# Vulnerability of Major Colorado Front Range Tree Species to Climate Change

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## Introduction

Forests and woodlands are a vital component of the Colorado Front Range landscape. Occupying millions of acres, Front Range forests and woodlands support myriad species (Latif et al. 2020; Peet 1981; Simonson et al. 2001) and regulate geological, hydrological, and chemical processes (Bradford et al. 2008; Burns 2004; Troendle and King 1985). They also provide the people of the Front Range and beyond with ecosystem services ranging from timber, food, and water production to recreational opportunities (Clement and Cheng 2011).

Climate change over the next several decades is expected to profoundly impact Front Range forests and woodlands through both direct and indirect mechanisms. Indeed, climate change and its impacts have already been observed. Mean annual temperatures during the last two decades averaged 1.5 °F (0.8 °C) warmer than those of the 20th century (Rangwala 2024, this report). While annual precipitation totals in the last two decades do not show a clear deviation from the long-term trend, warmer temperatures have led to an increase in measures of water stress, like climatic water deficit and vapor pressure deficit (Andrus et al. 2021; Rangwala 2024; Rodman et al. 2020a). These climatic changes have directly contributed to higher mature tree mortality rates and to lower tree seedling establishment rates (Andrus et al. 2018, 2021; Worrall et al. 2008). Mature tree mortality due to wildfires and insect and disease outbreaks, disturbances which themselves bear the marks of recent climatic changes, has also increased, and postdisturbance tree establishment has declined (Chapman et al. 2012; Lalande et al. 2020; Rodman et al. 2020a). Although precise details about the nature of future climate are unknown, additional climatic changes are nonetheless predicted to bring even more direct and indirect impacts to Front Range forests and woodlands (Crookston 2009; Malone et al. 2018b; Monahan et al. 2013; Rodman et al. 2020a; Temperli et al. 2015).

Detailed assessments of species' vulnerabilities to climate change—that is, the degree to which species are susceptible to, and unable to cope with, climate change effects (IPCC 2007)—can help land managers incorporate the anticipated effects of climate change into their planning and decision documents. In this chapter, we used the best available scientific information to assess the vulnerability of nine major tree species in the Colorado Front Range to climate change. We broke the chapter into four main sections, with the first two describing our vulnerability assessment area and assessment approach, and the last two containing our assessments and conclusions.

## Vulnerability Assessment Area

Our assessment area was the forested portion of the Colorado Front Range. As in the other chapters in this General Technical Report, we delineated the Front Range as a rectangular area surrounding the Pike-San Isabel (PSI) and the Arapaho-Roosevelt (AR) National Forests (fig. 1). A large proportion of the forested lands in the Front Range is under the management of these National Forests. Other forested public lands include those managed by the National Park Service, the Bureau of Land Management, and the State of Colorado. A small but noteworthy proportion of the forested lands in the Front Range is managed by local government agencies or is privately owned.

The Front Range encompasses three broadly defined major forest and woodland vegetation types, or macrogroups (table 1; fig. 1) (USNVC 2020). The Southern Rocky Mountain Twoneedle Pinyon–Juniper Woodland Macrogroup (hereafter pinyon–juniper woodland) is primarily found in the foothills and lower montane zones of the southern Front Range. This vegetation type occupies only about 1 percent of the PSI-AR, or about 0.1 million ac (< 0.1 million ha), almost all of which is on the PSI (ARP 2019; PSICC 2019). However, it is quite common on lower-elevation neighboring lands. The most ubiquitous tree species is twoneedle pinyon (*Pinus edulis*) (fig. 2). The Southern Rocky Mountain Lower Montane Forest Macrogroup (hereafter montane forest) occupies the lower montane zone of the Front Range. This vegetation type covers approximately 0.9 million ac (0.4 million ha), or 20 percent, of the PSI-AR (ARP 2019; PSICC 2019). The major tree species are ponderosa pine (*Pinus ponderosa* var. *scopulorum*) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) (fig. 3a-b). Finally, the Rocky Mountain Subalpine–High Montane Forest Macrogroup (hereafter subalpine forest) occurs from the upper portions of the montane zone to the subalpine zone. It occurs on about 41 percent of the PSI-AR, or on about 1.9 million ac (0.8 million ha) (ARP 2019; PSICC 2019). Quaking aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta* var. *latifolia*), limber pine (*Pinus flexilis*), Rocky Mountain bristlecone pine (*Pinus aristata*), subalpine fir (*Abies lasiocarpa* var. *lasiocarpa*), and Engelmann spruce (*Picea engelmannii* var. *engelmannii*) are the most common tree species (fig. 4a-e). The remaining 38 percent of the PSI-AR, encompassing 1.7 million ac (0.7 million ha), is primarily composed of vegetation types dominated by graminoids, forbs, and/or shrubs; it also includes minor tree-dominated vegetation types (e.g., riparian forests dominated by narrowleaf cottonwood [*Populus angustifolia*]), undefined vegetation types, and water.

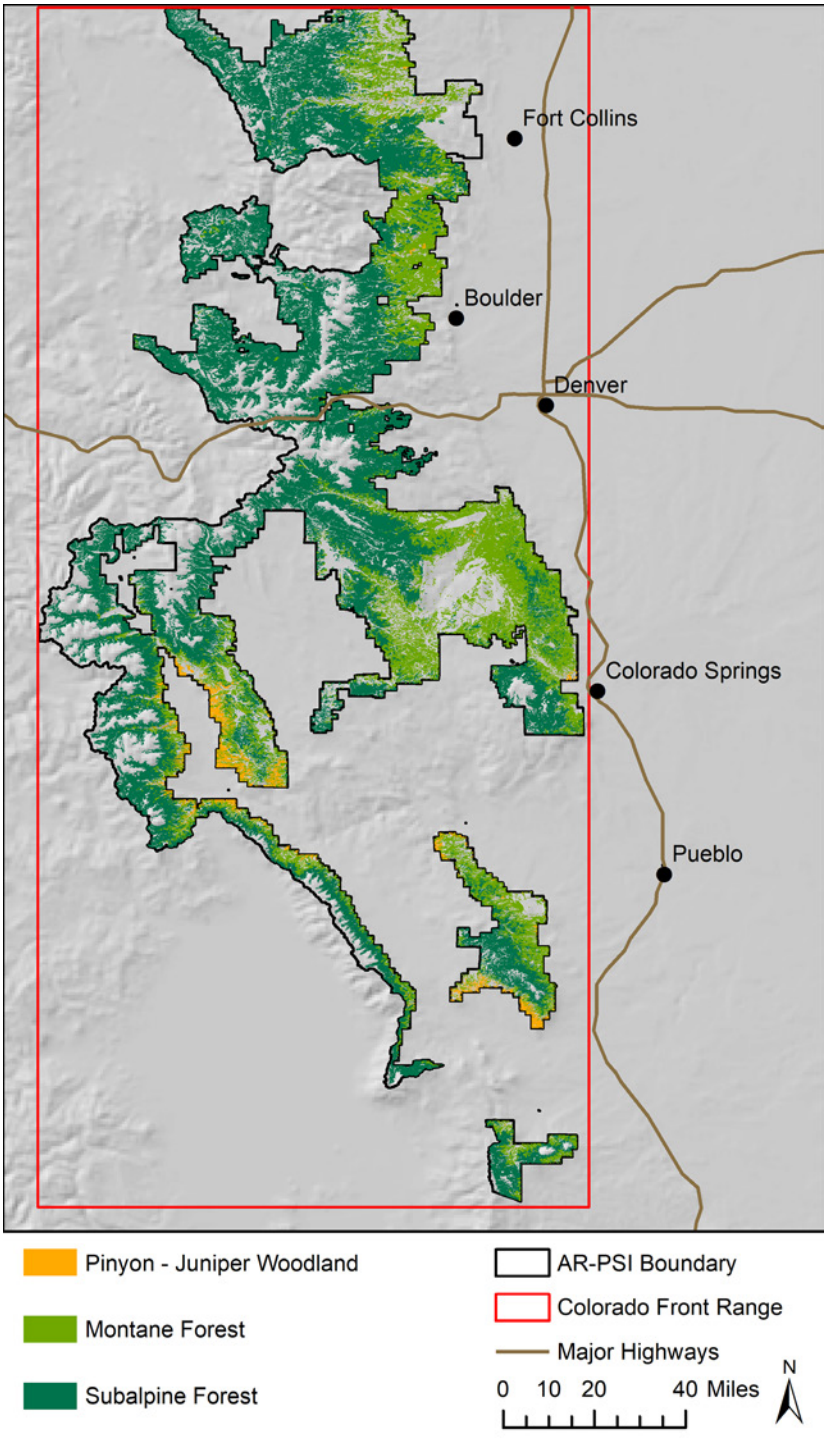



**Figure 1—**Map of the current distribution of the three major forest and woodland vegetation types on the Pike-San Isabel (PSI) and Arapaho-Roosevelt (AR) National Forests in the Colorado Front Range (ARP 2019; PSICC 2019). The vegetation types were derived by crosswalking USDA Forest Service Region 2 cover types to U.S. National Vegetation Classification macrogroups as described in table 1 (ARP 2019; PSICC 2019; USNVC 2020). Note that in some places the map reflects changes stemming from recent disturbances, such as the conversion of forest to nonforest by stand-replacing wildfire (e.g., the Hayman Fire northwest of Colorado Springs).

**Table 1—**The three major forest and woodland vegetation types of the Colorado Front Range. Vegetation types were defined by U.S. National Vegetation Classification (USNVC) macrogroups and Forest Service Region 2 (USFS R2) cover types (ARP 2019; PSICC 2019; USNVC 2020). The Front Range was defined as a box bounding the Arapaho-Roosevelt (AR) and Pike-San Isabel (PSI) National Forests.

| Vegetation type | Description |
|---|---|
| Pinyon-juniper woodland | The Southern Rocky Mountain Twoneedle Pinyon–Juniper Woodland Macrogroup (M897; hereafter pinyon-juniper woodland) occurs in the foothill and lower montane zones of the southern Front Range. It is present on about 0.1 million ac (< 0.1 million ha) of the PSI-AR National Forests; almost all of this is on the PSI (fig. 1). Twoneedle pinyon is the major tree species. Oneseed juniper and Rocky Mountain juniper are also common, with the former tending to be more prevalent on lower-elevation lands surrounding the PSI and the latter tending to be more prevalent on the PSI itself. Other species such as ponderosa pine and Douglas-fir are sometimes also present. We crosswalked this vegetation type to the USFS R2 pinyon-juniper cover type. |
| Montane forest | The Southern Rocky Mountain Lower Montane Forest Macrogroup (M022; hereafter montane forest) occurs throughout the lower montane zone of the Front Range. It covers about 0.9 million ac (0.4 million ha) of the PSI-AR (fig. 1). The major tree species are ponderosa pine and Douglas-fir. Occasionally other species, such as Rocky Mountain juniper, quaking aspen, white fir, and blue spruce, mix into the canopy or are dominant. The vegetation type was crosswalked to four USFS R2 cover types: ponderosa pine; Douglas-fir; white fir; and blue spruce. |
| Subalpine forest | The Rocky Mountain Subalpine–High Montane Forest Macrogroup (M020; hereafter subalpine forest) captures the upper montane and subalpine zones of the Front Range. It occurs on about 1.9 million ac (0.8 million ha) of the PSI-AR (fig. 1). The major tree species in this macrogroup are quaking aspen, lodgepole pine, limber pine, bristlecone pine, subalpine fir, and Engelmann spruce. Douglas-fir and other species can sometimes also occur. We crosswalked this vegetation type to five USFS R2 cover types: aspen; lodgepole pine; limber pine; bristlecone pine; and spruce-fir. |

**Figure 2—**Twoneedle pinyon, a major tree species of the pinyon-juniper woodland vegetation type, is abundant at this Bureau of Land Management site near Salida, Colorado. (USDA Forest Service photo by Mike Battaglia)


**Figure 3a-b—**Major tree species of the montane forest vegetation type. (a) Ponderosa pine dominates the landscape at the Manitou Experimental Forest on the Pike National Forest. (b) This Douglas-fir survived the 2002 Hayman Fire on the Pike National Forest. (USDA Forest Service photos by Paula Fornwalt.)

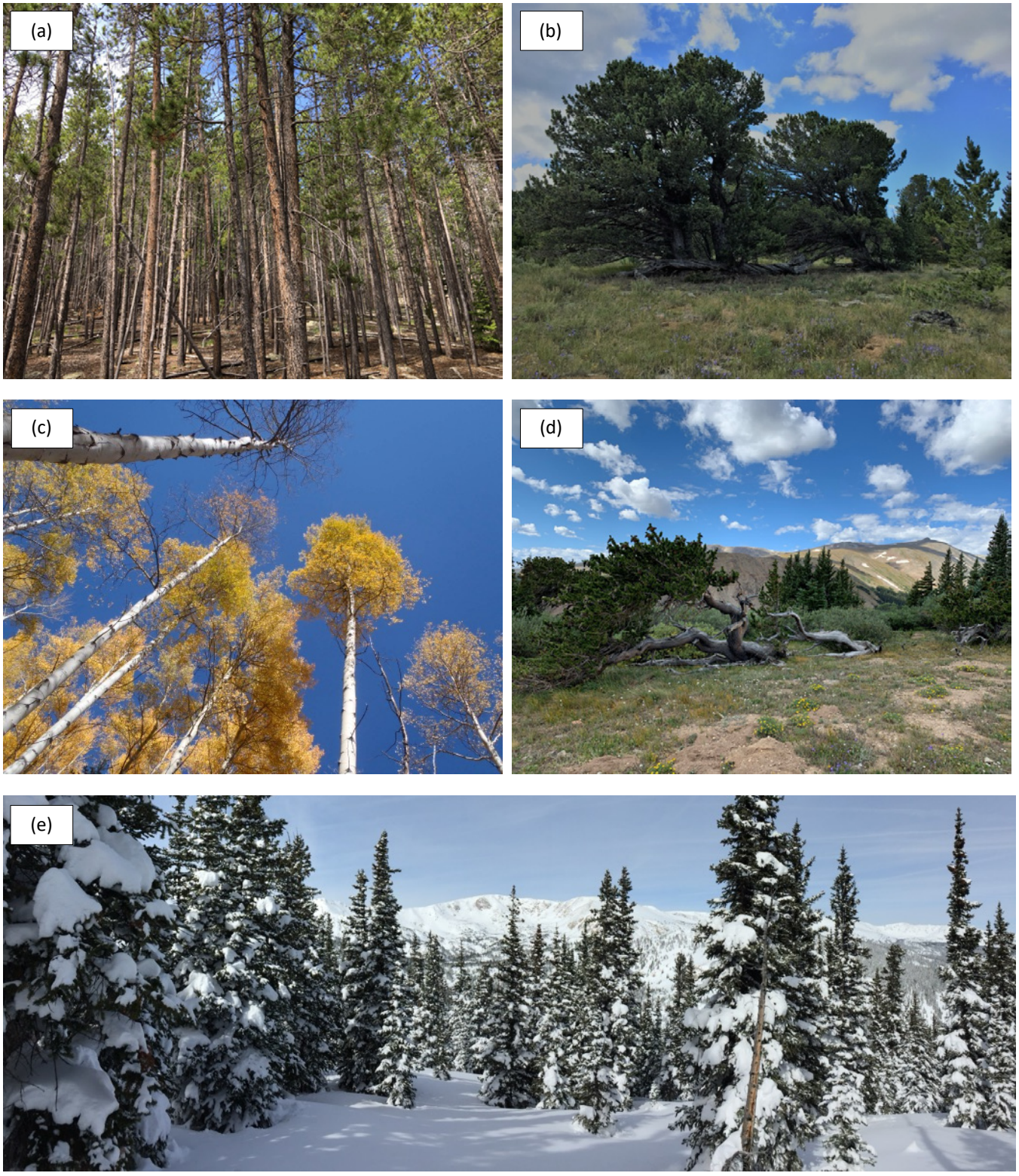



**Figure 4a-e—**Major tree species of the subalpine forest vegetation type. (a) Lodgepole pine occupies the upper portions of Crosier Mountain, Roosevelt National Forest. (b) Limber pine grows along the Brown's Lake Trail, Roosevelt National Forest. (c) Quaking aspen displays its fall colors at the Fraser Experimental Forest, Arapaho National Forest. (d) This twisted, old Rocky Mountain bristlecone pine helps form treeline on Pennsylvania Mountain, Pike National Forest. (e) Engelmann spruce and subalpine fir intermix near Uncle Bud's Hut, San Isabel National Forest. (USDA Forest Service photos by Paula Fornwalt (a, b, c, e) and John Frank (d))

## Vulnerability Assessment Approach

We assessed the vulnerability of the above nine major Front Range tree species—twoneedle pinyon, ponderosa pine, Douglas-fir, quaking aspen, lodgepole pine, limber pine, Rocky Mountain bristlecone pine, subalpine fir, and Engelmann spruce—using the general framework described by the Intergovernmental Panel on Climate Change (IPCC) and others (Glick et al. 2011; IPCC 2001, 2007; Swanston et al. 2016). This framework examines vulnerability by evaluating the potential impacts of climate change on a natural resource, such as a single species, a community of species, or an ecosystem service, and the capacity of the resource to adapt to it (fig. 5).

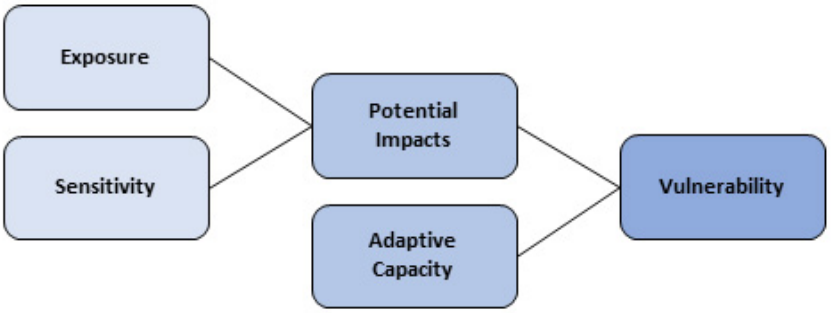



**Figure 5—**The components of climate change vulnerability. (Adapted from Glick et al. 2011.)

Potential impacts describe the consequences of climate change for a natural resource, and are a function of exposure, or how the climatic environment is expected to change, and sensitivity, or how the resource is expected to be affected by that change (fig. 5; Glick et al. 2011). Potential impacts can be either direct or indirect. Direct potential impacts are those of climate change per se, such as tree death due to warmer temperatures and more extreme weather events. Indirect potential impacts are those that are mediated through climate change's influence on other factors. Examples of indirect potential impacts are those due to a climate change-driven increase of the frequency, severity, or size of wildfires or insect and disease outbreaks.

