (Rejmánek and Richardson 1996). Species such as these will likely have more capacity to adapt to a changing climate (Dukes and Mooney 1999, Addo–Bediako et al. 2000, Calosi et al. 2008). By contrast, Garry oak is limited in its ability to disperse because its seeds are large and heavy and require continuous moisture until they germinate (Burns and Honkala 1990). Garry oak seeds are also dispersed by either gravity or food–gathering animals and thus have very limited dispersal distance.

Other studies have quantified vulnerability differently; for example, by multiplying sensitivity by exposure, but not directly incorporating adaptive capacity (see Gardali et al. 2012). We explored how vulnerability rankings would differ by (1) removing one of three of these components from the multivariate analysis, (2) using a multiplicative algorithm, and (3) using an additive algorithm. Although the additive and multiplicative algorithms resulted in the same rankings as the multivariate analysis, removing the sensitivity scores from the analysis resulted in different rankings – 9 of the 11 species change in their vulnerability rankings when sensitivity was excluded (Table 5). This finding highlights the need to include measures of sensitivity when calculating vulnerability.

Although we explored some of the ways in which our results are likely to be sensitive to methodological choices and approaches, there are other ways in which our choice of methods could have affected the results. For instance, we used the Bray-Curtis dissimilarity measure to compare each vulnerability component to a hypothetical reference species with high sensitivity, high exposure and low adaptive capacity. Although the Bray-Curtis dissimilarity measure is generally used to quantify the difference in species composition between sites, other multivariate distance metrics, such as Euclidean distance, produced similar rankings when compared to the same hypothetical reference species. Furthermore, as mentioned in the methods section, by using the Bray-Curtis dissimilarity measure, we were conservative in our estimates of vulnerability. An alternative technique would be to compare each vulnerability component to a hypothetical reference species with low sensitivity, low exposure and high adaptive capacity. Our approach of combining individual sensitivity, exposure, or adaptive capacity factors may also obscure high individual scores when other scores are all low, when in actuality, one high factor may affect vulnerability. One way to correct for this is to replace the existing multivariate analysis with a rule–based index that automatically assigns a high score when certain conditions are met. In addition, we used 11 biologically important climate variables to calculate exposure for one future time period. Alternative variables, time periods, and climate models may lead to different exposure estimates. Finally, we have chosen to weight all factors equally, but we recognize that some variables may be more important than others and that the importance could vary over time and across species.

Warming temperatures and changes in precipitation are affecting species around the world and some species are proving to be more susceptible to these changes than are others. Thus, climate change presents a particularly difficult challenge for natural resource managers

who will need to make decisions about which species should receive the benefits of limited funding. Vulnerability assessments, such as the one demonstrated here, are one of the tools that resource managers have at their disposal to better prepare for this uncertain future. Our approach, of quantifying inherent sensitivity, projected climatic changes, and adaptive capacity can facilitate, not only the identification of species that are relatively more vulnerable, but it can also identify the key aspects of vulnerability, which if addressed, could promote resilience in the face of climate change.

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Table 1. Bray-Curtis dissimilarity scores of sensitivity, exposure, adaptive capacity, and vulnerability for 11 tree species in western North America. Dissimilarity scores were calculated between each species and 1) highly sensitive reference species, 2) highly exposed reference species, 3) reference species with low adaptive capacity, and 4) highly vulnerable reference species. Bray-Curtis dissimilarity is bound between 0 (no difference) and 1 (large difference) and therefore lower scores represent relatively 1) higher sensitivity, 2) higher exposure, 3) lower adaptive capacity, and 4) higher vulnerability.

