How might the past and projected future changes in climate influence vegetation communities across the Greater Yellowstone Ecosystem (GYE) and the surrounding Rocky Mountains? This question is difficult to answer because of the complex interactions between climate and plant populations. Changes in climate will likely have direct effects on rates of establishment, growth, and death of plant populations. They will also have indirect effects via influence on other factors that interact with plant populations such as disturbance regimes (e.g., fire), pests (e.g., mountain pine beetle), and interactions with other species such as competition, facilitation, pollination, and dispersal. Scientists have some level of uncertainty about each of these potential direct and indirect effects of climate change on a given plant species. Consequently, analyses that consider all of these effects and interactions among them typically have levels of uncertainty that are too high to be very informative to resource managers (Huntley et al. 2010). An approach that is a reasonable first step for informing management is to represent projected changes in climate through the lens of the tolerances of plant species.

Controlling for other factors, plants tend to have viable populations in locations where climate conditions are within their range of tolerances for establishment, growth, survival, and reproduction. With this in mind, an approach termed “bioclimate envelope modeling” quantifies the climate conditions where a species is currently present and projects the locations of these climate conditions under future scenarios (Huntley et al. 1995, Pearson et al. 2003, Guisan and Thuiller 2005). More specifically, current presence of a species is assumed to be determined by climate in the context of disturbance, biotic interactions, and other factors that influence species distributions, so the projected areas of suitable climate are prefaced on the assumption that the interactions with disturbance and other ecological factors continue as at the present time. This method allows inference about potential climate suitability for a species (controlling for other factors). While this approach does not necessarily predict where a species will occur in the future (Pearson et al. 2003), it does project one foundational filter of where a species could exist in the future—climate suitability (Serra-Díaz et al. 2014).

The results of bioclimate envelope studies are very useful to resource managers for identifying which species may be most vulnerable to climate change and for developing management strategies for these species (Hansen and Phillips 2015). Whereas managers cannot manipulate climate over large landscapes, they can manipulate other factors that influence plant population viability: establishment, genetic composition, interactions with other species, and disturbances. Knowledge of climate suitability is a critical first filter for deciding where to use management actions to protect, restore, or establish certain populations under climate change. Species identified as vulnerable based on climate suitability are candidates for additional research used in vulnerability assessments (Dawson et al. 2011), which are typically more expensive and/or have higher uncertainty than climate suitability analyses.

We summarize three bioclimate envelope modeling studies for tree species across the U.S. Northern Rockies and within the GYE (figure 1). Hansen and Phillips (2015) integrated the results of published studies dealing with western North America tree species to assess their climate suitability within the Rocky Mountains of Wyoming, Montana, and Idaho. The results provide a broader context for interpreting potential changes in the GYE. In order to improve on the published studies within the GYE, Piekielek et al. (in review), used the newest Intergovernmental Panel on Climate Change (IPCC) climate projections, drew on the abundant plant field data for the GYE, and included consideration of habitat factors in addition to climate such as soil, water balance, and topography. Chang et al. (2014) focused on whitebark pine, the species found to be most vulnerable to changes in climate suitability in the Rocky Mountain analysis. This analysis used methods similar to Piekielek et al., but additionally examined the variability in climate suitability projected under different global circulation models (GCMs). These three studies all used two climate scenarios: a higher

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greenhouse gas emissions scenario termed A2 or RCP 8.5 in various IPCC iterations and a lower emissions scenario that assumes global reduction in the rate of emissions termed B1 or RCP 4.5 (IPCC 2007, Moss 2008). We report the results of both sets of scenarios in this synthesis.

U.S. Northern Rockies
The four studies evaluated by Hansen and Phillips (2015) all projected substantial declines in climate suitability for subalpine tree species across the Northern Rocky Mountains. Averaging among the studies, the proportion of the study area with suitable climate for whitebark pine dropped from 21% currently to 8.8% by 2070-2100 under the B1 scenario and to 11% under the A2 scenario (figure 2). Remaining suitable climate area by 2100 for Engelmann spruce, subalpine fir, and lodgepole pine was 18-25% under B1 and 16-25% under A2. Among the montane species, ponderosa pine and grand fir climate suitable areas were projected to increase substantially. The studies disagreed on Douglas-fir, with some studies projecting expansion and others contraction. Among the tree species now found in the more mesic Rocky Mountain westslope, mountain hemlock was projected to decrease dramatically under both climate scenarios while western red cedar and western hemlock were projected to increase moderately.