Adaptive capacity reflects the mechanisms that a biological natural resource has to cope with climate change by enabling it to either persist in its current location or migrate to a more suitable location (Glick et al. 2011; Jump and Peñuelas 2005). One factor that can influence the adaptive capacity of a resource is its phenotypic plasticity, or its ability to maintain high fitness in the face of environmental change by altering its morphology, phenology, or physiology (Nicotra et al. 2010). A resource with high phenotypic plasticity is therefore expected to be better able to tolerate changes in climate. Another factor that can influence a resource's adaptive capacity is its genetic diversity (Jump et al. 2009). Genetic diversity reflects the potential to adapt to climate change through evolution; a resource with high genetic diversity is more likely to contain individuals with heritable traits that increase its tolerance of climate change. A resource that can readily shift its

range—for example, because it can disperse long distances or because its distribution is broad and connected—is expected to be better able to adapt to climate change by migrating to an area with a more favorable climate (Corlett and Westcott 2013).

Even within the context of the IPCC framework, vulnerability can be assessed through a variety of approaches. These range from qualitative approaches that are based on expert opinions to quantitative approaches that use vulnerability assessment tools to integrate input data. Our approach took inspiration from that of Keane et al. (2018) and drew from the relevant available scientific literature to produce vulnerability assessment narratives. We particularly relied on literature describing studies conducted within the Front Range, supplementing it as appropriate with literature describing studies conducted in comparable areas elsewhere. We then used these narratives to produce overall vulnerability ratings and accompanying confidence ratings, as Brandt et al. (2014), Butler et al. (2015), Janowiak et al. (2018), and others have done.

## Vulnerability Assessment Narrative

### *Habitat*

We began our vulnerability assessment narrative for each tree species with a basic discussion of its habitat. Its current distribution was described, both in the western United States and in the Front Range. Its preferred environmental conditions in the Front Range were also described, as were its common tree, graminoid, forb, and shrub associates. We acquired much of this information from classic references like *Silvics of North America* (Burns and Honkala 1990a,b). We also routinely took information from the Field Sampled Vegetation Database, also known as FSVeg (ARP 2019; PSICC 2019).

### *Ecology*

Next, we synthesized the scientific literature to provide a foundational description of each species' basic ecology. Included in this portion of the vulnerability assessment narrative was information on its reproductive ecology, as well as information on its tolerance to drought, fire, insects, diseases, and other environmental stressors at seedling, sapling, and mature life stages.

### *Potential Direct and Indirect Impacts of Climate Change*

We broke our discussion of potential impacts into one section on direct impacts and another section on indirect impacts. Observational, experimental, and modeling studies were all used as input in these sections. In particular, we made extensive use of the west-wide bioclimatic envelope models developed by Crookston (2009) for our nine species. Bioclimatic envelope models relate the current geographic distribution of a species (or a community of species) to current climate variables to identify the climatic envelope within which it occurs, and then project the geographic distribution of the climatic envelope under various future climate scenarios. Please see box 1 for more information about bioclimatic envelope models in general, and about our use of Crookston's (2009) models specifically.

**Box 1**

## Bioclimatic envelope models

Bioclimatic envelope models are commonly used to assess the potential impacts of climate change on vegetation (Araújo and Peterson 2012). Bioclimatic envelope models relate the current geographic distribution of a species or a species assemblage to current climate variables to identify the climatic envelope under which it occurs. Potential climate change impacts are then explored by projecting the geographic distribution of the climatic envelope under future climate scenarios.

We drew from numerous studies that developed bioclimatic envelope models to investigate potential climate change impacts on Front Range tree species (e.g., Crookston 2009; Gray and Hamann 2013; Malone et al. 2018b). In particular, we made extensive use of a set of west-wide bioclimatic envelope maps developed by Crookston (2009) for more than 70 tree and shrub species. These maps depict the likelihood that climate at a given location and time period is (or is predicted to be) suitable for the species; values approaching 0 indicate that climate is very unsuitable and values approaching 1 indicate that climate is very suitable. West-wide maps for each of the 70 species were produced for the "current" (1990) climate and for seven potential future climates in 2030, 2060, and 2090.

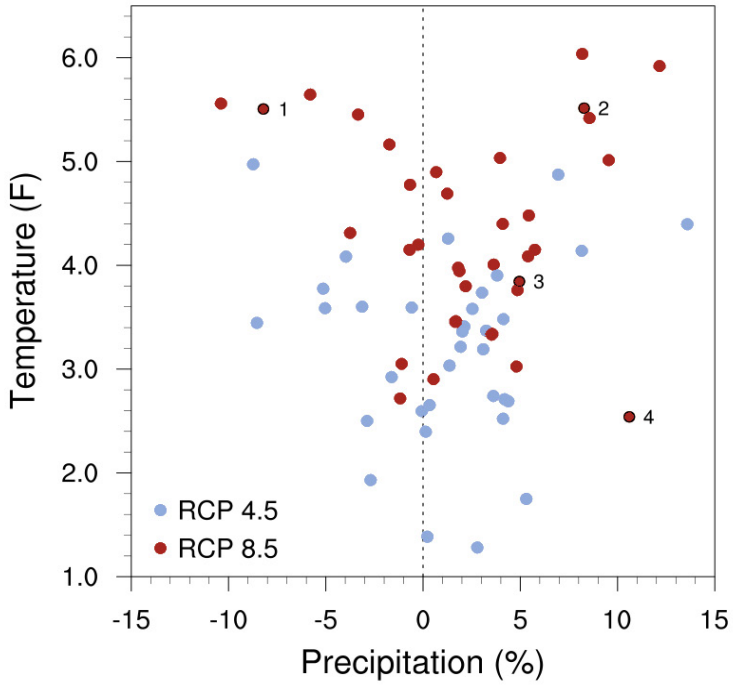
Unfortunately, none of the GCMs utilized by Crookston (2009) to represent the seven potential future climates were the same as those used in this GTR to represent the four potential future climate scenarios (Rangwala this report). However, HADCM3-A2, one of the GCMs used by Crookston (2009), seemed to crosswalk relatively well to CNRM-CM5.RCP85, the GCM representing the middle-of-the-road Hot scenario. In the Front Range, HADCM3-A2 predicts a ~4.5 °F (2.5 °C) increase in mean annual temperature and a 2 percent decrease in mean annual precipitation between the 2000 (1985–2015) and the 2050 (2035–2065) time periods. In comparison, CNRM-CM5.RCP85 predicts a ~3.8 °F (2.1 °C) increase in mean annual temperature and a 5 percent increase in mean annual precipitation between the 2000 and the 2050 time periods. We therefore chose to feature Crookston's (2009) bioclimate envelope maps under HADCM3-A2 in our chapter.

We integrated Crookston's (2009) current bioclimate envelope maps and the 2060 and 2090 bioclimate envelope maps under HADCM3-A2 to create Colorado-wide maps depicting potential future changes in climatic suitability for the major Front Range tree species (e.g., fig. 8). These changes were represented as four classes, as was done by Rehfeldt et al. (2015):

- Suitable climate lost (current suitability likelihood ≥ 0.5 and future suitability likelihood < 0.3);
- Suitable climate threatened (current suitability likelihood ≥ 0.5 and future suitability likelihood < 0.5 and ≥ 0.3);
- Suitable climate persistent (current and future suitability likelihood ≥ 0.5); and
- Suitable climate gained (current suitability likelihood < 0.5 and future suitability likelihood ≥ 0.5).

Bioclimatic envelope modeling is predicated on several assumptions (Araújo and Peterson 2012). Perhaps the most important assumptions are that distributions of species or species assemblages are governed first and foremost by climate, and that species or species assemblages inhabit all areas that are climatically suitable. While climate does in fact govern distributions at large spatial scales, non-climate factors such as species interactions and dispersal limitations may constrain them, particularly at small scales. For this reason, bioclimatic envelope models are best used at broad scales, such as across the Front Range.

To the extent the literature allowed, we examined potential impacts through the lens of four future climate scenarios, or exposures, for the 2035 to 2065 (hereafter 2050) time period. The scenarios, which are described in detail in Chapter 3, bracket the wide range of potential climates that have been projected for the Front Range by various CMIP5 general circulation models (GCMs; fig. 6; Rangwala 2024, this report). The first climate scenario, Hot (CNRM-CM5.rcp85), projects a future climate in which mean annual temperature is 3.8 °F (2.1 °C) warmer and mean annual precipitation is 5.0 percent greater than the 1985 to 2015 (hereafter 2000) baseline climate. Relative to the other three scenarios, the Hot scenario has the most middle-of-the-road 2050 temperature and precipitation anomalies, and so it may best represent a middle-of-the-road future climate scenario. The Very Hot and Wet (CanESM2.rcp85) climate scenario projects a 5.5 °F (3.1 °C) increase in mean annual temperature and an 8.3 percent increase in mean annual precipitation, while the Warm and Wet (GFDL-ESM2M.rcp85) climate scenario projects a 2.5 °F (1.4 °C) increase in mean annual temperature and a 10.6 percent increase in mean annual precipitation. The final climate scenario, Very Hot and Dry (IPSL-CM5A-MR.rcp85), projects a 5.5 °F (3.1 °C) increase and an 8.2 percent decrease in mean annual temperature and precipitation, respectively.




1 Very Hot & Dry (IPSL-CM5A-MR.rcp85)
2 Very Hot & Wet (CanESM2.rcp85)
3 Hot (CNRM-CM5.rcp85)
4 Warm & Wet (GFDL-ESM2M.rcp85)

**Figure 6—**Predicted changes in future (2050) precipitation and temperature on the Colorado Front Range based on the output from 34 CMIP5 general circulation models and two emissions scenarios (RCPs). The four future climate scenarios identified by Rangwala (this report), which approximately bracket the range of predicted changes, are labeled. The Front Range was defined as a box bounding the Pike-San Isabel (PSI) and Arapaho-Roosevelt (AR) National Forests. (Adapted from Rangwala, this report.)

### *Capacity to Adapt to Climate Change*

We assessed adaptive capacity for each species by reviewing the scientific literature to gather available information on its phenotypic plasticity, its genetic diversity, and its ability to migrate. As with potential climate change impacts, we incorporated results from observational, experimental, and modeling studies.

### *Overall Vulnerability Rating*

We assigned an overall climate change vulnerability rating of low, moderate, or high for each tree species by subjectively integrating the information on potential impacts and adaptive capacity (fig. 7a; Brandt et al. 2014; Butler et al. 2015; Janowiak et al. 2018). Vulnerability to climate change increased as potential impacts increased and as adaptive capacity decreased. We then qualified each vulnerability rating with a confidence rating (fig. 7b; Brandt et al. 2014; Butler et al. 2015; Janowiak et al. 2018). The confidence rating characterizes both the amount of information supporting the vulnerability rating (limited, moderate, abundant) and the level of agreement among that information (low, moderate, high). The amount of information was considered limited when the vulnerability rating was supported by a small number of studies, and abundant when it was supported by numerous studies that collectively employed a range of observational, experimental, and modeling approaches. Agreement among the information was considered low when individual studies generally led to different vulnerability ratings, and high when they led to similar vulnerability ratings. Finally, we supported our overall vulnerability rating for each species with a brief paragraph that captured the key points.

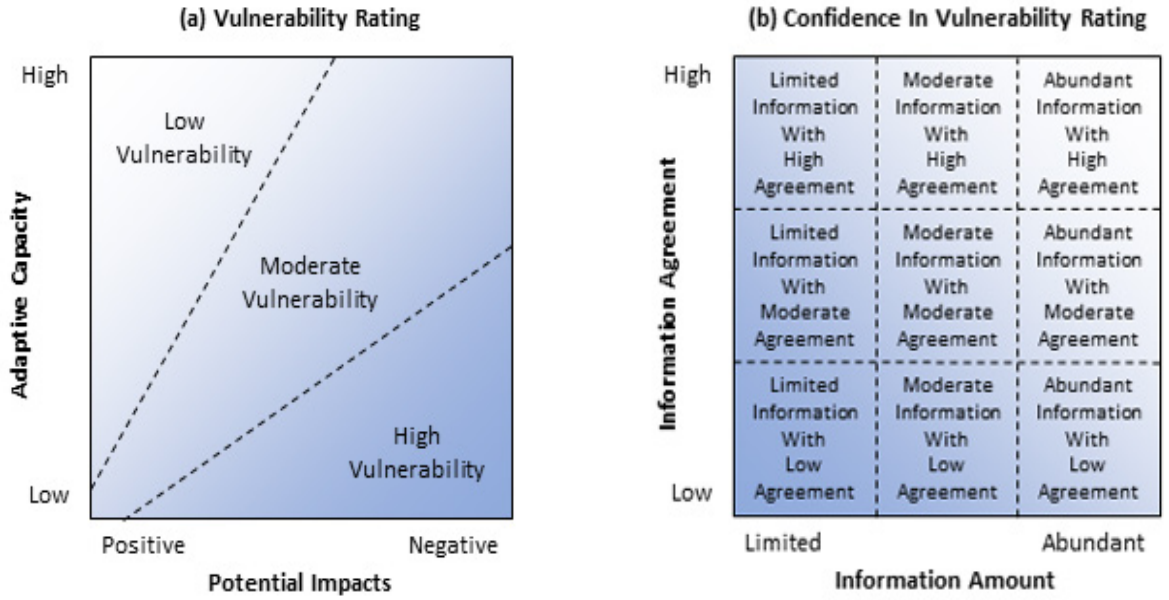



**Figure 7a-b—**The approach used to determine (a) the climate change vulnerability rating for a tree species and (b) the confidence in the climate change vulnerability rating. (Adapted from Brandt et al. 2014; Butler et al. 2015; Janowiak et al. 2018; and Mastrandrea et al. 2010.)

## Twoneedle Pinyon (*Pinus edulis*)

**Climate change vulnerability rating:** moderate

**Confidence in climate change vulnerability rating:** limited information with moderate agreement

Our ability to confidently assess the vulnerability of Front Range twoneedle pinyon populations to climate change is constrained by a lack of local research. There is already considerable evidence of high tree mortality and low regeneration due to climate-change driven drought events, wildfires, and pinyon ips outbreaks across much of twoneedle pinyon's range, and such trends are expected to be exacerbated under a changing climate. However, it is unclear how well these range-wide trends transfer to the Front Range specifically. Bioclimatic envelope modeling suggests that twoneedle pinyon in the Front Range could potentially benefit under a warmer future climate through a net gain of suitable climate space, although capitalizing on it seems unlikely without human intervention (i.e., assisted migration) because the species is slow to regenerate naturally. Moreover, a warmer climate would likely increase the severity, frequency, and extent of drought, wildfires, and pinyon ips outbreaks, to twoneedle pinyon's detriment.

### *Habitat*

Twoneedle pinyon is a short-statured tree that occupies dryland habitats across the southwestern United States, including Arizona, Colorado, New Mexico, and Utah, with isolated populations in southern California, eastern Oklahoma, northern Texas, and southern Wyoming (fig. 2; Little 1971; NRCS 2020; Ronco 1990). Its distribution in the Front Range is largely restricted to the southern counties; very little twoneedle pinyon occurs in the northern counties (ARP 2019; Little 1971; NRCS 2020; PSICC 2019). Indeed, it is not mapped as a major component of forests and woodlands on the AR at all (ARP 2019). On the PSI, it is a major component on 0.1 million ac (< 0.1 million ha) (PSICC 2019). It is also a major component of forests and woodlands adjacent to the PSI, such as Bureau of Land Management lands.

Twoneedle pinyon is typically found in areas with hot, dry conditions. On the PSI, long-term (1981 to 2010) mean annual precipitation in the twoneedle pinyon zone generally ranges from 11 to 27 in (29 to 68 cm) and mean annual temperature generally ranges from 40 to 48 °F (4 to 9 °C) (PRISM 2020; PSICC 2019); however, across the full distribution of the species, mean annual precipitation can be as low as 10 in (25 cm) and mean annual temperature can be as high as 61 °F (16 °C) (Ronco 1990). The elevational range of twoneedle pinyon on the PSI generally spans from 7,100 to 9,500 ft (2,100 to 2,900 m), but it can extend down to around 5,200 ft (1,600 m) elsewhere (PSICC 2019; Ronco 1990; USGS 2020). Twoneedle pinyon occurs across a variety of topographic conditions, including mountain slopes, rocky plateaus, mesas, foothill terraces, and, to a

lesser extent, intervening valleys (Ronco 1990). It also occurs on a variety of soil types, ranging from shallow soils with exposed bedrock to deep soils (Romme et al. 2009).

Twoneedle pinyon is a foundational species of pinyon–juniper woodlands, where it often co-occurs with various species of juniper (table 1; figs. 1, 2). On the PSI, it is commonly found with Rocky Mountain juniper (*Juniperus scopulorum*), but rarely with oneseed juniper (*Juniperus monosperma*) (PSICC 2019). However, oneseed juniper is a common associate on Bureau of Land Management and other surrounding lands in drier areas. Stand structure can vary across the broad set of environmental conditions that support twoneedle pinyon. A sparse, savanna-like structure with a strong grass component commonly occurs in hotter and drier areas with greater monsoonal precipitation, while a closed-canopy structure commonly occurs in cooler and wetter locations (Romme et al. 2009). Twoneedle pinyon is also occasionally found in montane forests, co-occurring with ponderosa pine and Douglas-fir (PSICC 2019); in these forests, pinyon generally achieves a taller stature.

## *Ecology*

### *Reproductive Ecology*

Twoneedle pinyon regeneration occurs exclusively from seed. It is a mast-seeding species, with mast events (i.e., large seed production years) typically occurring every 3 to 7 years (Redmond et al. 2012; Wion et al. 2020). Twoneedle pinyon seeds take over 2 years to mature following seed cone initiation, which occurs in late summer (Little 1938; Mirov 1967). Large mast years are associated with cool and wet climatic conditions during seed cone initiation and seed cone fertilization, which occur in summer two years prior and spring one year prior to mature seed formation, respectively (Forcella 1981; Redmond et al. 2012; Wion et al. 2020). Twoneedle pinyon seeds disperse from seed cones following maturation. Seeds are heavy and lack wings, and therefore they disperse poorly via wind (Vander Wall and Balda 1977). However, seeds are highly nutritious and commonly collected by a wide array of wildlife species, including various corvids (e.g., Clark's nutcracker [*Nucifraga columbiana*]) and rodents (e.g., pinyon mouse [*Peromyscus truei*]), which can disperse these seeds over 13 mi (22 km) (Vander Wall and Balda 1977). Following dispersal, seeds typically remain viable for about a year (Meeuwig and Bassett 1983).