Species	Common name	Species Code	A) Sensitivity Bray-Curtis Score	B) Exposure Bray-Curtis Score	C) Adaptive Capacity Bray-Curtis Score	D) Vulnerability Bray-Curtis Score
Quercus garryana	Garry oak	QUGA	0.18	0.56	0.19	0.51
Larix lyallii	Subalpine larch	LALY	0.17	0.56	0.27	0.54
Pinus albicaulis	Whitebark pine	PIAL	0.17	0.57	0.27	0.54
Abies procera	Noble fir	ABPR	0.33	0.42	0.30	0.56
Taxus brevifolia	Pacific yew	TABR	0.33	0.45	0.29	0.56
Abies amabilis	Pacific silver fir	ABAM	0.50	0.35	0.34	0.60
Pinus monticola	Western white pine	PIMO	0.35	0.50	0.39	0.61
Thuja plicata	Western redcedar	THPL	0.42	0.48	0.37	0.62
Abies grandis	Grand fir	ABGR	0.42	0.54	0.34	0.63
Larix occidentalis	Western larch	LAOC	0.45	0.63	0.27	0.64
Acer macrophylla	Big leaf maple	ACMA	0.65	0.43	0.59	0.70

Table 2. Bray-Curtis dissimilarity scores of sensitivity for 11 tree species in western Northwest with six factors (A) and combinations of a subset of five of the six sensitivity factors (B-G) and additive sensitivity scores (H). Smaller values represent higher sensitivity for columns A-G and larger values represent higher sensitivity for column H. Tree species codes are the same as in Table 1.

Species Code	(A) Six-Factor Sensitivity Bray-Curtis Score	(B) No Generalist/ Specialist	(C) No Physiology	(D) No Habitat	(E) No Disturbance Regimes	(F) No Ecology	(G) No Non-Climatic Stressors	(H) Additive Sensitivity Score
LALY	0.17	0.17	0.19	0.21	0.15	0.19	0.11	71
PIAL	0.17	0.15	0.13	0.21	0.15	0.17	0.21	71
QUGA	0.18	0.15	0.15	0.23	0.21	0.19	0.19	69
ABPR	0.33	0.37	0.35	0.27	0.40	0.32	0.30	48
TABR	0.33	0.32	0.32	0.27	0.40	0.37	0.32	50
PIMO	0.35	0.37	0.37	0.30	0.37	0.37	0.35	50
THPL	0.42	0.43	0.43	0.37	0.46	0.43	0.43	40
ABGR	0.42	0.43	0.43	0.37	0.46	0.43	0.43	40
LAOC	0.45	0.43	0.43	0.40	0.46	0.49	0.49	38
ABAM	0.50	0.49	0.52	0.46	0.46	0.52	0.56	33
ACMA	0.65	0.67	0.63	0.63	0.67	0.67	0.63	21

Table 3. Averaged difference between future and historical climate variables averaged across the distribution for each tree species. Climate variable codes are as follows: Hargreaves climatic moisture deficit (CMD), mean annual temperature (MAT), mean temperature during the coldest month (MCMT), precipitation as snow (PAS), mean temperature during the warmest month (MWMT), mean total precipitation for the driest month (PPT_Dry), mean total precipitation during the wettest month (PPT_Wet), mean total precipitation during autumn (PPT_AT), temperature difference between the warmest month and the coldest month (TD), mean maximum temperature during spring (TMAXSP), and mean maximum temperature during winter (TMAXWT). Temperature variables (i.e., MAT, MCMT, MWMT, TD, TMAXSP, TMAXWT) are measured in degrees Celsius and precipitation variables (i.e., PAS, PPT_Dry, PPT_Wet, PPT_AT) are measured in millimeters.

Species Code	CMD	MAT	MCMT	MWMT	PAS	PPT_Dry	PPT_Wet	PPT_AT	TD	TMAXSP	TMAXWT
ABAM	52.2	3.3	3.5	4.2	-348.9	34.8	89.4	147.2	0.7	2.6	3.1
ABGR	92.7	3.5	3.7	4.5	-146.3	15.9	50.2	41.5	0.9	2.8	3.1
ABPR	99.2	3.3	3.2	4.5	-204.3	9.9	65.6	40.9	1.3	2.6	2.9
ACMA	83.5	3.2	3.2	4.2	-160.5	15.7	60.7	78.4	1	2.7	3
LALY	66.7	3.7	4.3	4.6	-120.9	22.4	36	38.1	0.4	2.9	3.3
LAOC	95.6	3.8	4.3	4.8	-143.1	15.1	26.7	23.5	0.5	3	3.3
PIAL	70.8	3.7	4.2	4.6	-140.8	16.1	33.8	44.9	0.4	3	3.3
PIMO	84.4	3.5	3.8	4.5	-182.6	16	51.9	56	0.8	2.8	3.1
QUGA	105.8	3.2	3.1	4.4	-52.5	1.6	37.1	20.9	1.2	2.7	2.9
TABR	75.8	3.3	3.4	4.3	-196	22.5	62.7	88.2	0.9	2.7	3
THPL	60.4	3.4	3.7	4.3	-208.1	26.1	62.2	101.4	0.6	2.6	3.1