The spatial patterns of change in climate suitability projected for the next century help place the GYE in the context of the surrounding Rocky Mountains. Climate suitability for the subalpine species decreased on the westside of the Continental Divide and in lower elevations around the GYE. In contrast, Douglas-fir and especially ponderosa pine climate suitability were projected to expand throughout the westslope and in lower to mid-elevations of the GYE under both climate scenarios.

Four metrics derived from these climate suitability analyses were used to rank vulnerability of the tree species. Whitebark pine and mountain hemlock had the highest vulnerability scores (figure 3). These species and the other subalpine species (Engelmann spruce, subalpine fir, and lodgepole pine) were placed in the High vulnerability class because of the large decline in projected suitable area and low gain in newly suitable areas. Western hemlock, western redcedar, western larch, and Douglas-fir were considered Medium in vulnerability. Ponderosa pine and grand fir were projected to gain substantially in area of suitable habitat and were considered Low in vulnerability.

Greater Yellowstone Ecosystem
To what extent do more detailed habitat models for the GYE confirm or differ from the Rocky Mountain climate suitability projections described above? Piekielek et al. (in review) found subalpine species declined dramatically in projected area of suitable habitat by 2099 under RCP 4.5 (50-77% decrease) and RCP 8.5 (80-90% decrease) (table 1). The montane species aspen, Douglas-fir, and lodgepole pine also showed substantial decreases in suitable habitat area with decreases of 10-53% under RCP 4.5 and decreases of 60-85% under RCP 8.5. Some lower treeline communities were projected to increase substantially in suitable habitat. The juniper community type was projected to increase 32% and 55% in suitable habitat area under RCP 4.5 and RCP 8.5. The sagebrush community was projected to increase 31% and 40% in suitable area under the two scenarios.

The habitat variables that consistently contributed to the best habitat models included early growing-season snowpack, late season soil water-deficit, mid-season soil moisture, and soil texture. These predictors are consistent with hypotheses on factors that limit tree species in the GYE and indicate that consideration of water balance and soil are improvements on models that only consider climate.

Maps of projected changes in climate suitability illustrate sagebrush and juniper communities, now at the warmer and drier lower forest treeline, expanding by...
Figure 2. Projected change in the proportion of the Northern Rockies study area with suitable climate for each tree species averaging the results of the four studies considered in Hansen and Phillips (2015) under the B1 and A2 climate scenarios.

2100 onto the mid-elevations of the Yellowstone Plateau (e.g., figure 4). Douglas fir was projected to contract from current mid- to lower elevation settings and expand onto the Yellowstone Plateau under RCP 4.5 but not RCP 8.5. Lodgepole pine was projected to continue to have suitable habitat on the Yellowstone Plateau under both scenarios. Habitat suitability for subalpine fir and Engelmann spruce was projected to remain only in the highest elevations under both scenarios.

Whitebark pine is of special interest in GYE. It is considered a keystone species in the subalpine (Logan et al. 2010). It provides a food source for wildlife, including the grizzly bear. It also serves the ecosystem functions of stabilizing soil, moderating snow melt and runoff, and facilitating establishment by other conifer species. Whitebark pine has experienced a notable decline in the past decade due to high rates of infestation from the mountain pine beetle (Dendroctonus ponderosae) and infections from white pine blister rust (Cronartium ribicola) (MacFarlane et al. 2012). Furthermore, whitebark pine was found to have the highest vulnerability to climate change in the Rocky Mountain analysis described above.

Chang et al. (2014) found the presence of whitebark pine in the GYE was associated with lower summer maximum temperatures and higher springtime snowpack. Patterns of projected habitat change by the end of the century suggested a constant decrease in suitable area from a 2010 baseline. Among nine GCMs, percent suitable climate area estimates in 2100 averaged 16.5% and 3% of the 2010 baseline for RCP 4.5 and 8.5 respectively (figure 5). Projected suitable area for individual GCMs varied from 29-2% and 10-0.04% by 2099 for RCP 4.5 and 8.5, illustrating that GCMs differ in climate projections that are relevant to climate suitability projections for this species. However, the agreement among all the GCMs in substantial declines in whitebark pine climate suitability suggests a high level of concern for this species in GYE is warranted. Projected suitable habitats for this species by 2100 are only in the highest elevations of the GYE, largely on the Beartooth Plateau, the Absaroka Range, and the Wind River Range.