### *Ecology of Seedlings, Saplings, and Mature Trees*

Twoneedle pinyon is considered highly drought-tolerant (drought tolerance score of 4.9 out of 5.0; Niinemets and Valladares 2006). Yet, because it occurs in hot, dry climates, seedling establishment generally occurs during consecutive cool, wet years and in cool microsites beneath nurse trees and shrubs (Barger et al. 2009; Redmond et al. 2018; Urza et al. 2019). Similarly, twoneedle pinyon growth is greatest during years with high winter precipitation and low summer vapor pressure deficits (Adams and Kolb 2005; Macalady and Bugmann 2014; Redmond et al. 2017).

Twoneedle pinyon ranks as one of the most shade-intolerant tree species in the Front Range, receiving a shade tolerance score of 1.4 out of 5.0 (Niinemets and Valladares 2006; Ronco 1990). However, its shade tolerance is dependent on life stage. It strongly relies on shading from nurse plants to facilitate seedling establishment (Redmond et al. 2015, 2018; Sthultz et al. 2007). As seedlings age, the effect of nurse plants shifts from facilitative to competitive (Redmond et al. 2018).

Twoneedle pinyon experienced considerable variability in historical fire regimes across its range, with infrequent high-severity fire regimes being the most prevalent (Romme et al. 2009). Fire regimes of twoneedle pinyon have yet to be studied in the Front Range, but studies from relatively nearby areas suggest that infrequent high-severity fire regimes were common (Floyd et al. 2004, 2017; Huffman et al. 2008). Fire regimes of Mesa Verde National Park in southwest Colorado, for example, were characterized by high-severity events that burned with a rotation of 400 years or longer; fire years were coincident with periods of severe drought (Floyd et al. 2004). The tendency of twoneedle pinyon to have historically experienced a high degree of mortality due to wildfire is a product of its relatively thin bark, short stature, and low-growing branches (Stevens et al. 2020). Postfire recovery processes were often protracted historically because of climatic and microclimatic conditions and seed dispersal limitations (Floyd et al. 2017; Huffman et al. 2012; Vander Wall and Balda 1977).

Twoneedle pinyon can be affected by a variety of insects and diseases, of which the most damaging is the pinyon ips beetle (*Ips confusus*) (Eager 1999). Pinyon ips beetles are native beetles that attack damaged or stressed adult twoneedle pinyon pine trees. Extensive and severe mortality events have been caused by these insects across pinyon's range, often in combination with drought, dwarf mistletoe, or high stand densities (Breshears et al. 2005; Negrón and Wilson 2003). Pinyon ips beetles preferentially attack larger-diameter trees (Negrón and Wilson 2003). As with fire, the establishment of twoneedle pinyon seedlings following pinyon ips outbreaks can be limited by climate and microclimate (Redmond and Barger 2013).

### *Potential Direct Impacts of Climate Change*

While twoneedle pinyon is considered highly drought-tolerant relative to other Front Range tree species, within its range, it still appears to be vulnerable to recent hotter droughts. Mature twoneedle pinyon trees have already been found to be highly sensitive to recent increases in aridity associated with climate change. Extensive twoneedle pinyon mortality has occurred in many portions of the Four Corners States in the past two decades due to a combination of hotter droughts and drought-driven pinyon ips outbreaks (Breshears et al. 2005; Floyd et al. 2009; Shaw et al. 2005). As a result, a suite of metrics has been developed to forecast future twoneedle pinyon mortality (Breshears et al. 2018), which suggest projected increases in the frequency and severity of drought events in the region will drive additional twoneedle pinyon

mortality events over upcoming decades. In fact, twoneedle pinyon radial growth is tightly linked to cool and wet climate conditions and growth declines have also already been observed in southwestern Colorado and in northern Arizona (Adams and Kolb 2004; Redmond et al. 2017).

Twoneedle pinyon recruitment also appears to be highly sensitive to recent increases in aridity. Cool and wet climate conditions during seed cone initiation and fertilization are associated with years of higher seed cone production (Forcella 1981; Parmenter et al. 2018; Redmond et al. 2012; Wion et al. 2020) and recent declines in twoneedle pinyon cone production have occurred in New Mexico and Oklahoma in association with recent warming (Redmond et al. 2012). Additionally, twoneedle pinyon seedling establishment is often limited to cool and wet climate periods (Barger et al. 2009; Shinneman and Baker 2009) and to microsites beneath nurse trees and shrubs that provide cooler microenvironments (Redmond et al. 2018; Urza et al. 2019). This apparent reliance on cool and wet conditions for seed production and seedling establishment is likely why recovery following recent tree mortality events has been limited in many areas, including in western Colorado, northern Arizona, and New Mexico (Redmond et al. 2015, 2018).

However, while this body of research shows that twoneedle pinyon has been adversely affected by ongoing climate change already, to our knowledge only one study included data from the Front Range. This study utilized a spatially extensive dataset collected by the U.S. Department of Agriculture, Forest Service's Forest Inventory and Analysis program to examine recent climate-driven twoneedle pinyon mortality (Shaw et al. 2005). It revealed that mortality in the Front Range has been fairly low in comparison to other portions of twoneedle pinyon's range.

In fact, bioclimatic modeling suggests twoneedle pinyon in the Front Range could potentially benefit from a warmer climate through a net gain of suitable climate space (Cole et al. 2008; Crookston 2009). The results of Crookston (2009), for example, indicated that 1.4 million ac (0.6 million ha) in the Front Range are currently climatically suitable for this species (box 1; table 2; fig. 8). By 2060, results predicted that 2.0 million ac (0.8 million ha) of suitable climate space will be gained, while 0.4 million ac (0.2 million ha) will be lost. By 2090, gains were predicted to be 2.2 million ac (0.9 million ha) and losses were predicted to be 0.8 million ac (0.3 million ha). Crookston (2009) utilized a GCM that is fairly analogous to the one representing the Hot future climate scenario.

**Table 2—**Characteristics of the wildfires > 1,000 ac (400 ha) affecting Colorado Front Range forests and woodlands, 1984 to 2020. Areas are from the Monitoring Trends in Burn Severity program (MTBS 2022). The Front Range was defined as a box bounding the Pike-San Isabel (PSI) and Arapaho-Roosevelt (AR) National Forests.

| Wildfire | On PSI-AR? | Year | Area (ac) | Major forest and woodland vegetation type(s) |
|---|---|---|---|---|
| Canyon | Yes | 1988 | 1,092 | Montane forest |
| Grace Creek | Yes | 1988 | 1,455 | Montane forest; subalpine forest |
| #6 | Yes | 1989 | 1,547 | Montane forest |
| Sunnyside | Yes | 1989 | 1,416 | Montane forest |
| Unnamed | Yes | 1989 | 1,305 | Montane forest |
| Buffalo Creek | Yes | 1996 | 11,690 | Montane forest |
| Bobcat | Yes | 2000 | 10,444 | Montane forest; subalpine forest |
| Eldorado | No | 2000 | 1,001 | Montane forest |
| High Meadows | Yes | 2000 | 9,607 | Montane forest |
| Big Elk | Yes | 2002 | 4,348 | Montane forest; subalpine forest |
| Hayman | Yes | 2002 | 129,417 | Montane forest; subalpine forest |
| Million | No | 2002 | 7,424 | Montane forest; subalpine forest |
| Mt. Zirkel Complex | No | 2002 | 15,478 | Subalpine forest |
| Schoonover | Yes | 2002 | 2,821 | Montane forest |
| Snaking | Yes | 2002 | 2,080 | Montane forest |
| Unnamed | Yes | 2002 | 1,104 | Montane forest |
| Overland | Yes | 2003 | 3,232 | Montane forest |
| Picnic Rock | Yes | 2004 | 9,014 | Montane forest |
| Mason | Yes | 2005 | 11,023 | Pinyon-juniper woodland; montane forest |
| Mato Vega | No | 2006 | 13,126 | Subalpine forest |
| Mauricio Canyon | No | 2006 | 4,370 | Montane forest |
| Nash Ranch | No | 2008 | 1,107 | Montane forest |
| Fourmile Canyon | Yes | 2010 | 5,865 | Montane forest |
| Medano | Yes | 2010 | 4,887 | Montane forest; subalpine forest |
| Crystal | Yes | 2011 | 2,855 | Montane forest; subalpine forest |
| Duckett | Yes | 2011 | 4,705 | Montane forest; subalpine forest |
| Fern Lake | No | 2012 | 2,549 | Subalpine forest |
| High Park | Yes | 2012 | 90,769 | Montane forest; subalpine forest |

Table 2 continued.

| Wildfire | On PSI-AR? | Year | Area (ac) | Major forest and woodland vegetation type(s) |
|---|---|---|---|---|
| Lower North Fork | Yes | 2012 | 3,436 | Montane forest |
| Springer | Yes | 2012 | 1,665 | Montane forest |
| Waldo Canyon | Yes | 2012 | 20,112 | Montane forest; subalpine forest |
| Wetmore | Yes | 2012 | 2,293 | Pinyon-juniper woodland |
| East Peak | Yes | 2013 | 10,082 | Montane forest; subalpine forest |
| Galena Fire | No | 2013 | 1,319 | Montane forest |
| Beaver Creek | No | 2016 | 44,221 | Subalpine forest |
| Beulah Hill | No | 2016 | 5,769 | Pinyon-juniper woodland; montane forest |
| Hayden Pass | Yes | 2016 | 17,977 | Pinyon-juniper woodland; montane forest; subalpine forest |
| Junkins | Yes | 2016 | 19,023 | Montane forest; subalpine forest |
| Chateau | No | 2018 | 1,414 | Montane forest |
| Silver Creek | No | 2018 | 20,725 | Subalpine forest |
| Spring Creek | Yes | 2018 | 10,7108 | Pinyon-juniper woodland; montane forest; subalpine forest |
| Sugarloaf | Yes | 2018 | 1,216 | Subalpine forest |
| Weston Pass | Yes | 2018 | 13,169 | Montane forest; subalpine forest |
| Decker | Yes | 2019 | 9,875 | Pinyon-juniper woodland; montane forest; subalpine forest |
| Calwood | Yes | 2020 | 9,836 | Montane forest |
| Cameron Peak | Yes | 2020 | 208,910 | Montane forest; subalpine forest |
| East Troublesome | Yes | 2020 | 188,924 | Montane forest; subalpine forest |
| Mullen | No | 2020 | 179,894 | Montane forest; subalpine forest |
| Williams Fork | Yes | 2020 | 14,679 | Subalpine forest |

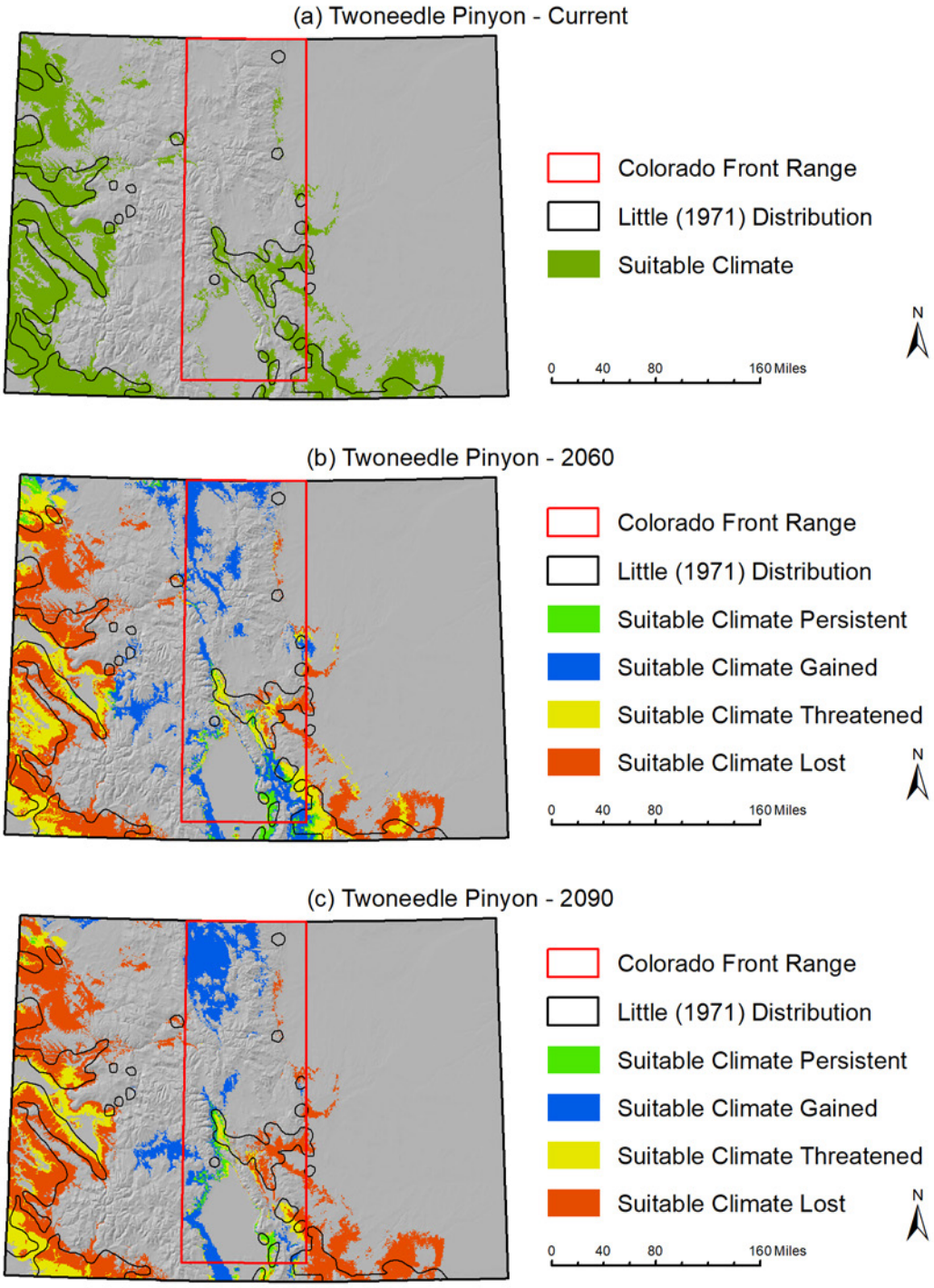



**Figure 8a-c—**The current and potential future suitable climate space of twoneedle pinyon (Crookston 2009). Panel (a) depicts areas in Colorado where the current climate is suitable for the species. Panels (b) and (c) depict areas in Colorado where suitable climate in the future is predicted to be either lost, threatened, persistent, or gained under the HADCM3-A2 general circulation model (GCM), a GCM that crosswalks relatively well to the one representing our Hot future climate scenario. See box 1 for more information about how current and potential future climate suitability were determined. For all panels, the map of Little (1971) is used to represent the general current distribution of the species.

## *Potential Indirect Impacts of Climate Change*

### *Wildfire*

Recent hotter drought events across the range of twoneedle pinyon have not only caused widespread mortality due to increased tree water stress, but have also caused mortality by driving an increase in spatially extensive stand-replacing wildfires (Floyd et al. 2004, 2017; Kennard and Moore 2013). An uptick in wildfires has also occurred in recent decades in the Front Range twoneedle pinyon zone, and while the extent and amount of mortality is unknown, it is likely that this climate change interaction is already underway here (table 3). A warmer, drier future would portend more wildfires and more pinyon mortality in the Front Range (Rangwala 2024, this report; Rocca et al. 2014).

**Table 3—**The area of current and potential future climate space for nine major Colorado Front Range tree species, per Crookston (2009). Current climate space is categorized as either suitable (suit) or unsuitable (unsuit), while future climate spaces is categorized as either lost, threatened (threat), persistent (pers), or gained (gain). Area values (ac, millions) are for the Front Range, defined as a box bounding the PSI-AR. See box 1 for more information about how current and potential future climate suitability were calculated.

| | Current | | 2060 | | | | 2090 | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Species | Suit | Unsuit | Lost | Threat | Pers | Gain | Lost | Threat | Pers | Gain |
| Twoneedle pinyon | 1.4 | 14.4 | 0.4 | 0.7 | 0.3 | 2.0 | 0.8 | 0.3 | 0.3 | 2.2 |
| Ponderosa pine | 3.0 | 12.8 | 1.3 | 0.8 | 0.9 | 0.9 | 2.3 | 0.6 | 0.1 | 0.6 |
| Douglas-fir | 3.0 | 12.7 | 1.7 | 0.9 | 0.5 | 1.1 | 2.5 | 0.5 | < 0.1 | 0.3 |
| Lodgepole pine | 5.6 | 10.1 | 4.4 | 0.7 | 0.6 | 0.6 | 5.6 | < 0.1 | < 0.1 | 0.3 |
| Quaking aspen | 7.4 | 8.4 | 2.7 | 1.3 | 3.4 | 0.9 | 5.1 | 1.2 | 1.1 | 1.3 |
| Limber pine | 8.0 | 7.8 | 3.8 | 2.1 | 2.0 | 0.4 | 6.6 | 1.0 | 0.4 | 0.3 |
| Rocky Mountain bristlecone pine[1] | 3.1 | 12.6 | 2.7 | 0.2 | 0.2 | < 0.1 | NA | NA | NA | NA |
| Subalpine fir | 4.5 | 11.3 | 1.5 | 0.8 | 2.3 | 0.3 | 3.5 | 0.9 | 0.1 | 0.2 |
| Engelmann spruce | 5.8 | 10.0 | 2.9 | 0.6 | 2.3 | 0.2 | 4.2 | 1.4 | 0.2 | 0.1 |

[1] 2090 data are unavailable for this species.

Climate change-driven wildfires may already be leading to contractions in twoneedle pinyon across its range due to limited postfire recovery, and further contractions are likely (Floyd et al. 2021). Twoneedle pinyon is strongly seed limited following disturbances due to its poor dispersal ability in the absence of animals (Vander Wall and Balda 1977) and, as a result, new seedling establishment following disturbances is strongly limited to areas with remaining adult live pinyon seed sources (Redmond et al. 2015). Further, twoneedle pinyon is strongly reliant on nurse trees and shrubs

for seedling establishment and survival (Redmond and Barger 2013; Redmond et al. 2015; Sthultz et al. 2007), and thus losses in tree and shrub canopy cover following disturbances further negatively impact twoneedle pinyon recovery.