Table 4. Bray-Curtis dissimilarity scores of adaptive capacity for 11 tree species in western North America with three factors (A) and combinations of a subset of two of the three adaptive capacity factors (B-D) and additive adaptive capacity scores (E). Smaller values represent lower adaptive capacity for columns A-E. Tree species codes are the same as in Table 1.

Species Code	(A) Three-Factor Adaptive Capacity Bray-Curtis Score	(B) No Reproductive Strategy	(C) No Dispersal Ability	(D) No Climate Breadth	(E) Additive Adaptive Capacity Score
QUGA	0.19	0.20	0.31	0.10	1.08
PIAL	0.27	0.33	0.39	0.12	1.56
LALY	0.27	0.35	0.27	0.22	1.66
LAOC	0.27	0.28	0.39	0.19	1.54
TABR	0.29	0.36	0.40	0.14	1.71
ABPR	0.30	0.25	0.46	0.24	1.61
ABAM	0.34	0.31	0.51	0.24	1.83
ABGR	0.34	0.31	0.51	0.24	1.84
THPL	0.37	0.36	0.55	0.24	2.02
PIMO	0.39	0.32	0.64	0.27	2.04
ACMA	0.59	0.52	0.75	0.51	3.00

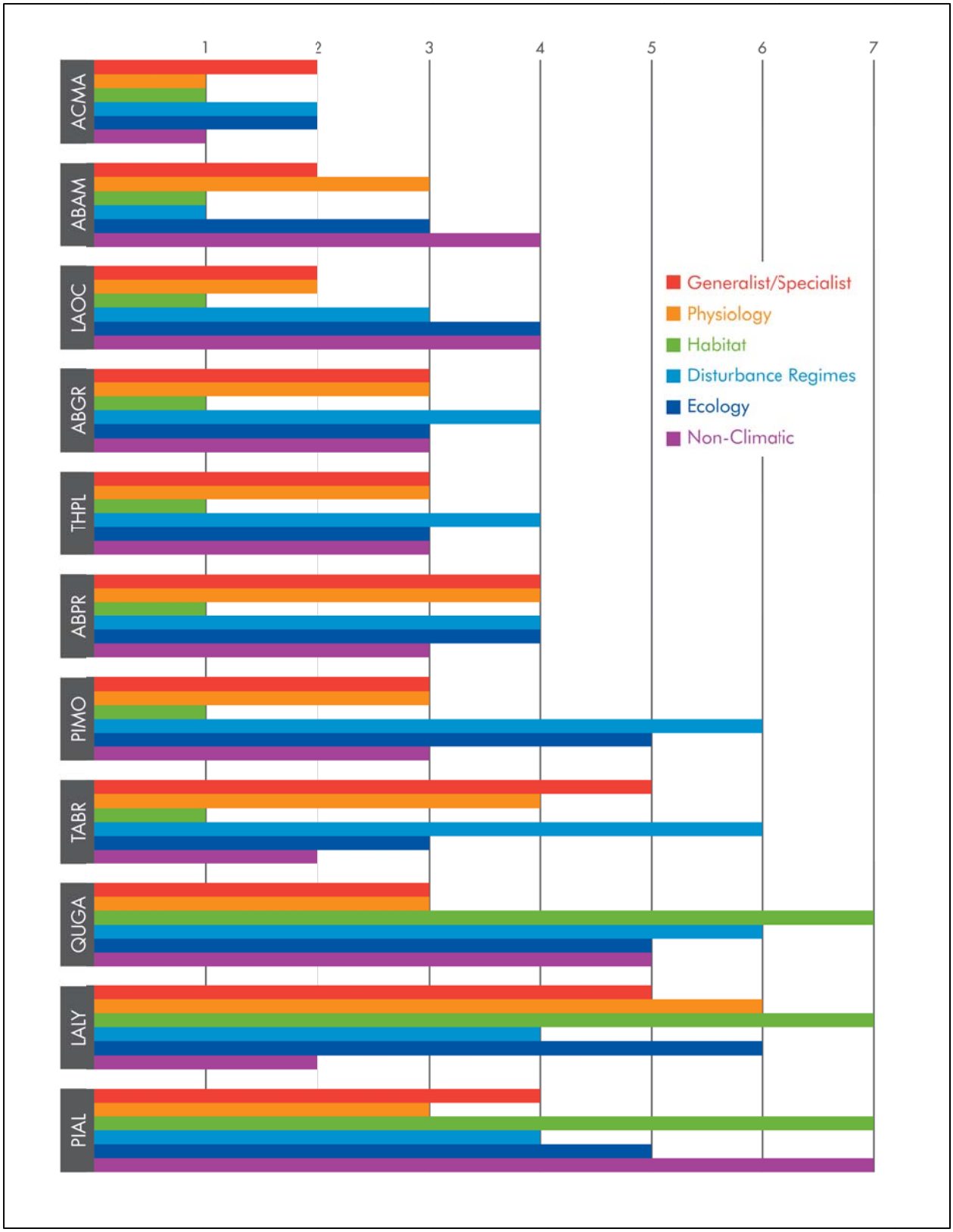
Table 5. Bray-Curtis dissimilarity scores of vulnerability for 11 tree species in western Northwest with three factors (A) and a subset of two of the three vulnerability factors (B-D), additive vulnerability scores (E), and multiplicative vulnerability scores (F). Smaller values represent relatively higher vulnerability for columns A-D and larger values represent relatively higher vulnerability for columns E and F. Tree species codes are the same as in Table 1.