Implications for Research and Management

The results of the three studies described above suggest the climate suitability for forests of the GYE will change substantially in the coming century. The warming temperatures, decreasing springtime snowpack and decreasing late season soil moisture projected by the GCMs would
result in a longer, warmer, and drier growing season than present. In general, vegetation types are projected to shift upward in elevation. Sagebrush and juniper communities are projected to expand from valley bottoms upslope into the lower forest zone and the Yellowstone Plateau. Climate suitability for the dense and productive Douglas-fir and aspen forests now in the lower forest zone is projected to deteriorate for these species. Ponderosa pine, a species not currently found in the GYE, is projected to have suitable habitat in this zone by the end of the century.

Projections for the Yellowstone Plateau, which occupies the central portion of Yellowstone National Park, are complex and vegetation patterns there are further complicated by soils. The coarse textured and nutrient poor rhyolitic soils on the plateau are thought to currently limit the distribution of Douglas-fir and aspen on the plateau (Despain 1990) and this may continue to be the case even if climate becomes more suitable for these species. Given that the Yellowstone Plateau is projected to provide suitable habitats for sagebrush, juniper, and lodgepole pine, the actual distributions of these species are likely to be governed by disturbance and other ecological factors. Subalpine species are projected to have reduced climate suitability in much of their current range while higher elevations become more suitable in climate for these species. Many of these high-elevation locations, however, are now dominated by rock which will likely constrain the area of suitable habitat for these species.

Given the projected changes in habitat suitability described above, a number of questions arise as to the consequences for vegetation of the indirect effects of climate change. How will climate change influence fire regimes and what will be the consequences for vegetation patterns? Based on climate change alone, fire frequency was projected to increase dramatically across all elevations of the GYE (Westerling et al. 2011). How will change in climate influence forest pests? Buotte et al. (2015) project increasingly favorable climate conditions for mountain pine beetles to the north and west, and the development of new pest populations may be expected across the region.

Table 1. Percent change in projected area of suitable habitat across the GYE in 2040, 2070, and 2100 under two climate scenarios. From Piekielek et al. (in review).

<table>
<thead>
<tr>
<th>Common Tree Species Name</th>
<th>RCP 4.5</th>
<th>RCP 8.5</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2040</td>
<td>2070</td>
</tr>
<tr>
<td>Sagebrush</td>
<td>17</td>
<td>23</td>
</tr>
<tr>
<td>Juniper</td>
<td>18</td>
<td>26</td>
</tr>
<tr>
<td>Limber pine</td>
<td>-13</td>
<td>-8</td>
</tr>
<tr>
<td>Aspen</td>
<td>-1</td>
<td>-5</td>
</tr>
<tr>
<td>Lodgepole pine</td>
<td>-20</td>
<td>-42</td>
</tr>
<tr>
<td>Englemann spruce</td>
<td>-46</td>
<td>-61</td>
</tr>
<tr>
<td>Subalpine fir</td>
<td>-43</td>
<td>-56</td>
</tr>
</tbody>
</table>

Figure 3. Results of vulnerability assessment ranking averaged among studies under the A2 scenario. (From Hansen and Phillips 2015).
beetles. How will changes in forest habitat suitability, fire regimes, and pest outbreaks interact to influence patterns of vegetation across the GYE? We speculate these interacting factors will result in vegetation in GYE later in the century being dominated by nonforest communities and remaining forest communities being earlier in seral stage and lower in canopy cover.

Whitebark pine was projected to have the greatest loss in area of suitable habitat in the GYE. The areal extent of adult reproductive aged stands has already declined dramatically across the GYE due to mortality from mountain pine beetles (Logan et al. 2010). Will whitebark pine be entirely lost from the GYE? Hope for the persistence of whitebark pine in GYE is bolstered by its history. Pollen records indicate that five-needle pine (whitebark and/or limber pine) remained in the region over the past 10,000 years even during the relatively warm hypsithermal period (Iglesias et al, in revision). More research is needed, but various hypothesis suggest viable populations can re- main through the projected harsher climate in 2100 (Hansen et al. in prep):