### *Insects and Diseases*

Recent hotter droughts have made twoneedle pinyon more susceptible to insect attacks and mortality by pinyon ips beetles (Gaylord et al. 2013). The widespread and severe twoneedle pinyon mortality event that occurred following the 2002 to 2003 drought coincided with a pinyon ips outbreak (Breshears et al. 2005). In a study spanning New Mexico, Colorado, and Arizona, all adult trees that died during that mortality event had evidence of pinyon ips beetle attack, highlighting how drought and insect infestations can—and will likely continue to—interact to lead to widespread dieoff events in twoneedle pinyon (McDowell et al. 2019).

### *Capacity to Adapt to Climate Change*

While twoneedle pinyon as a species appears vulnerable to climate change, certain populations are likely better adapted to handle projected future conditions and may provide refugia as well as seed sources for assisted migration. For instance, radial growth among populations in the warmer and drier portions of the species' range appear to be more sensitive to annual fluctuations in climate (Barger and Woodhouse 2015; Redmond et al. 2017), suggesting that populations located in more mesic habitats may serve as refugia to future drought. In addition, variation in stomata shape and density can influence a tree's water use efficiency and thereby influence the effects of drought and warmer temperature (Lawson and Blatt 2014). Previous research on twoneedle pinyon found heritable differences in stomata shape between populations that were associated with differences in soil water availability (Mitton and Duran 2004; Mitton et al. 1998), suggesting that some populations, and even individuals within a population, are likely better able to persist and recover following projected hotter droughts.

Despite the projected future increase in suitable climate space in the Front Range due to climate change, in the absence of human intervention (i.e., assisted migration), twoneedle pinyon will likely be unable to take advantage of this space by rapidly shifting its range. Its ability to migrate at the pace of changing climatic suitability is low due to its low seed viability after one year, its poor seed dispersal ability, and its slow rates of recovery following disturbances (Meeuwig and Bassett 1983; Redmond et al. 2013, 2015). Indeed, Minott and Kolb (2020) found no evidence of recent upward twoneedle pinyon migration into adjacent ponderosa pine forests in northern Arizona.

## Ponderosa Pine (*Pinus ponderosa* var. *scopulorum*)

**Climate change vulnerability rating:** moderate

**Confidence in climate change vulnerability rating:** moderate information with high agreement

Ponderosa pine in the Front Range is expected to be moderately vulnerable to climate change. All four future climate scenarios indicate that temperatures will increase, which will likely decrease ponderosa pine reproduction, survival, and growth across its current range, particularly in lower-elevation areas. Reproduction, survival, and growth of ponderosa pine will likely be most compromised for the Hot and Very Hot and Dry scenarios, where increases in temperature are not coupled with notable increases in precipitation. Moreover, all four scenarios are likely to interact with disturbances, including past land management, wildfire, and mountain pine beetle outbreaks, to exacerbate the adverse effects of climate change on ponderosa pine. This is particularly true for wildfire, the extent and severity of which already bear a clear mark of a changing climate. That said, several factors may help ameliorate adverse climate change effects. Ponderosa pine can modify some aspects of its morphology, phenology, and physiology in response to climatic changes. Populations within the Front Range are broadly distributed and well-connected, which may create some opportunity for latitudinal and upslope range shifts, particularly where climate change and climate change × disturbance interactions reduce the abundance of other preexisting species. Populations are also fairly genetically diverse, which may allow for evolutionary adaptation.

### *Habitat*

The Rocky Mountain variety of ponderosa pine is a prominent tree species in forests of the interior western United States, including in the Front Range. The core of its range extends from Idaho and Montana, through Wyoming, Colorado, Utah, and Nevada, and into Arizona and New Mexico (Little 1971; NRCS 2020; Oliver and Ryker 1990). Ponderosa pine populations also grow outside this core range, in South Dakota, Nebraska, and elsewhere (Little 1971; NRCS 2020; Oliver and Ryker 1990). Ponderosa pine occurs along the entire length of the Front Range from north to south, but it is largely restricted to the eastern side of the Continental Divide from west to east (ARP 2019; Little 1971; NRCS 2020; PSICC 2019). It dominates or co-dominates 0.9 million ac (0.4 million ha) of forest managed by the PSI-AR, as well as other forested acres in the Front Range that are managed by private, county, state, and other Federal entities (ARP 2019; PSICC 2019).

The ideal ponderosa pine habitat is dry and warm relative to that of other tree species in the region. Long-term (1981 to 2010) mean annual precipitation and temperature for the PSI-AR ponderosa pine zone generally range from around 13 to 27 in (34 to 68 cm) and from around 38 to 48 °F (3 to 9 °C), respectively (ARP 2019; PRISM 2020; PSICC

2019); elevations in this zone range from around 6,700 to 9,600 ft (2,000 to 2,900 m) (ARP 2019; PSICC 2019; USGS 2020). Ponderosa pine also extends into drier, warmer, and lower-elevation locales on other lands closer to the Front Range urban corridor, such as Lory State Park just west of Fort Collins (Peet 1981). Ponderosa pine occurs on a variety of soil types in the Front Range, including those that are poorly developed with limited organic matter as well as those that are well-developed with moderate amounts of organic matter (Veblen and Donnegan 2005).

In the Front Range, ponderosa pine is one of the most common tree species in montane forests (table 1; figs. 1, 3). In xeric areas, such as at low elevations or on south-facing slopes, ponderosa pine commonly occurs either in pure stands or in stands mixed with Rocky Mountain juniper and/or Douglas-fir (ARP 2019; Peet 1981; PSICC 2019). Understory communities in these stands are typically diverse and frequently include prairie sagewort (*Artemisia frigida*), blue grama (*Bouteloua gracilis*), and alderleaf mountain mahogany (*Cercocarpus montanus*) (Fornwalt et al. 2009; Keith et al. 2010; Peet 1981). In mesic areas, such as at high elevations or on north-facing slopes, ponderosa pine commonly grows in stands with Douglas-fir, lodgepole pine, quaking aspen, blue spruce (*Picea pungens*), and (on the PSI) white fir (*Abies concolor*) (ARP 2019; Peet 1981; PSICC 2019). Common understory associates in mesic areas include kinnikinnick (*Arctostaphylos uva-ursi*), Virginia strawberry (*Fragaria virginiana*), and common juniper (*Juniperus communis*), among many others (Fornwalt et al. 2009; Keith et al. 2010; Peet 1981). Ponderosa pine tends to be a climax species in xeric areas and a seral species in mesic areas (Oliver and Ryker 1990).

### *Ecology*

#### *Reproductive Ecology*

Ponderosa pine is a seed-obligate species. Trees in the southern Rockies can produce seed cones by as early as 28 years of age, and by 52 years of age on average (Rodman et al. 2021). Seed production takes more than 2 full years, beginning with seed cone initiation in the summer of the first year, continuing with pollination in the spring of the second year, and ending with seed ripening and dispersal in the fall of the third year (Owens and Blake 1985). Seed production is highly episodic. In the Front Range, trees produce good crops of viable seeds one to several times a decade; few viable seeds are produced in intervening years (Rodman et al. 2020b; Shepperd et al. 2006). A clear and consistent relationship between seed production and climate has not been found for ponderosa pine populations across the Front Range, although above-average moisture availability during the year of seed cone initiation appears to be important (Mooney et al. 2011). Seeds mostly disperse within two tree heights of parent trees (Barrett 1966; McDonald 1980; Oliver and Ryker 1990). Seed predators such as birds and small mammals can greatly reduce the number of viable seeds reaching the soil seedbank (Krannitz and Duralia 2004; Shepperd et al. 2006). Seeds in the soil seedbank remain viable for only a couple years (Bai et al. 2004).

### *Ecology of Seedlings, Saplings, and Mature Trees*

Ponderosa pine is very drought tolerant. Niinemets and Valladares (2006) assigned ponderosa pine a mean drought tolerance score of 4.3 out of 5.0, a score higher than the one assigned to all of its common tree associates except Rocky Mountain juniper and limber pine. Nonetheless, ponderosa pine can be affected by drought. Germination studies show that ponderosa pine seedling emergence is negatively impacted by high temperatures and low moisture availability (Petrie et al. 2016). Dendrochronological studies likewise show that fewer seedlings emerge during drought years than during cool, wet years (League and Veblen 2006; Rother and Veblen 2017). Additionally, mature trees tend to produce less woody growth in drought years than in cool, wet years (McCullough et al. 2017). Indeed, in severe drought years, such as 1851, 1880, and 2002 in the Front Range, mature trees may not produce woody growth at all. Multiple consecutive years of drought can exacerbate growth declines and even cause mortality (Peltier and Ogle 2019).

In the Front Range, ponderosa pine historically occurred in spatially heterogeneous, yet generally open forests, and correspondingly, it tends to establish and grow best in open forest environments (Battaglia et al. 2018; Malone et al. 2018a; Schubert 1971). While ponderosa pine can benefit from some shade, particularly in the seedling stage, it does not tolerate heavy shade well. Niinemets and Valladares (2006) gave ponderosa pine a shade tolerance score of 1.6 out of 5.0; they consider Rocky Mountain juniper, limber pine, lodgepole pine, and aspen to be less shade-tolerant associates, and Douglas-fir to be more shade-tolerant.

Ponderosa pine is fairly fire-tolerant, making it well-adapted to survive the relatively frequent, low- to mixed-severity wildfires that historically regulated montane Front Range forests (Brown et al. 1999, 2015; Sherriff and Veblen 2007). That said, its fire tolerance is dependent on life stage. Even low-severity fire can result in high levels of mortality for seedlings; flame lengths of only 2 in (5 cm) were sufficient to kill most seedlings under 24 in (60 cm) tall during a prescribed fire in South Dakota, for example (Battaglia et al. 2009). As trees mature, their lower branches self-prune and they develop thick bark, an open crown architecture, thick bud scales, and deep roots, which together increase their ability to survive fire (Fornwalt et al. 2018; Stevens et al. 2020). Ponderosa pine can survive a considerable amount of crown loss due to fire, although it can rarely survive complete crown loss such as occurs from high-severity fire (Sieg et al. 2006).

Ponderosa pine is also well-adapted to regenerate after low- to mixed-severity wildfires. Such fires leave behind some surviving mature ponderosa pine trees to serve as necessary seed sources (Fornwalt et al. 2018; Malone et al. 2018a; Rodman et al. 2020b). But by killing smaller ponderosa pine trees and/or trees of less fire-tolerant associates, these fires also foster the open forest environment that promotes seedling establishment and growth (Fornwalt et al. 2018; Malone et al. 2018a; Rodman et al. 2020b).

Ponderosa pine can be affected by a variety of insects and diseases, of which the most damaging in the Front Range is the mountain pine beetle (*Dendroctonus ponderosae*). This native beetle can kill trees by mass attack, with large and/or stressed trees preferentially targeted (McCambridge et al. 1982; Negrón and Popp 2004). It can cause considerable mortality during epidemics, which can be tied to periods of drought (Bentz et al. 2010). For more information on this and other insects and diseases of ponderosa pine, please see Chapter 8 (Negrón 2024, this report).

### *Potential Direct Impacts of Climate Change*

Bioclimatic envelope modeling done by Crookston (2009) suggests that ponderosa pine will probably experience a net loss of suitable climate space in the Front Range under a changing climate. Model results indicated that 3.0 million ac (1.2 million ha) are currently climatically suitable for ponderosa pine (box 1; table 2; fig. 9). However, under a future climate that is fairly analogous to the Hot climate scenario, model results predicted that 1.3 million of these acres (0.5 million ha) will no longer be suitable by 2060, and that suitability will be threatened for an additional 0.8 million acres (0.3 million ha). Model results also predicted that 0.9 million previously unsuitable acres (0.4 million ha) will become suitable. Areas where suitable climate was predicted to be lost generally occurred at lower elevations, while areas where suitable climate was predicted to be gained generally occurred at higher elevations.

Bioclimatic envelope modeling done by Gray and Hamann (2013) and Rehfeldt et al. (2014) also indicates that the suitable climate space of ponderosa pine will shift to higher elevations due to climate change. For example, Gray and Hamann (2013) predicted that in the U.S. Rockies, the suitable climate space for ponderosa pine in 2050 will shift upward in elevation by nearly 1,000 ft (294 m) relative to that of the 1961 to 1990 reference period. Because the authors of both studies used GCM ensembles, their future climate may best approximate our most middle-of-the-road future climate scenario, the Hot scenario.

A field-based experiment by Rother et al. (2015) suggests that the Hot future climate scenario will negatively impact the survival and height growth of ponderosa pine seedlings, at least in open areas near lower treeline. Working in Boulder County in 2012 and 2013, the authors used open-top chambers to warm the growing season air temperature around planted seedlings by about 2.7 °F (1.5 °C). They found that the warming treatment decreased both survival and height growth. For example, in 2012, median survival was around 40 percent for the warming treatment and around 90 percent for the control treatment, and in 2013, median survival was around 70 percent for the warming treatment and 100 percent for the control treatment.

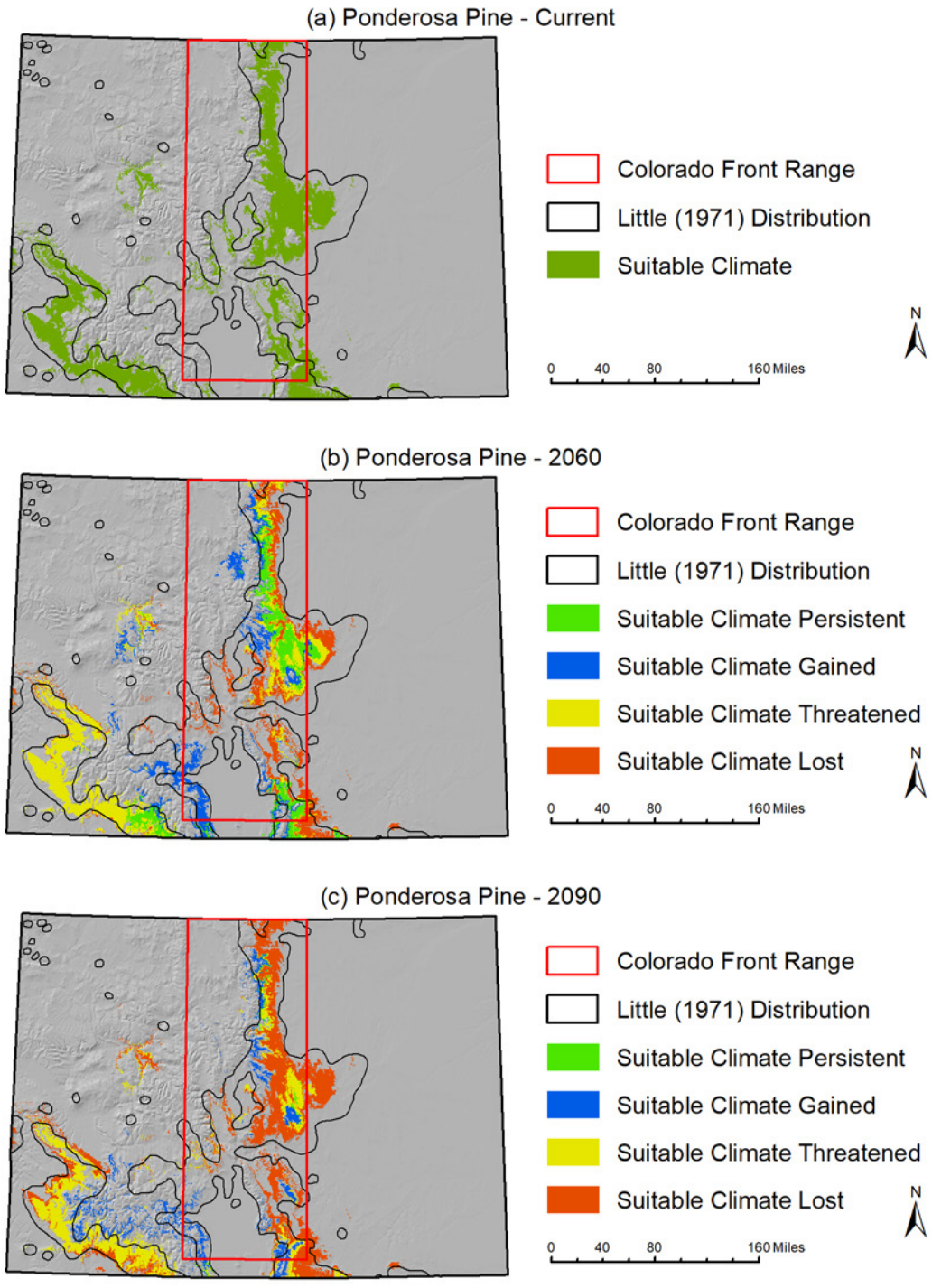



**Figure 9a-c—**The current and potential future suitable climate space of ponderosa pine (Crookston 2009). Panel (a) depicts areas in Colorado where the current climate is suitable for the species. Panels (b) and (c) depict areas in Colorado where suitable climate in the future is predicted to be either lost, threatened, persistent, or gained under the HADCM3-A2 general circulation model (GCM), a GCM that crosswalks relatively well to the one representing our Hot future climate scenario. See box 1 for more information about how current and potential future climate suitability were determined. For all panels, the map of Little (1971) is used to represent the general current distribution of the species.

Relative to the Hot future climate scenario, the Warm and Wet scenario will probably have less of an adverse impact on ponderosa pine owing to cooler, wetter conditions (Rangwala 2024, this report). The experiment by Rother et al. (2015) also supports this notion. When the authors coupled the warming treatment with a watering treatment, they found that the declines in survival and height growth were less severe than the declines for the warming treatment alone. Meanwhile, the Very Hot and Dry scenario will probably have a greater adverse impact on ponderosa pine than the Hot scenario. The Very Hot and Wet scenario may have an impact comparable to the Hot scenario if the effects of higher temperatures are offset by the effects of greater precipitation.