Species Code	A) Three-Factor Vulnerability Bray-Curtis Score	B) No Sensitivity	C) No Exposure	D) No Adaptive Capacity	E) Additive Vulnerability Score	F) Multiplicative Vulnerability Score
QUGA	0.51	0.58	0.30	0.58	1.19	1.57
LALY	0.54	0.61	0.37	0.57	1.05	1.08
PIAL	0.54	0.62	0.37	0.58	1.04	1.08
ABPR	0.56	0.57	0.52	0.58	0.98	1.06
TABR	0.56	0.57	0.51	0.59	0.93	0.98
ABAM	0.60	0.55	0.62	0.62	0.86	0.76
PIMO	0.61	0.64	0.58	0.62	0.71	0.71
THPL	0.62	0.62	0.60	0.64	0.64	0.62
ABGR	0.63	0.63	0.59	0.66	0.57	0.57
LAOC	0.64	0.64	0.57	0.69	0.49	0.49
ACMA	0.70	0.67	0.72	0.69	0.12	0.25

Figures

Figure 1. Study area. The map denotes the combined extent of all 11 tree species ranges and the area for which climate data were downscaled.

Figure 2. Climate change sensitivity factors for 11 tree species, low values represent low relative sensitivity and high values represent high relative sensitivity. Overall sensitivity scores are summarized in Table 1 (A). Tree species codes are: ABAM – Pacific silver fir (*Abies amabilis*), ABGR – grand fir (*Abies grandis*), ABPR – noble fir (*Abies procera*), ACMA – big leaf maple (*Acer macrophylla*), LALY – subalpine larch (*Larix lyallii*), LAOC – western larch *(Larix occidentalis*), PIAL – whitebark pine (*Pinus albicaulis*), PIMO – western white pine (*Pinus monticola*), QUGA – Garry oak (*Quercus garryana*), TABR – Pacific yew (*Taxus brevifolia*), and THPL – western redcedar (*Thuja plicata*).


1
2
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ACMA
ABAM
LAOC
ABGR
THPL
ABPR
PIMO
TABR
QUGA
LALY
PIAL
Generalist/Specialist
Physiology
Habitat
Disturbance Regimes
Ecology
Non-Climatic

Figure 3. The average Euclidean distance between historical climate (1961–1990) and five general circulation models for the time period 2070 to 2099 for the A2 emissions scenario. Tree species codes are the same as in Figure 2.