- About 960 km$^2$ of suitable habitat is projected to remain, even under the more extreme RCP 8.5 scenario (Chang et al. 2014), possibly allowing the population to persist, albeit at a greatly reduced size. This projected suitable habitat is at the highest elevations in GYE and an unknown, but probably substantial portion of this is rock and unsuitable for the species.
- Some locations projected to become unsuitable may actually have small pockets that remain suitable due to microsite characteristics. Local steep, north-facing slopes may maintain cooler temperatures and later snowpack than projected by the 800-m climate data used in the climate suitability analyses. Such sites may serve as microrefugia (Dobrowski 2011) where whitebark pine is able to persist even while the surrounding landscape becomes unsuitable.
- Within the whitebark pine population, genetic variants may exist that are better able to tolerate more extreme climate conditions. These variants likely would be favored by selection as climate warms.
- The current distribution is thought to be strongly limited by competition with other conifer species and the species may be able to persist in warmer conditions in the absence of competition (GYCC 2011). This raises the possibility that active management to reduce competition from lodgepole pine and subalpine fir could favor whitebark pine under a changing climate.
- Some of the current mortality of this species is caused by white pine blister rust. Seedlings that are genetically

Figure 4. Oblique view from the southwest of the GYE showing change in modeled spatial distribution of climate suitable areas for tree species from the reference period to 2100 under the RCP 8.5 climate scenario based on majority agreement of nine GCM model runs. Data from Pielieke et al. (in review). Photos by A. Hansen and the YNP photo archive.
resistant to the rust have been propagated and are being planted. If these seedlings are planted in locations projected to maintain suitable climate, competing vegetation is controlled, and mountain pine beetles do not cause mortality, these seedlings may contribute to the maintenance of a viable population.

The changes in the aerial extent of vegetation projected above would likely have large consequences for the provisioning of ecosystem services across the GYE. Loss of coniferous forest cover would likely further exacerbate reductions in snowpack due to warming spring temperatures with large consequences for stream flows and temperature, cold-water fish populations, and downstream water availability for irrigation and human consumption. Habitat quality would be expected to deteriorate for the many species of wildlife now dependent on forest habitats and snow cover. Implications for the quality of visitor experiences and recreational opportunities are poorly understood.

**Tools to Address Climate Change**

Projected climate change represents a very significant challenge to natural resource managers. There is high uncertainty about the magnitude of climate change, the ecological response to it, the effectiveness of various management treatments, and even the appropriateness of active management in some wildlands. Fortunately, approaches are being developed and tested. “Climate adaptation planning” (e.g., Stein et al. 2014) involves multiple steps that link climate science and management. Research is used to project potential future response to climate change and reduce uncertainty. Monitoring in fast changing places provides information on actual rates of change and ecological response to this change. Vulnerability assessments can reveal which species or ecosystems are most at risk, where these are located, and why they are at risk. Education programs for natural resource staff and the public can help promote an understanding of the issues and formulating effective policy. Agency planning
documents can incorporate consideration of climate change in order to mitigate undesirable climate change impacts on projects. Passive management such as allowing fires to burn can sometimes favor species vulnerable to climate change. Finally, a variety of types of active management are being developed and evaluated aimed at protecting existing populations until newly suitable habitats develop, facilitating natural establishment in newly suitable habitats, and assisted migration to suitable areas.

There is currently much discussion and debate about the use of active management on some federal lands. The enabling legislation for restricted federal land types such as national parks, roadless areas, and designated wilderness areas encourage or require minimal human intervention (Long and Biber 2014). The three studies summarized above all found projected suitable habitat for vegetation increasingly shifts from unrestricted federal lands to the restricted federal lands which dominate the higher elevations. While the debate over active management in wildlands facing climate change will continue, it should be noted that research, monitoring, education, vulnerability assessment, and passive management are all viable options for managers of restricted federal lands.

**Literature Cited**


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**“Assisted migration”**

“Assisted migration” or managed relocation is the act of deliberately assisting plant or wildlife species to colonize new habitats. The method is intended to facilitate conservation of valued species by shifting populations to alternative areas that are predicted to be suitable habitat for these target species (IPCC Climate Change Synthesis Report). The consequences of assisted migration have been subject to limited case studies. It is difficult to predict the ultimate success, or failure, of assisted migration or the unintended impacts to native flora and fauna from introduction of species into new regions. However, the use of assisted migration as a climate change adaptation tool may be a viable option for several species in the GYE, such as whitebark pine.


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