### *Potential Indirect Impacts of Climate Change*

#### *Past Land Management*

Overly dense stands are currently widespread throughout the Front Range ponderosa pine zone due to past land management, particularly unregulated logging and livestock grazing from the 1850s to the 1900s and fire suppression from the 1900s to present (fig. 10a-b; Battaglia et al. 2018; Brown et al. 2015; Kaufmann et al. 2001). These activities allowed for substantial tree recruitment, particularly of ponderosa pine's more shade-tolerant and fire-intolerant associate, Douglas-fir (Battaglia et al. 2018; Brown et al. 2015). Lower-elevation stands now have basal areas that are 179 percent higher than they were in the mid-1800s, while higher-elevation stands now have basal areas that are 139 percent higher (Battaglia et al. 2018). Overly dense stand conditions can decrease the vigor of ponderosa pine (Bottero et al. 2017; Bradford et al. 2022); decreased vigor may in turn predispose it to higher mortality under warmer and drier conditions, such as would be encountered under the Hot and Very Hot and Dry future climate scenarios, and probably under the Very Hot and Wet scenario as well. For example, a west-wide study found that as climatic conditions became warmer and drier, the rate of ponderosa pine mortality increased more dramatically for high basal area stands than for low basal area stands (Bradford et al. 2022). Front Range stands were particularly sensitive to this phenomenon (Bradford et al. 2022).

#### *Wildfire*

Climate change will likely interact with wildfire through multiple mechanisms to reduce the abundance and distribution of ponderosa pine in the Front Range. One mechanism is by driving increases in the total area experiencing tree-killing, high-severity burning (fig. 11). Indeed, dramatic increases in total high-severity area have occurred since the 1990s, and while uncharacteristically dense forest conditions are thought to be contributing to increases, so too is a warmer, drier climate (Chapman et al. 2020; Coop et al. 2022; Parks et al. 2018; Picotte et al. 2016). For example, the Hayman Fire burned with high severity across approximately 77,000 ac (31,000 ha) of predominantly ponderosa pine forest, and occurred during the most severe drought in decades (Chapman et al. 2020; Graham 2003). Continued climate change in upcoming decades will likely further exacerbate total high-severity area, with the area likely greatest under the Very Hot and Dry scenario (Coop et al. 2022; Heidari et al. 2021; Rangwala 2024, this report; Rocca et al. 2014).

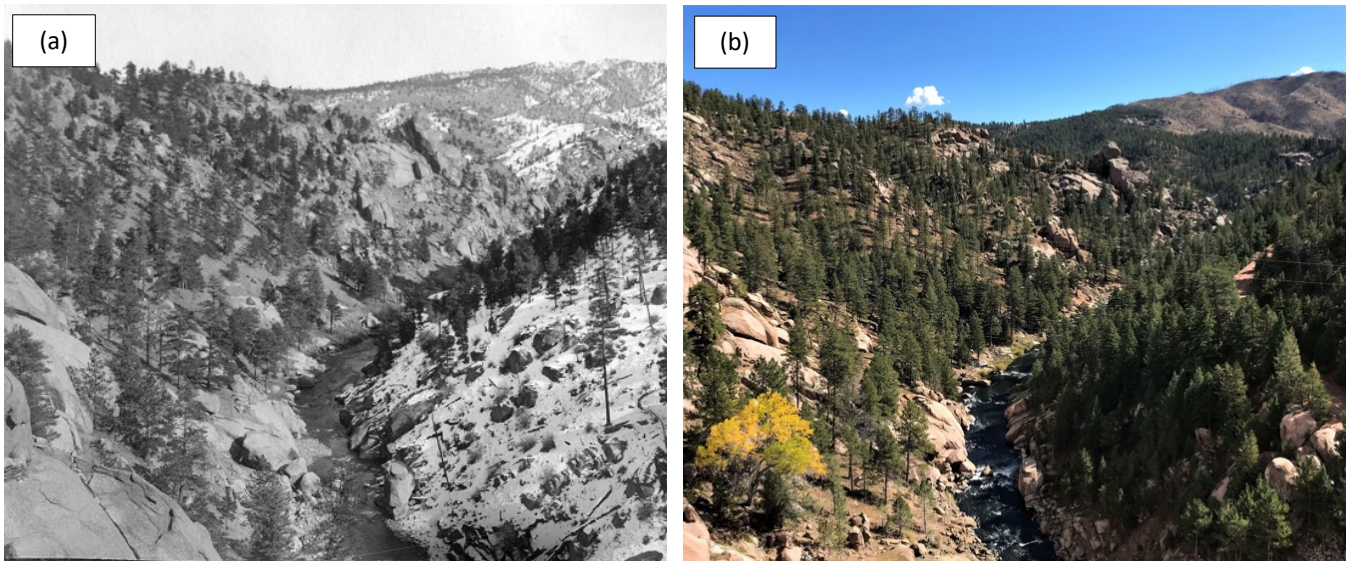



**Figure 10a-b—**Paired photographs demonstrating montane forest conditions along the South Platte River on the Pike National Forest in (a) 1903 and (b) 2022. In general, historical montane forests across the Front Range were considerably less dense and had proportionately more ponderosa pine and less Douglas-fir than current forests (Battaglia et al. 2018; Brown et al. 2015; Kaufmann et al. 2001). Uncharacteristically dense forest conditions can predispose trees to mortality under a changing climate through several mechanisms, including wildfire, as seen in the background of (b) (Coop et al. 2022; Parks et al. 2018; Rocca et al. 2014). Courtesy photo (a) by Denver Water; USDA Forest Service photo (b) by Paula Fornwalt.

**Figure 11—**A portion of a large treeless patch created by the 2002 Hayman Fire on the Pike National Forest. Driven by severe drought and dense stand conditions, this fire burned more than 129,000 ac (52,000 ha) of montane forest dominated by ponderosa pine and Douglas-fir (Chapman et al. 2020; Graham 2003). Courtesy photo by Matt Cooney, Colorado College, used with permission.

Climate-driven increases in the contiguous area of high-severity burning, or high-severity patch area, will also likely negatively impact ponderosa pine by constraining its ability to regenerate. High-severity patch area is an important metric because ponderosa pine is dependent on seeds dispersed from surviving trees to regenerate, and these seeds generally do not disperse long distances (Barrett 1966; McDonald 1980; Oliver and Ryker 1990). Chambers et al. (2016) identified 164 ft (50 m) from surviving trees as a critical threshold distance for Front Range ponderosa pine, with areas beyond it generally having very little postfire regeneration. Rother and Veblen (2016) and Rodman et al. (2020b) found similar patterns. While high-severity burning was a component of the historical fire regime in Front Range forests dominated or co-dominated by ponderosa pine, high-severity patches were not thought to be greater than 124 to 247 ac (50 to 100 ha), and so surviving trees were generally in close proximity (Fornwalt et al. 2016; Graham 2003; Sherriff et al. 2014). However, as with total high-severity area, high-severity patch area appears to have already increased in recent decades, and patches larger than 247 ac are now commonly created (Chapman et al. 2020; Coop et al. 2022). Referencing back to the Hayman Fire, for example, more than 60 percent of the total high-severity area was in patches over 247 ac in size (Chambers et al. 2016). Uncharacteristically large high-severity patches will probably continue to be created under all future climate scenarios, but especially under the Very Hot and Dry scenario (Heidari et al. 2021; Rangwala 2024, this report).

Assuming that ponderosa pine's ability to regenerate is not constrained by seed dispersal, a third mechanism through which climate change × wildfire interactions will likely adversely impact this species is by creating climatic conditions that are unfavorable for seedling establishment. Chambers et al. (2016) found that elevation was a strong driver of postfire ponderosa pine regeneration density, with higher elevations (where climate tends to be cooler and wetter) having higher densities than lower elevations (where climate tends to be warmer and drier). These results suggest that a warmer and drier future climate will likely constrain tree establishment across the current range of ponderosa pine, although upslope opportunities outside the current range may be created. Meanwhile, Rodman et al. (2020a) found that climatic water deficit, a metric that integrates climate and topography to provide an indication of water stress, was a strong predictor of postfire ponderosa pine regeneration density in recent wildfires across the southern Rocky Mountains. Moreover, through the use of an ensemble of GCMs, they found that future increases in climatic water deficit would drive declines in postfire regeneration density across much of the species' current range, and that declines would be greater under more extreme emissions scenarios than under less extreme emissions scenarios.

### *Insects and Diseases*

Interactions between climate change and insects, particularly mountain pine beetle, will likely negatively impact ponderosa pine's abundance. As with other climate change × disturbance interactions, negative impacts are already thought to have occurred. A recent epidemic in the northern Front Range killed ponderosa pine trees across thousands of acres (Chapman et al. 2012; Meddens and Hicke 2014; West et al. 2014). The epidemic began in higher-elevation lodgepole pine forests in the late 1990s and grew rapidly due, at least in part, to a severe regional drought that stressed trees and reduced the mortality of overwintering beetles (Chapman et al. 2012; Negrón and Cain 2019). The epidemic subsequently transitioned into lower-elevation ponderosa pine forests (Chapman et al. 2012; Mitton and Ferrenberg 2012; West et al. 2014). It is likely that mountain pine beetle epidemics will continue to impact ponderosa pine under all four future climate scenarios in the near-term; however, over longer time frames, climate change may cause conditions to be outside the beetle's climatic niche (Sidder et al. 2016). Moreover, while beetle-caused canopy openings may create opportunities for seedling establishment, these opportunities may be increasingly difficult to capitalize on under the future climate scenarios (Rother et al. 2015).

### *Capacity to Adapt to Climate Change*

The work of Carroll et al. (2017) suggests that ponderosa pine trees at mid elevations may be able to tolerate, or even benefit from, a warmer climate in situ by modifying some aspects of their morphology, phenology, and physiology. These researchers implemented an experiment in the northern Front Range, wherein ponderosa pine seedlings were grown from seeds collected at an intermediate-temperature site in the middle of the species' local elevational range and then planted at a low-temperature, an intermediate-temperature, and a high-temperature site. They found that ponderosa pine seedlings put on larger needles at the high-temperature site than at the intermediate- and low-temperature site, and that they burst their buds earlier at the high- and intermediate-temperature site than at the low-temperature site; together these traits may enable seedlings to maintain or even increase growth under warmer conditions. Additionally, these seedlings maintained a constant photosynthetic rate across the sites, suggesting that they may not need to close stomates to reduce water loss due to warming.

Genetics research suggests that ponderosa pine may have some ability to adapt evolutionarily to climate change. Relative to the isolated, disjunct populations of ponderosa pine found elsewhere in the west, the fairly well-connected Front Range populations have high genetic diversity within them (Potter et al. 2015). This high genetic diversity should enhance the capacity of ponderosa pine to adapt to a changing climate. However, Front Range populations are somewhat inbred, suggesting somewhat limited gene flow between them despite their connectedness, which may constrain

adaptive capacity (Potter et al. 2015). Moreover, the capacity of ponderosa pine to adapt may be constrained by its irregular seed production and by its relatively long generation time (Oliver and Ryker 1990; Rodman et al. 2020b, 2021; Shepperd et al. 2006).

Several aspects of ponderosa pine's current distribution could potentially enable it to migrate in response to climate change. Its range currently extends well beyond the Front Range latitudinally, not only to the south but also to the north, suggesting that any latitudinal migration the species undergoes will probably not result in range contractions in the Front Range in the foreseeable future (Oliver and Ryker 1990). Opportunities for upslope migration, into areas where it is not currently found, also exist in the Front Range. For example, while 1.3 million ac (0.5 million ha) that are currently climatically suitable for ponderosa pine are predicted to be lost by 2060 under a future climate similar to the Hot scenario, 0.9 million ac (0.4 million ha) are predicted to be gained (box 1; table 3; fig. 9; Crookston 2009). These predicted gains typically occurred in higher-elevation locales where subalpine tree species dominate, at least at the moment. Moreover, because forests currently dominated or co-dominated by ponderosa pine are fairly well-connected in the Front Range, there are few geographic barriers that would impede latitudinal or upslope migration. However, migration may not occur rapidly enough to keep pace with climate change because good seed crops are somewhat infrequently produced, seeds do not disperse long distances, and seedlings require two or more decades to grow into reproductively mature trees (Barrett 1966; McDonald 1980; Rodman et al. 2021; Shepperd et al. 2006).

## Douglas-fir (*Pseudotsuga menziesii* var. *glauca*)

**Climate change vulnerability rating:** moderate

**Confidence in climate change vulnerability rating:** moderate information with high agreement

Climate change is expected to have a negative impact on Douglas-fir in the Front Range, through both direct and indirect mechanisms. Douglas-fir reproduction, survival, and growth can be adversely affected by increases in temperature and decreases in available moisture, making the species vulnerable to all four future climate scenarios, and especially vulnerable to the Hot and Very Hot and Dry scenarios. Douglas-fir's primary disturbance agents—wildfire, Douglas-fir beetle, western spruce budworm, and Douglas-fir tussock moth—can also be promoted by warmer and drier conditions, suggesting that they will drive further increases in Douglas-fir vulnerability. That said, Douglas-fir on the Front Range appears to have some opportunity for upslope migration and evolutionary adaptation, which may buffer some populations against future changes in climate.

### *Habitat*

The Rocky Mountain variety of Douglas-fir is widely distributed throughout interior western North America. Its core range extends from British Columbia and Alberta south to Arizona and New Mexico, and from Oregon east to Wyoming, Colorado, and New Mexico (Hermann and Lavender 1990; Little 1971; NRCS 2020). Small, often discontinuous, populations also occur outside this core range, including in Washington, Montana, Texas, and northern Mexico (Hermann and Lavender 1990; Little 1971; NRCS 2020). Douglas-fir is found throughout the Front Range, although it is much more prevalent east of the Continental Divide than west of it (ARP 2019; Little 1971; NRCS 2020; PSICC 2019). It is a major constituent of 1.0 million ac (0.4 million ha) of forest on the PSI-AR alone (ARP 2019; PSICC 2019).

In the Front Range, Douglas-fir is most commonly found in montane forests, but it also occurs in some subalpine forests (table 1; figs. 1, 3). Douglas-fir rarely grows in pure stands in the Front Range (ARP 2019; PSICC 2019). It typically grows in mixed stands alongside ponderosa pine in more xeric environments, and alongside lodgepole pine, limber pine, aspen, subalpine fir, and/or Engelmann spruce in more mesic environments (ARP 2019; Peet 1981; PSICC 2019). Herbaceous and shrubby understory associates are numerous and often include Ross' sedge (*Carex rossii*), alderleaf mountain mahogany (*Cercocarpus montanus*), and mountain muhly (*Muhlenbergia montana*) in xeric areas and heartleaf arnica (*Arnica cordifolia*), common juniper (*Juniperus communis*), and kinnikinnick (*Arctostaphylos uva-ursi*) in mesic areas (Johnston 1987; Peet 1981). Douglas-fir is best characterized as a climax species in montane forests and a seral species in subalpine forests (Hermann and Lavender 1990).

As suggested by its broad geographic extent, Douglas-fir grows under a wide variety of environmental conditions (Hermann and Lavender 1990). On the PSI-AR National Forests, long-term (1981 to 2010) mean annual precipitation in the Douglas-fir zone ranges from ca. 13 to 29 in (34 to 73 cm), while long-term mean annual temperature ranges from ca. 36 to 46 °F (2 to 8 °C) (ARP 2019; PRISM 2020; PSICC 2019). Elevations in the PSI-AR Douglas-fir zone range from ca. 7,000 to 10,200 ft (2,100 to 3,100 m) (ARP 2019; PSICC 2019; USGS 2020). Closer to the Front Range urban corridor, Douglas-fir extends even lower in elevation, to around 5,500 ft (1,700 m) (Peet 1981). Douglas-fir grows on a variety of soils, but grows best in those that are deep and well-aerated (Hermann and Lavender 1990).

## *Ecology*

### *Reproductive Ecology*

Douglas-fir reproduces solely from seeds. Trees can begin producing seeds as early as 12 to 15 years after establishment (Hermann and Lavender 1990). Seed production is irregular, with heavy crops occurring about every 7 years (Hermann and Lavender 1990). Climatic controls on seed production are unclear in the Front Range, but at the continental scale, larger trees in warmer, drier locations appear to be the most fecund (Clark et al. 2021). The small seeds are wind-dispersed, with most falling within 330 ft (100 m) of the source tree, although a proportion of seeds may travel farther (Hermann and Lavender 1990). Seeds entering the soil seedbank probably remain viable for only about a year.

### *Ecology of Seedlings, Saplings, and Mature Trees*

Douglas-fir is moderately drought-tolerant, with a drought tolerance score of 2.6 out of 5.0 (Niinemets and Valladares 2006). Seedlings are especially sensitive to drought, with warm, dry conditions yielding lower levels of germination and establishment than cool, wet conditions (Davis et al. 2019; Foster et al. 2020; Rother and Veblen 2017). Mature trees also grow more slowly under warm, dry conditions than under cool, wet conditions (Restaino et al. 2016).

Douglas-fir tends to grow best in environments with some shade. Seedling establishment, in particular, benefits from shade, especially on warm, dry sites like south-facing slopes (Ryker and Potter 1970). Niinemets and Valladares (2006) assigned Douglas-fir a shade tolerance score of 2.8 out of 5.0, higher than all of the other major Front Range tree species except subalpine fir and Engelmann spruce.

Prior to the 1900s, forests supporting Douglas-fir in the Front Range primarily burned with a mixed-severity wildfire regime, defined by wildfire events that burned with a mosaic of low-, moderate-, and high-severity fire effects at multi-decadal intervals (Brown et al. 1999; Schoennagel et al. 2011; Sherriff and Veblen 2007). Douglas-fir is only moderately tolerant of this regime (Giunta et al. 2016). Douglas-fir seedlings and saplings are commonly killed by even low-severity wildfires due to their low-growing branches, dense crown architecture, and thin bark (Fornwalt et al. 2018; Steinberg

2002). The bark of Douglas-fir becomes thicker with age, rendering mature trees less susceptible to wildfire-caused mortality (Steinberg 2002; Stevens et al. 2020). However, mature Douglas-fir trees are still more susceptible to mortality than those of its most common associate, ponderosa pine (Fornwalt et al. 2018; Steinberg 2002; Stevens et al. 2020). Douglas-fir can regenerate readily after wildfire, including high-severity wildfire, so long as living trees are nearby to serve as seed sources (Malone et al. 2018a; Rodman et al. 2020a,b; Rother and Veblen 2016). Regeneration after wildfire is also enhanced by relatively cool, wet conditions (Chambers et al. 2016; Rodman et al. 2020a,b).

One of the principal biotic disturbance agents of Douglas-fir in the Front Range is the western spruce budworm (*Choristoneura occidentalis*), a moth defoliator that can cause a considerable amount of mortality and decline, especially to seedlings, saplings and other subcanopy trees (Giunta et al. 2016; Hadley and Veblen 1993). The Douglas-fir tussock moth (*Orgyia pseudotsugata*), another moth defoliator, and the Douglas-fir beetle (*Dendroctonus pseudotsugae*), a bark beetle, can also cause damage to this species in the Front Range (Giunta et al. 2016). Western spruce budworm and Douglas-fir tussock moth consume new shoot growth, seeds, and cones; though they rarely cause mortality in large-diameter, canopy dominant individuals, they will often weaken them, leading to slower growth rates and predisposing them to attacks from Douglas-fir beetles (Cole et al. 2022; Hadley and Veblen 1993; Negrón et al. 2014). Douglas-fir beetles also attack trees weakened by drought, competition, fire, or other stressors (Gibson and Negrón 2009; Negrón 1998). For more information on these and other insects and diseases of Douglas-fir, please see Chapter 8 (Negrón 2024, this report).

### *Potential Direct Impacts of Climate Change*

A field study by Restaino et al. (2016) highlights how future increases in vapor pressure deficit, a measure of water stress that integrates temperature and relative humidity, will negatively affect mature Douglas-fir growth in the northern Front Range and across much of the western United States. Historically (1916 to 2006) at the northern Front Range site, vapor pressure deficit exceeded values associated with extremely low growth rates only 10 percent of the time. However, under a changing climate, vapor pressure deficit was predicted to exceed this threshold about 60 percent of the time by the 2040s and about 90 percent of the time by the 2080s. The study used an ensemble of GCMs, making the findings most relatable to the middle-of-the-road Hot future climate scenario.

Two other field studies provide insight into the potential effects of climate change on Douglas-fir seedling survival and growth. Rother et al. (2015) used open-top chambers at a lower-elevation northern Colorado site to increase growing season air temperature around a subset of the planted seedlings by about 2.7 °F (1.5 °C); they also used weekly watering treatments to approximate an upper quartile growing season precipitation regime for a subset of the seedlings. They found that seedling survival was highest for the control (unwarmed and unwatered), intermediate for the warmed and watered seedlings, and lowest for the warmed and unwatered seedlings. They also found that

seedling growth was higher for the control and the warmed and watered seedlings than for the warmed and unwatered seedlings, though differences between the former two groups of seedlings were less apparent. Taken together, these results suggest that the higher temperatures for all four future climate scenarios will result in decreased Douglas-fir seedling survival and growth, particularly for scenarios where higher temperatures are not accompanied by increased precipitation. In a water manipulation field study, Foster et al. (2020) found that soil moisture and warmer temperatures strongly limited Douglas-fir seedling establishment at the upper elevation limit of Douglas-fir's range in northern Colorado, highlighting how increasingly warm and dry conditions may lead to recruitment failure, even at the leading edge of the species' distribution.

Bioclimatic envelope models have predicted a notable change in the suitable climate space of Douglas-fir due to future climate change. Crookston (2009) found that 3.0 million ac (1.2 million ha) were currently considered climatically suitable for Douglas-fir in the Front Range, but that under a climate change scenario akin to the Hot scenario, only 2.5 million ac (1.0 million ha) were predicted to be suitable in 2060 and 0.9 million ac (0.4 million ha) were predicted to be suitable in 2090 (box 1; table 3; fig. 12). Furthermore, 35 percent (2060) and 59 percent (2090) of these future suitable acres were threatened, meaning that their climatic suitability was predicted to be marginal. Areas where suitable climate was predicted to be lost generally occurred at lower elevations, while areas where suitable climate was predicted to be gained generally occurred at higher elevations. Gray and Hamann (2013) and Rehfeldt et al. (2014) also found similar trends with elevation, with the former predicting that by 2050, Douglas-fir populations across the U.S. Rocky Mountains will lag behind their baseline (1961 to 1990) climatic niche by approximately 587 ft (179 m).

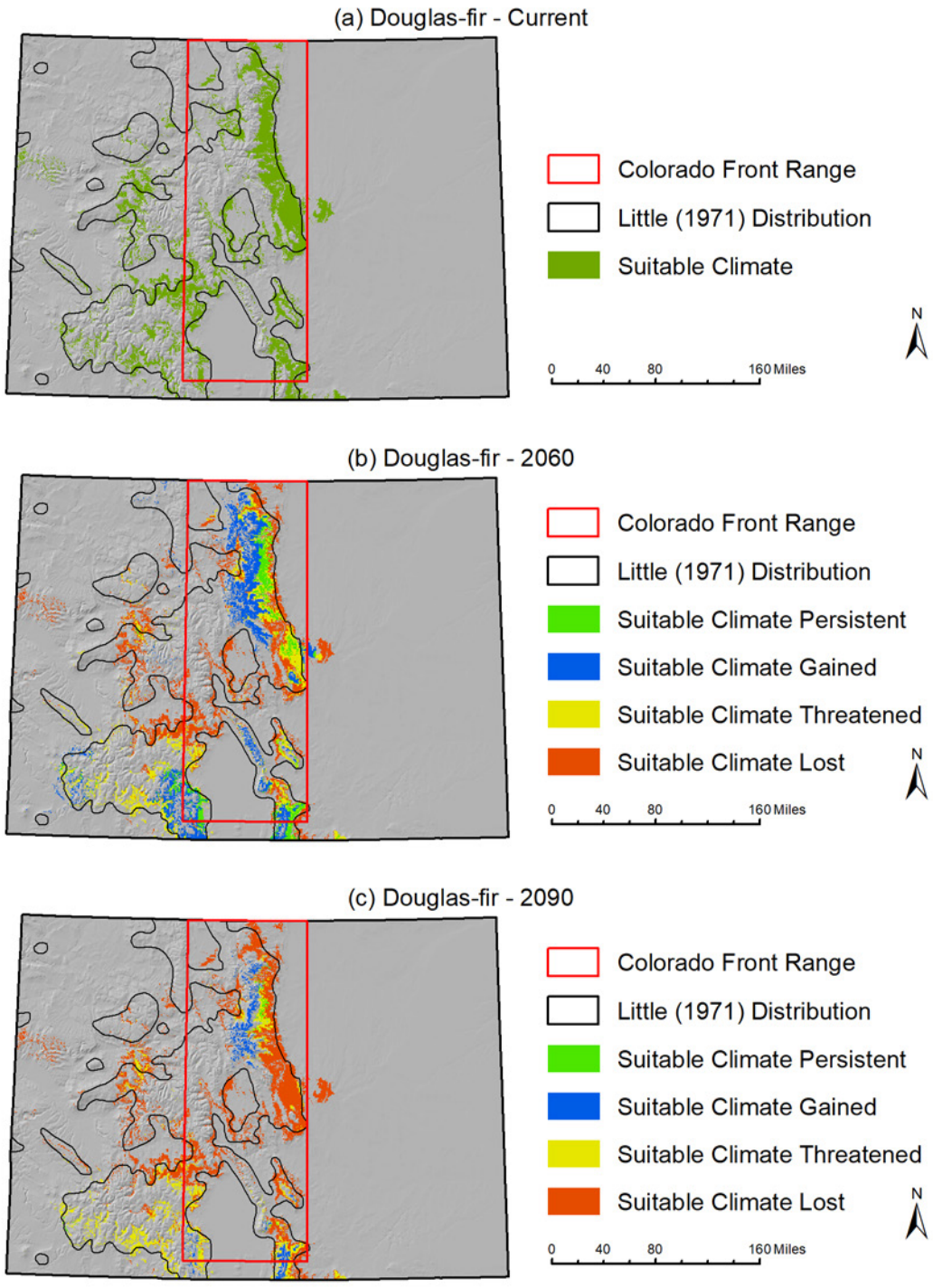



**Figure 12a-c—**The current and potential future suitable climate space of Douglas-fir (Crookston 2009). Panel (a) depicts areas in Colorado where the current climate is suitable for the species. Panels (b) and (c) depict areas in Colorado where suitable climate in the future is predicted to be either lost, threatened, persistent, or gained under the HADCM3-A2 general circulation model (GCM), a GCM that crosswalks relatively well to the one representing our Hot future climate scenario. See box 1 for more information about how current and potential future climate suitability were determined. For all panels, the map of Little (1971) is used to represent the general current distribution of the species.

### *Potential Indirect Impacts of Climate Change*

#### *Past Land Management*

Lower-elevation montane forests supporting Douglas-fir have experienced dramatic increases in tree density since the mid to late 19th century due to past management (fig. 10). Fire exclusion, logging, livestock grazing, and other management activities since Euro-American settlement have disrupted the historical wildfire regime, wherein predominately mixed-severity events occurred every few decades (Brown et al. 1999, 2015; Sherriff and Veblen 2007). This disruption allowed for substantial tree recruitment, particularly of relatively shade-tolerant and fire-intolerant species like Douglas-fir (Battaglia et al. 2018; Brown et al. 2015). Uncharacteristically dense stand conditions may contribute to decreased vigor, which may in turn predispose the species to increased mortality under a warmer future climate (Restaino et al. 2016).

The effects of past management are less clear at higher elevations, such as in the upper montane and lower subalpine zones. Mixed-severity wildfire regimes were also in effect historically, but fire events tended to be less frequent (Schoennagel et al. 2011; Sherriff and Veblen 2007). While many of these higher-elevation forests, particularly those that have not burned for over a century, appear to be uncharacteristically dense and therefore vulnerable to mortality from climate change, the density increases are less dramatic compared to lower montane forests (Battaglia et al. 2018; Brown et al. 2015). For example, Battaglia et al. (2018) reconstructed a 350 percent increase in density for lower montane forests of the Front Range since Euro-American settlement, but only an 82 percent increase in density in upper montane forests.

#### *Wildfire*

Climate change, together with overly dense forest conditions, has driven large increases in the annual area burned in the Front Range montane zone (table 2; fig. 11; Chapman et al. 2020; Coop et al. 2022; Parks et al. 2018; Picotte et al. 2016). This has, in turn, driven large increases in the amount of Douglas-fir mortality. Douglas-fir was a major component of forests impacted by the 2002 Hayman Fire, for example, which burned approximately 129,000 ac (52,000 ha) during a period of extreme drought (Chapman et al. 2020; Fornwalt et al. 2018; Graham 2003). Douglas-fir was also a major component of the forests that were burned by the drought-driven 2012 High Park and 2020 Cameron Peak Fires, among others (Chapman et al. 2020; Coop et al. 2022). Continued increases in the annual area burned and resultant Douglas-fir mortality are expected under all four future climate scenarios, particularly the Very Hot and Dry scenario (Heidari et al. 2021; Rangwala 2024, this report; Rocca et al. 2014).

Climate change has also exacerbated the risk of postfire Douglas-fir regeneration failures, and this risk will likely continue to grow in the future. Main contributors to this risk are not only the amount of high-severity area, but also the contiguity of this area (Davis et al. 2020). Douglas-fir regenerates primarily from seeds produced by nearby

living trees (Hermann and Lavender 1990); however, for recent fires, a considerable proportion of high-severity area is too distant from seed-bearing trees to have a reliable seed source (Chapman et al. 2020; Rodman et al. 2020a). A trend of greater and more contiguous high-severity area is expected to continue under all four future climate change scenarios (Heidari et al 2021; Rangwala 2024, this report). Another contributor to the risk of Douglas-fir regeneration failure after wildfire is the occurrence of suitable climatic conditions. For example, Rodman et al. (2020a) forecasted future climatic suitability for postfire regeneration across the southern Rockies using an ensemble GCM approach (likely corresponding best to the Hot future climate scenario), finding strong declines in Douglas-fir climatic suitability through the mid and end of the 21st century. Similar analyses using the other three future climate scenarios would likely also show declines in climatic suitability (Rangwala 2024, this report).

### ***Insects and Diseases***

Stands with abundant Douglas-fir can sustain irruptive populations of insects such as Douglas-fir beetle, western spruce budworm, and Douglas-fir tussock moth. All four future climate scenarios will result in warmer temperatures, which will probably allow Douglas-fir beetle to expand. In the Colorado Front Range, the beetle's activity builds throughout the early growing season, peaking in mid to late June (Negrón et al. 2011). Temperatures reaching to 60 °F (15.5 °C) earlier in spring and lasting longer into the fall would extend its activity period and potentially drive spikes in its population (Bentz et al. 2010). The defoliator western spruce budworm is also expected to increase under the warmer conditions predicted by the future climate scenarios (Régnière and Nealis 2019). Moreover, warmer and drier summers, as well as dense stand conditions and wildland fires, stress Douglas-fir, increasing its susceptibility to the three insects alone and in combination (Gibson and Negrón 2009; Negrón 1998, 2014). For example, Douglas-fir beetle populations commonly increase in stressed trees during defoliation events; eventually defoliators can kill smaller-diameter and understory trees while Douglas-fir beetles can kill the larger-diameter trees (Negrón et al. 2014).

However, mountain pine beetle outbreaks that kill co-occurring lodgepole pine trees may provide Douglas-fir with opportunities for growth and expansion. Renwick et al. (2016) conducted an observational study in beetle-impacted lodgepole pine stands of Rocky Mountain National Park, including in some lower-elevation stands that also contained Douglas-fir. They found that in these stands, the decline in lodgepole pine basal area was partially offset by an increase in Douglas-fir basal area. They also found that Douglas-fir seedling densities increased, with greater increases in areas of higher mountain pine beetle mortality. Because these increases in basal area and seedling establishment occurred at Douglas-fir's leading edge, the species should be able to maintain them, and possibly even expand them, under a changing climate.

### *Capacity to Adapt to Climate Change*

Despite extensive logging, centuries-old Douglas-fir trees can be found across the Front Range (Fornwalt et al. 2016; Huckaby et al. 2001, 2003; Kaufmann et al. 2000). These trees have persisted through a wide range of historical climate conditions, and may indicate that Douglas-fir has some ability to plastically modify aspects of its morphology, phenology, and/or physiology to tolerate climate variation.

Southern populations of Douglas-fir in the Interior West, such as those in the Front Range, have fairly high genetic diversity among them (Li and Adams 1989). This variation may allow for gene exchange and in turn promote evolutionary adaptation to climate change. That said, southern populations also have relatively limited genetic diversity within populations, which may limit adaptive capacity (Li and Adams 1989). Adaptive capacity may also be limited by Douglas-fir's reproductive ecology, including its irregular seed production, its relatively short seed dispersal distances, and its relatively long generation time (Hermann and Lavender 1990).

Douglas-fir has some potential opportunity to migrate in the Front Range with a changing climate. For example, under a future climate scenario comparable to the Hot scenario, 1.1 million ac (0.4 million ha) of climatically suitable area may be gained by 2060, most of which is above Douglas-fir's current elevational range (Crookston 2009). Because low moisture availability limits Douglas-fir establishment, the Warm and Wet scenario would likely provide Douglas-fir with even more opportunity to migrate, while the Very Hot and Dry scenario would likely provide it with less opportunity (Foster et al. 2020). However, regardless of the future climate scenario, the reproductive ecology of Douglas-fir may not allow migration to keep pace with climatic change (Hermann and Lavender 1990).

## Lodgepole Pine (*Pinus contorta* var. *latifolia*)

**Climate change vulnerability rating:** moderate to high

**Confidence in climate change vulnerability rating:** moderate information with moderate agreement

Lodgepole pine will be moderately to highly vulnerable to climate change by mid-century. Under a middle-of-the-road Hot climate change scenario, the vast majority of the area that is currently climatically suitable for lodgepole pine will no longer be so, with losses concentrated at mid to lower elevations; moreover, gains in climatically suitable area at higher elevations will be small relative to losses. High-severity wildfires have long played an important role in maintaining lodgepole pine in the Front Range, particularly where serotinous trees are present. Climate change driven increases in the frequency of high-severity wildfires may favor lodgepole pine establishment over other tree species, including into upslope areas that have become climatically suitable; however, establishment potential may be diminished in areas where climatic suitability has been lowered. The 1990s to 2000s mountain pine beetle outbreak further complicates predictions of postfire lodgepole establishment, but it is possible that this prior disturbance could restrict establishment by reducing the availability of viable seeds.

### *Habitat*

The Rocky Mountain variety of lodgepole pine is the inland form of the species. It occurs from British Columbia, Alberta, and Saskatchewan in the north to the Utah and Colorado mountains in the south (Little 1971; Lotan and Critchfield 1990; NRCS 2020). Lodgepole pine is widespread in Front Range forests, particularly in the northern counties (ARP 2019; Little 1971; NRCS 2020; PSICC 2019). It is a major component of forests on 1.1 million ac (0.5 million ha) on the PSI-AR National Forests alone (ARP 2019; PSICC 2019).

Lodgepole pine occupies a wide range of environments. In the PSI-AR lodgepole pine zone, long-term (1981 to 2010) mean annual precipitation largely ranges from 16 to 35 in (41 to 88 cm), while long-term mean annual temperature largely ranges from 32 to 42 °F (0 to 6 °C) (ARP 2019; PRISM 2020; PSICC 2019). Precipitation mostly falls as snow. Elevations supporting lodgepole pine on the PSI-AR are typically between 8,100 and 11,100 ft (2,400 to 3,400 m) (ARP 2019; PSICC 2019; USGS 2020). Lodgepole pine grows on a wide variety of soil types, including those that are poorly developed, shallow, and infertile (Lotan and Critchfield 1990).

Lodgepole pine in the Front Range is a keystone member of the subalpine forest vegetation type (table 1; figs. 1, 4). It commonly grows in pure stands (ARP 2019; Peet 1981; PSICC 2019). It also grows alongside ponderosa pine and Douglas-fir in warmer, lower-elevation areas of the upper montane zone, and alongside quaking aspen,

subalpine fir, and Engelmann spruce in cooler, higher-elevation areas of the subalpine zone (ARP 2019; Peet 1981; PSICC 2019). Understory communities can be relatively depauperate in stands containing lodgepole pine, with the shrubs kinnikinnick (*Arctostaphylos uva-ursi*), common juniper (*Juniperus communis*), and blueberry (*Vaccinium* spp.) being some of the most common understory community members (Peet 1981). Lodgepole pine is described as a shade-intolerant seral species that establishes right after stand-replacing disturbances, particularly wildfire; however, it can be a climax or near-climax species where such disturbances are relatively frequent or where other, more shade-tolerant species do not co-occur (Alexander 1974; Huckaby and Moir 1998; Peet 1981).

## *Ecology*

### *Reproductive Ecology*

Lodgepole pine reproduction is dependent on seeds. Trees can begin producing annual seed crops when they are as young as 5 to 10 years of age in open stands, and 15 to 20 years of age in closed stands (Alexander 1974). Large seed crops are generally produced at 1- to 3-year intervals thereafter (Lotan and Critchfield 1990). Individual trees have predominantly either serotinous cones that remain closed after seeds mature and open following exposure to intense sunlight or fire, or nonserotinous cones that open at seed maturity; however, serotiny is not expressed until trees are 30 to 60 years old (Alexander 1974). The proportion of trees with serotinous cones is highly variable across stands in the Rocky Mountains, with greater levels of serotiny potentially favored where lodgepole pine's native stand-replacing fire regime is more frequent (Alexander 1974; Decker and Fink 2015). Serotinous cones are persistent, storing viable seeds in tree crowns for many decades (Alexander 1974). Seeds from both serotinous and nonserotinous cones are primarily dispersed by wind, but some seeds may be dispersed by rodents or birds. Seeds are usually dispersed less than 200 ft (60 m), although strong winds may carry seeds much farther (Alexander 1974). Once seeds are dispersed and enter the soil seedbank, they likely remain viable for only a few years.

### *Ecology of Seedlings, Saplings and Mature Trees*

Lodgepole pine is highly drought-tolerant; with a drought tolerance score of 4.2 out of 5.0, it needs less water than its major tree associates Douglas-fir, quaking aspen, Engelmann spruce and subalpine fir (Niinemets and Valladares 2006). Even so, it can be adversely affected by drought. Young seedlings are shallow-rooted and can be particularly drought-sensitive (Kaufmann and Eckard 1977; Petrie et al. 2016; Shepperd and Noble 1976). Mature trees can also be sensitive (Andrus et al. 2021).

Lodgepole pine is a shade-intolerant species (shade tolerance score of 1.5 out of 5.0; Niinemets and Valladares 2006). Optimal germination and seedling establishment occur in full sunlight, although shading can be beneficial on warm, dry sites (Alexander 1974). Once established, trees grow quickly, with the greatest growth in full sunlight (Alexander 1974).

As previously alluded to, high-severity, stand-replacing wildfires are the major disturbance agent in the Front Range lodgepole pine zone. Such wildfire events, which historically occurred roughly every 150 to 350 years, are often associated with infrequent, extreme regional droughts (Kulakowski and Jarvis 2011; Schoennagel et al. 2011; Sibold and Veblen 2006; Sibold et al. 2006). Stand-replacing wildfires generally spread rapidly through the forest canopy and result in the complete or near-complete mortality of lodgepole pine across large areas (Schoennagel et al. 2004). Although less severe wildfires that burn on the forest floor can also sometimes occur in the lodgepole pine zone, particularly at lower elevations, these fires can also result in significant mortality because lodgepole pine's bark is relatively thin (Schoennagel et al. 2011; Sibold et al. 2006; Stevens et al. 2020). A dense pulse of lodgepole pine trees often establishes and grows rapidly following wildfires, particularly where prefire stands exhibited a high degree of serotiny (Guz et al. 2021; Schoennagel et al. 2011; Sibold et al. 2006).

Lodgepole pine is highly susceptible to infestations by insects and diseases. The most common and damaging insect and disease agent of lodgepole pine is the mountain pine beetle, a native species. Epidemic outbreaks of these beetles, which are commonly driven by drought and warmer-than-average winters, have long caused extensive mortality events in the Colorado Front Range and across the southern Rocky Mountains (Chapman et al. 2012; Jarvis and Kulakowski 2015; Negrón and Huckaby 2020). Trees that are large, old, or stressed are more likely to be killed (Klutsch et al. 2009; Kulakowski and Jarvis 2013; Negrón and Huckaby 2020). While mountain pine beetle outbreaks can trigger a pulse of regeneration, they tend not to trigger as dense of a pulse as fire or harvesting do because they do not dramatically increase light availability in the understory, expose mineral soil, or open most serotinous cones (Pelz et al. 2018; Rhoades et al. 2020a). For more information about insects and diseases affecting lodgepole pine, please see Negrón 2024, this report.

### *Potential Direct Impacts of Climate Change*

Climate change may directly lead to increased mortality of mature lodgepole pine trees in the Front Range (Andrus et al. 2021; Smith et al. 2015). Indeed, recent (1982 to 2019) increases in annualized mortality rates of lodgepole pine have already been documented at Niwot Ridge in the northern Front Range, albeit nonsignificantly (Andrus et al. 2021). Higher mortality rates were correlated with higher frequencies of extremely warm (90th percentile) summer days, higher summer climatic water deficits, and cooler phases (i.e., La Niña events) of the El Niño–Southern Oscillation (Andrus et al. 2021). Looking forward, it is likely that all four future climate change scenarios would spur additional increases in mortality rates, but also that rates would be lowest under the Warm and Wet scenario and highest under the Very Hot and Dry scenario.

Bioclimatic envelope models provide insight into how shifts in suitable climate space may affect lodgepole pine's distribution. Bioclimatic envelope models developed by Crookston (2009) suggest that lodgepole pine will likely experience a considerable loss of suitable climate space by mid-century in the Front Range (box 1; table 3; fig. 13). Results indicated that 5.6 million ac (2.3 million ha) are currently climatically suitable for lodgepole pine. However, under a future climate that is fairly analogous to the Hot climate scenario, model results predicted that around 79 percent of these acres will no longer be suitable in 2060, and that suitability will be threatened for an additional 18 percent. Model results also predicted that 0.6 million previously unsuitable acres (0.2 million ha) will become suitable. Additionally, bioclimatic envelope models developed by Gray and Hamann (2013) estimated that today's lodgepole pine populations across the U.S. Rocky Mountains already lag behind their baseline (1961 to 1990) suitable climate space by approximately 105 mi (168 km) in latitude and 245 feet (74 m) in elevation. The models further predicted that, relative to the baseline suitable climate space, the suitable climate space for lodgepole pine in 2050 will shift upward by 335 mi (542 km) in latitude or 780 ft (238 m) in elevation.

A warming and watering experiment conducted by Conlisk et al. (2018) at Niwot Ridge showed that temperature increases negatively impacted first-year lodgepole pine seedling establishment, but that this impact was partially to fully alleviated by moisture increases that compensated for warming-induced evaporative losses. Interestingly, this pattern held for all sites (forest, treeline, and alpine), as well as for all seed provenances (low-elevation and high-elevation). This pattern also held through time, although seedlings became less sensitive to the effects of warmer and/or wetter conditions as they approached 3 years of age.

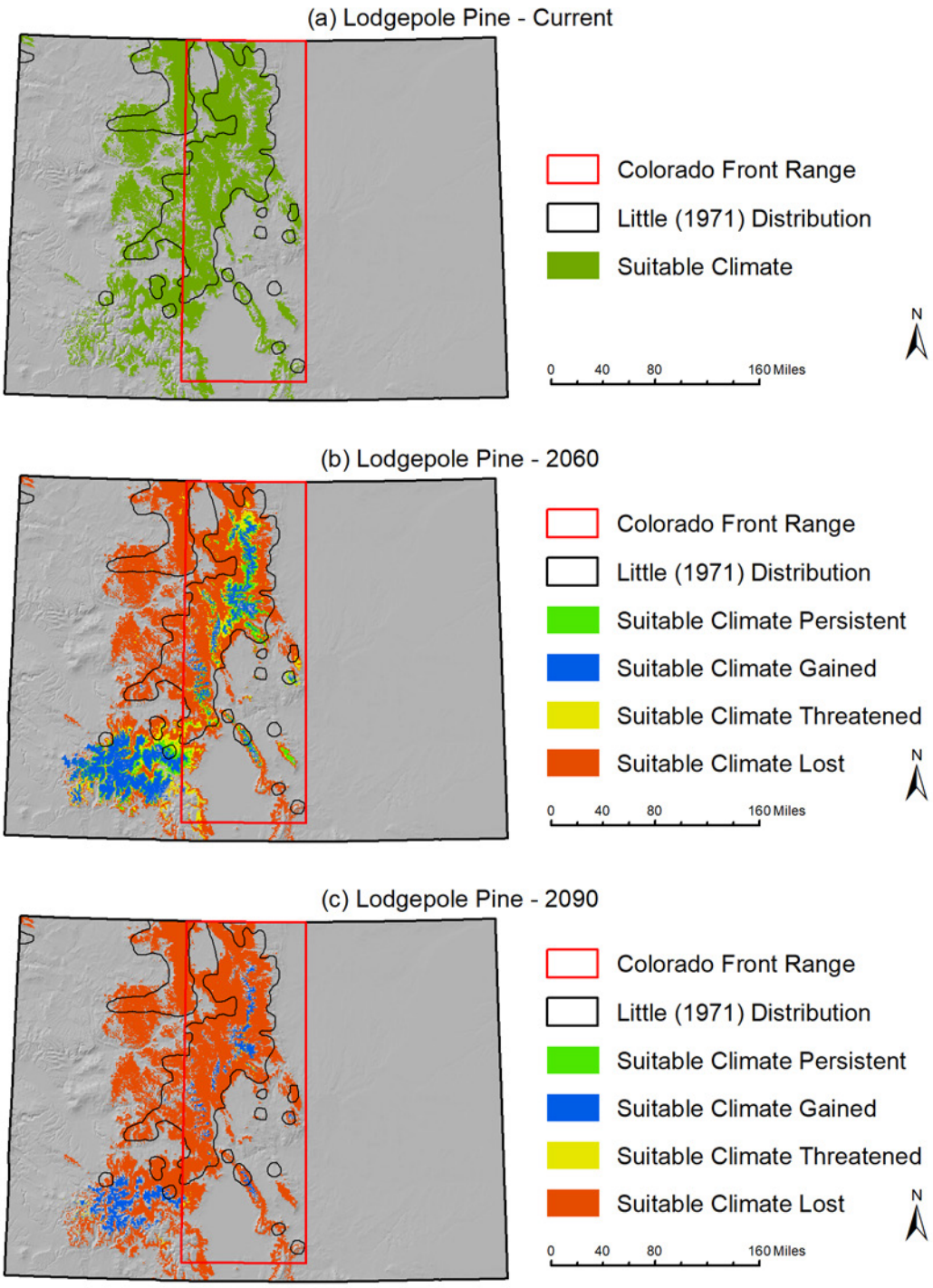



**Figure 13a-c—**The current and potential future suitable climate space of lodgepole pine (Crookston 2009). Panel (a) depicts areas in Colorado where the current climate is suitable for the species. Panels (b) and (c) depict areas in Colorado where suitable climate in the future is predicted to be either lost, threatened, persistent, or gained under the HADCM3-A2 general circulation model (GCM), a GCM that crosswalks relatively well to the one representing our Hot future climate scenario. See box 1 for more information about how current and potential future climate suitability were determined. For all panels, the map of Little (1971) is used to represent the general current distribution of the species.

### *Potential Indirect Impacts of Climate Change*
### *Insects and Diseases*

The mountain pine beetle outbreak that unfolded across Colorado from the 1990s to 2000s affected millions of acres of forest in the lodgepole pine zone, killing hundreds of millions of trees (fig. 14; Chapman et al. 2012; Meddens and Hicke 2014). Climate change played a key role in triggering and sustaining the outbreak: ongoing increases in temperature and decreases in precipitation bolstered beetle survival and reproduction, and also stressed trees and reduced their capacity to defend against attacks (Bentz et al. 2010; Chapman et al. 2012; Creeden et al. 2014; Mitton and Ferrenberg 2012; Sidder et al. 2016). An abundance of suitable high-density stands with large-diameter trees also contributed to the outbreak (Negrón and Cain 2019). Assuming suitable stands and trees remain available, additional warming and drying are expected to exacerbate future outbreaks, at least at higher elevations; however, at lower elevations, additional warming and drying may result in conditions that are outside the climatic niche of the beetle (Hicke et al. 2006; Sidder et al. 2016).

**Figure 14—**The recent mountain pine beetle outbreak resulted in a considerable amount of lodgepole pine mortality across the northern Front Range and elsewhere in Colorado. Ongoing climate change played a key role in triggering and sustaining the outbreak (Bentz et al. 2010; Chapman et al. 2012; Creeden et al. 2014; Mitton and Ferrenberg 2012; Sidder et al. 2016). USDA Forest Service photo by Paula Fornwalt.

Lodgepole pine regeneration events triggered by mountain pine beetle outbreaks may be compromised under a changing climate, particularly at the lower-elevation margins of lodgepole's range. In fact, such reductions may already be occurring. Renwick et al. (2016) found that at three low-elevation lodgepole pine sites in Rocky Mountain

National Park that experienced recent beetle disturbance, lodgepole seedling densities were very low, ranging from only 17 to 36 stems $ac^{-1}$ (42 to 90 stems $ha^{-1}$). Moreover, lodgepole pine seedlings were completely absent at the lowest-elevation portions of the sites. Meanwhile, at high-elevation lodgepole pine sites that experienced beetle disturbance, seedling densities were considerably higher, ranging from 55 to 115 stems $ac^{-1}$ (136 to 284 stems $ha^{-1}$). The authors suggested that the differences in regeneration rates between low- and high-elevation sites provide insight into how future mountain pine beetle outbreaks and climatic changes could interact to drive trailing-edge contractions in lodgepole pine's range.

### *Wildfire*

In their review on climate change × fire regime interactions in the southern Rocky Mountains, Rocca et al. (2014) concluded that subalpine forests will continue to burn with high severity as they did historically, but will burn with greater frequency. Increases in fire frequency already seem to be unfolding: largely because of the record-setting, drought-driven fire season of 2020, the 21st century fire rotation interval for subalpine forests in and adjacent to the Front Range is now 117 years, a rate that is nearly double that of the past 2,000 years (Higuera et al. 2021). Because lodgepole pine is poorly adapted to survive even low-severity burning, future increases in fire frequency can be expected to drive considerable increases in mortality (Stevens et al. 2020). But, if prefire stands contain live trees with serotinous cones, future fires could encourage lodgepole pine to regenerate, so long as climate is favorable (Guz et al. 2021; Schoennagel et al. 2011; Sibold et al. 2006). Unfortunately, ongoing climate change has already reduced the probability of postfire seedling establishment in the southern Rockies and elsewhere in the West, and future changes in climate over the next 10 to 30 years are expected to lead to further reductions (Davis et al. 2023).

Stands that were impacted by mountain pine beetle outbreaks prior to burning could potentially experience additional obstacles to regeneration under a warmer, drier climate. This is primarily because the viability of seeds stored in the serotinous cones of beetle-killed trees diminishes as time since outbreak passes. Research conducted shortly after the onset of the recent beetle outbreak in Rocky Mountain National Park reported that on average, the germination rate of seeds stored in serotinous cones on recently beetle-killed trees exceeded 50 percent (Aoki et al. 2011). However, a subsequent study conducted on the AR and the adjacent Medicine Bow-Routt National Forests found that the germination rate of seeds in serotinous cones on long-dead trees averaged only 34 percent (Rhoades et al. 2022). The regeneration challenges created by declining seed viability could be exacerbated by the low fuel moistures of dead trees and by dead tree fall rates, increasing the likelihood of cone consumption during fire (Rhoades et al. 2018, 2020b). This said, Davis et al. (2023) did not find an effect of prior bark beetle outbreaks on postfire lodgepole pine regeneration, highlighting the uncertainty surrounding the interactive effects of climate change, mountain pine beetle outbreaks, and wildfire.

### *Capacity to Adapt to Climate Change*

Lodgepole pine's phenological plasticity may help it adapt to climate change in situ, and possibly even benefit from it. Carroll et al. (2017) conducted a common garden experiment in the northern Front Range, where lodgepole pine seedlings were grown from seeds collected at an intermediate-temperature site in the middle of the species' local elevational range and then planted at a low-temperature, an intermediate-temperature, and a high-temperature site. They found that seedlings burst their buds earlier at the high- and intermediate-temperature site than at the low-temperature site, extending the growing season; longer growing seasons under a changing climate could result in greater growth. Moreover, lodgepole may not need to close stomates to reduce water loss due to warming, as seedlings maintained a constant photosynthetic rate across the sites; this may also enable greater growth.

Lodgepole pine appears to have some potential to adapt evolutionarily to a changing climate. West-wide studies indicate that populations are highly adapted to their local climate, resulting in considerable genetic diversity across the species' range (Rehfeldt et al. 1999; Yang and Yeh 1993, 1995). Genetic diversity within populations is also high due to high gene flow rates (Yang and Yeh 1993, 1995). The adaptive capacity provided by these diversity patterns is likely augmented by lodgepole's short (relative to other Front Range conifers) generation time and its ability to produce an abundance of seedlings.

Lodgepole pine's distribution in the Front Range may both hurt and help its ability to migrate as climate changes. It reaches the southern extent of its range in the southern Front Range, thus limiting latitudinal migration opportunities. The topography in the Front Range suggests that ample opportunities for upslope migration exist, although bioclimatic envelope modeling indicates that this topographic variation does not fully translate into suitable climate space under a future climate akin to that of the Hot scenario (Crookston 2009).

## Quaking Aspen (*Populus tremuloides*)

**Climate change vulnerability rating:** moderate

**Confidence in climate change vulnerability rating:** moderate information with moderate agreement

Quaking aspen has a low tolerance of warm, dry conditions. Such conditions reduce survival and growth, as well as reproduction from both sprouts and seeds. Bioclimatic envelope models indicate that, under a warmer climate similar to the Hot future climate scenario, quaking aspen in the Front Range may experience 24 to 42 percent net loss of suitable climate space by the middle of the century. Consistent with drought-driven dieback events already observed across Colorado, the suitable climate space that was predicted to be either lost or threatened tended to occur at lower elevations. That said, quaking aspen has the potential to benefit from climate-change driven increases in disturbances like wildfire and mountain pine beetle and spruce beetle outbreaks. By killing aspen and/or co-occurring conifers, wildfires and outbreaks may create opportunities for this disturbance-stimulated species to regenerate not only within climatically suitable portions of its current range via sprouting, but also above its current range via seedling establishment as climate there becomes suitable.

### *Habitat*

Quaking aspen is the most broadly distributed native tree species in North America. In the northern portion of its range, it extends west to east from Alaska and British Columbia to Newfoundland and Labrador and Nova Scotia (Little 1971; NRCS 2020; Perala 1990). It then extends down through mountainous regions in the west to Arizona and New Mexico, while in the east it extends to Iowa, Illinois, and over to New Jersey (Little 1971; NRCS 2020; Perala 1990). Very small, disjunct populations also occur farther south in both the west and the east (Little 1971; NRCS 2020; Perala 1990). In the Front Range, quaking aspen is a major component of about 1.1 million forested acres (0.4 million ha) on the PSI-AR alone, and likely occurs on tens of thousands of acres on adjacent lands (ARP 2019; Little 1971; NRCS 2020; PSICC 2019).

Given its broad distribution, it follows that quaking aspen tolerates a wide variety of environmental conditions. On the PSI-AR, areas where quaking aspen is a major forest component predominately have long-term (1981 to 2010) mean annual temperature values between 32 and 44 °F (0 and 7 °C) and long-term mean annual precipitation values between 14 and 33 in (36 and 83 cm) (ARP 2019; PRISM 2020; PSICC 2019). Elevations in these areas mostly fall between 7,700 and 11,000 ft (2,300 and 3,400 m) (ARP 2019; PSICC 2019; USGS 2020). Aspen grows in a wide range of soil types in the Front Range, so long as they are moist (Peet 1981); where soils are on the drier end of aspen's soil moisture spectrum, they are typically well-developed and fertile (Peet 1981).

In the Front Range, quaking aspen is an important member of subalpine forests, and to a lesser extent, montane forests (table 1; figs. 1, 4). Quaking aspen can sometimes grow in pure stands in the Front Range, but it most commonly grows in mixed-species stands (ARP 2019; PSICC 2019). Its most common associates in mixed stands are ponderosa pine, Douglas-fir, lodgepole pine, subalpine fir, and Engelmann spruce (ARP 2019; PSICC 2019). It is also commonly associated with limber pine and Rocky Mountain bristlecone pine in mixed stands (ARP 2019; PSICC 2019). Stands containing aspen tend to support understories that are species-rich and productive relative to adjacent, purely coniferous, stands, although composition is highly variable (Peet 1981).

## *Ecology*

### *Reproductive Ecology*

Quaking aspen most commonly reproduces vegetatively, by suckering along a shallow, extensive lateral root system (Perala 1990). Suckering in quaking aspen is suppressed by aboveground stems, and released when stems are killed or removed by disturbances such as wildfire or logging (Perala 1990). That said, aspen can also reproduce from seed; indeed, recent genetics work suggests that, while rare, seed reproduction is more common than previously thought (Landhäusser et al. 2019; Long and Mock 2012; Mock et al. 2008). Aspen begins to flower at 2 to 3 years of age and begins to produce large seed crops at 10 to 20 years of age (Perala 1990; Schopmeyer 1974). The seeds are attached to a pappus of long, silky hairs that facilitates long-distance dispersal by wind (Perala 1990). Dispersed seeds tend to have high viability, although this viability lasts for only a few weeks at best (Maini and Cayford 1968).

### *Ecology of Seedlings, Saplings, and Mature Trees*

Quaking aspen can have a low tolerance of warm, dry conditions. Its drought tolerance score is 1.8 out of 5.0, the lowest of all the major Front Range tree species (Niinemets and Valladares 2006). Mature stems are shallowly rooted, and warm, dry conditions can diminish their vigor or even cause mortality (Perala 1990). For example, in USDA Forest Service Region 2, a mid-2000s rapid dieback event (sometimes referred to as SAD, or sudden aspen decline) was triggered by the extreme temperature and precipitation conditions that occurred in the years prior to the event (Rehfeldt et al. 2009). Warm, dry conditions can also negatively impact regeneration, especially from seeds, which require water-saturated soils to germinate (Perala 1990).

As a disturbance-stimulated species, aspen does not tolerate shade well. It has a shade tolerance score of 1.2 out of 5.0, the lowest of all tree species in the Front Range (Niinemets and Valladares 2006).

Wildfires play a key role in quaking aspen's persistence in the Front Range. While aspen stands can be stable in the absence of wildfire or other disturbance, many experience decline due to mortality of the relatively short-lived stems coupled with low regeneration rates and invasion by longer-lived and more shade-tolerant conifers (Bretfield et al. 2016; Kashian et al. 2007; Zier and Baker 2006). When wildfire burns

through an aspen stand, aspen stems are typically killed; the stems' very thin bark makes them highly susceptible to mortality by even low-intensity wildfires (Rodman et al. 2020b; Shinneman et al. 2013; Wooten et al. 2022). Yet this mortality often triggers rapid, prolific suckering from the root system (Rodman et al. 2020b; Shinneman et al. 2013; Wooten et al. 2022). Because wildfires tend to reduce competition and expose a mineral soil seedbed, aspen establishment from seed can sometimes also be promoted by them (Kreider and Yocom 2021; Nigro et al. 2022; Shinneman et al. 2013).

Quaking aspen stems are highly susceptible to mortality from a diversity of insects and diseases. Among the most damaging insects are various species of wood borers, bark beetles, and defoliators (Dudley et al. 2015; Perala 1990). A host of pathogenic fungi cause cankers and butt, root, and trunk rots (Dudley et al. 2015; Hinds and Wengert 1977; Perala 1990). For more information on insects and diseases of aspen, please see Negrón 2024, this report). Aspen also is an important forage for wildlife and livestock, which may result in mortality through heavy browsing, trampling, and rubbing (Dudley et al. 2015; Perala 1990).

### *Potential Direct Impacts of Climate Change*

The bioclimatic envelope models of Crookston (2009) revealed that quaking aspen could experience a net loss of 24 to 42 percent of suitable climate space in the Front Range under the Hot future climate scenario by mid-century (box 1; table 3; fig. 15). Model results indicated that 7.4 million ac (3.0 million ha) are currently climatically suitable for quaking aspen. However, model results predicted that 2.7 million of these acres (1.1 million ha) will no longer be suitable in 2060, and that suitability will be threatened for an additional 1.3 million of these acres (0.5 million ha). While model results also predicted that 0.9 million previously unsuitable acres (0.2 million ha) will become suitable, these gains are insufficient to balance losses. Suitable climate space was generally predicted to be either lost or threatened at lower elevations, while suitable climate was generally predicted to be gained at higher elevations.

Similarly, bioclimatic envelope models developed by Gray and Hamann (2013) for the U.S. Rocky Mountains estimated that the current (1997 to 2006) suitable climate space for quaking aspen already exceeds the baseline (1961 to 1990) suitable climate space by approximately 130 ft (40 m) in elevation. Moreover, relative to the baseline suitable climate space, the suitable climate space for quaking aspen in 2050 will potentially shift upward by 540 ft (164 m) in elevation. Bioclimatic envelope models developed by Rehfeldt et al. (2009) for U.S. Forest Service Region 2 predicted even greater elevational shifts in suitable climate space for quaking aspen by 2090 (as high as 3,280 ft (1,000 m)).

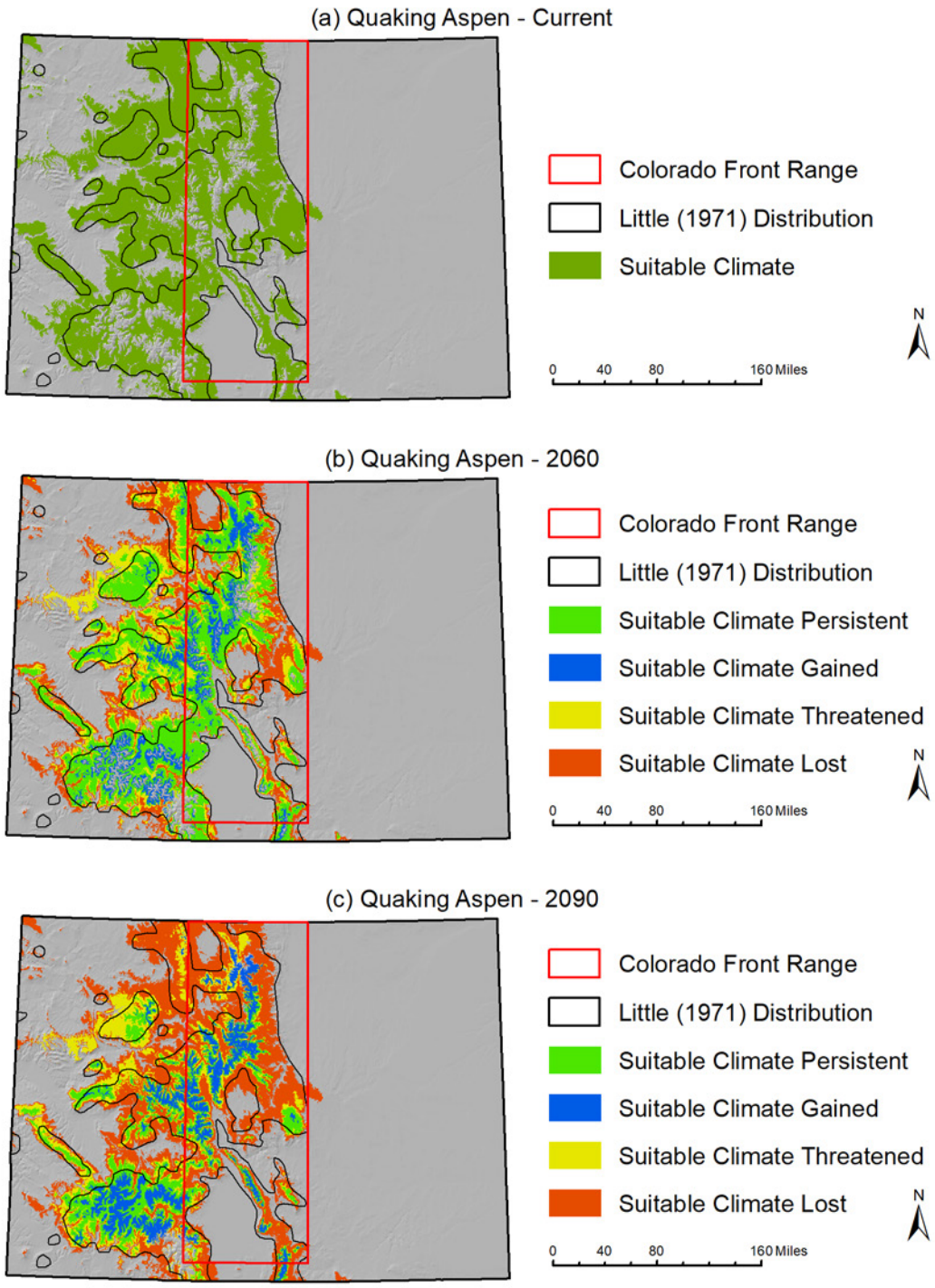



**Figure 15a-c—**The current and potential future suitable climate space of quaking aspen (Crookston 2009). Panel (a) depicts areas in Colorado where the current climate is suitable for the species. Panels (b) and (c) depict areas in Colorado where suitable climate in the future is predicted to be either lost, threatened, persistent, or gained under the HADCM3-A2 general circulation model (GCM), a GCM that crosswalks relatively well to the one representing our Hot future climate scenario. See box 1 for more information about how current and potential future climate suitability were determined. For all panels, the map of Little (1971) is used to represent the general current distribution of the species.

Rehfeldt et al. (2009) also used a bioclimatic envelope modeling approach to examine the climatic factors that triggered a rapid quaking aspen dieback event in U.S. Forest Service Region 2 during the mid-2000s, and to predict where dieback events may be likely to occur in the future. Analyses suggested that the dieback event was triggered by the extremely warm, dry conditions that occurred from 2000 to 2003, and that dieback was largely concentrated within lower-elevation portions of aspen's current suitable climate space. Analyses using an ensemble of GCMs further indicated that aspen's suitable climate space could potentially shift upslope so as to exclude 58 percent of the dieback area by 2030 and 76 percent of the dieback area by 2060. These findings highlight the extent to which dieback events could play a major role in adjusting aspen's lower-elevation distribution under a changing climate.

### *Potential Indirect Impacts of Climate Change*

#### *Wildfire*

Continued climate change in the upcoming decades is expected to further exacerbate wildfire activity by increasing the number of high, very high, and extreme fire danger days (Rangwala 2024, this report). While greater wildfire activity will drive increases in the mortality of aspen stems, it could also promote ample regeneration from suckers, so long as severity is not high enough to damage aspen's shallow root system (Rodman et al. 2020b; Shinneman et al. 2013; Wooten et al. 2022). Greater wildfire activity could also promote aspen regeneration from seed by reducing competition and exposing a mineral soil seedbed (Kreider and Yocom 2021; Shinneman et al. 2013). Indeed, Nigro et al. (2022) documented aspen seedling establishment following recent wildfires on the Rio Grande National Forest, Colorado, including establishment 239 to 1,296 ft (73 to 395 m) above prefire aspen stands, suggesting that postfire upslope establishment could help aspen successfully shift its range in response to climate change. However, postfire regeneration from both suckers and seeds would likely be compromised by future warming and drying, particularly at lower elevations (Perala 1990).

#### *Insects and Diseases*

Future deviations from normal temperature and precipitation regimes may lead to conditions that stress quaking aspen, increasing its susceptibility to damage from insects and diseases. The recent aspen dieback events that occurred across Colorado and the Interior West serve as a case in point. While extremely warm, dry conditions triggered the events, insects and diseases then commonly infiltrated the stressed trees to serve as the proximate agents of mortality. Working in five National Forests of central Colorado and Wyoming (including the PSI), Dudley et al. (2015) found that aspen stands experiencing dieback were not only on warmer, drier sites than healthy stands, but also had higher incidence of damage from wood borers, bark beetles, and Cytospora (*Cytospora* spp.) canker. These findings largely track those documented elsewhere in Colorado (Marchetti et al. 2011; Worrall et al. 2008).

In some areas, aspen has been a beneficiary of recent bark beetle epidemics that killed co-occurring conifers. Rodman et al. (2022a) synthesized field plot data from 16 studies conducted across subalpine forests that were recently impacted by bark beetles in the southern Rocky Mountains. They found that aspen dominated only 2 percent of the sampled plots prior to the outbreaks. However, aspen dominated 6 percent of the plots after the outbreaks, and simulations using the Forest Vegetation Simulator indicated that aspen would dominate 10 percent of the plots after 30 years. Aspen may be able to maintain dominance under changing climate in some of these expanded areas, particularly those that are in cooler, wetter environments.

### *Capacity to Adapt to Climate Change*

An experiment implemented in the northern Front Range by Carroll et al. (2017, 2019) suggests that quaking aspen may have only a limited ability to withstand climate change by plastically modifying its morphology, phenology, and physiology. The authors grew aspen seedlings from seeds collected at an intermediate-temperature site in the middle of the species' local elevational range and then planted the seedlings at a low-temperature, an intermediate-temperature, and a high-temperature site. They found that aspen displayed a strong degree of temperature sensitivity in photosynthesis, leaf size, and growth efficiency, with traits achieving their greatest values at the intermediate elevation site closest to the seed source location. Together, these findings suggest that warmer temperatures will constrain aspen growth. While they also found that warmer temperatures lengthened the growing season by triggering earlier bud break, they predicted that any resultant growth benefits will be insufficient to overcome the observed other constraints on growth.

The capacity of quaking aspen to evolve or migrate in response to climate change will be highly dependent on seed-based reproduction. While random mutations within clones contribute to aspen's high level of genetic diversity, given the pace of climatic changes expected, reproduction from seeds will be needed to support the rapid evolution of favorable traits (Mitton and Grant 1996; Mock et al. 2008). Similarly, while clonal expansion enables some migration, reproduction from seeds will be crucial if aspen is to move along with its suitable climate space (Elliott and Baker 2004; Mock et al. 2008; Nigro et al. 2022). However, aspen's ability to reproduce from seeds is constrained. Aspen produces large quantities of seeds that readily disperse long distances, but seeds rarely grow into seedlings due to very short seed viability windows and highly exacting moisture requirements for seed germination and seedling establishment (Landhäusser et al. 2019; Long and Mock 2012; Maini and Cayford 1968; Perala 1990; Schopmeyer 1974).

## Limber Pine (*Pinus flexilis*)

**Climate change vulnerability rating:** high

**Confidence in climate change vulnerability rating:** moderate information with moderate agreement

If climate change was the only factor challenging limber pine, we may hypothesize that the species could fare better than other less drought-tolerant species. It is a generalist and has broad climatic tolerances. However, limber pine is highly susceptible to disturbances, especially white pine blister rust but also mountain pine beetle and wildfire. These disturbances greatly exacerbate the vulnerability of limber pine to climate change. A key limitation to projecting limber pine's population trajectories under a changing climate is the paucity of data on the frequency of quantitative resistance to blister rust.

### *Habitat*

Limber pine, a five-needle white pine, has a very broad distribution in North America[1]. Its core range extends from the Canadian Rockies (British Columbia, Alberta) south through the central (Montana, Idaho, Wyoming) and southern Rockies (Colorado, New Mexico) and west into the Great Basin (Utah, Nevada) and southern Sierra Nevada (California). It occurs in small populations across much of this range; the largest, most connected populations occur in Montana, Wyoming, Utah, and Colorado (Little 1971; NRCS 2020; Steele 1990). Limber pine occurs throughout the Front Range (ARP 2019; Little 1971; NRCS 2020; PSICC 2019). It is a dominant or co-dominant tree species on approximately 0.3 million ac (0.1 million ha) of forest on the PSI-AR (ARP 2019; PSICC 2019). Limber pine also occurs on other forested lands in the Front Range, such as in Rocky Mountain National Park and Great Sand Dunes National Park and Preserve.

Limber pine tends to be most abundant on xeric sites, growing in harsh habitats where other tree species cannot (Schoettle 2004; Tomback et al. 2011). However, it can establish on more mesic sites if competition is low. On the PSI-AR, long-term (1981 to 2010) mean annual precipitation for sites where limber pine is dominant or co-dominant ranges from about 15 to 34 in (39 to 86 cm) (ARP 2019; PRISM 2020; PSICC 2019). Long-term mean annual temperature for these same sites ranges from about 32 to 44 °F (0 to 7 °C). Limber pine has a very broad elevational range across its distribution and especially in the Front Range, where it extends from the grassland to

[1]In the 1970s, geneticists reported hybridization between limber pine and southwestern white pine (*Pinus strobiformis*) (Steinhoff and Andresen 1971). Recently, the broad hybrid zone has been confirmed using genomic tools to span the U.S. portion of the southwestern white pine's range and into southern Colorado (Menon et al. 2018). For this discussion, we refer to the full distribution of limber pine as mapped by Little (1971) as being limber pine, although ongoing research may lead to changes in the taxonomic designation of some populations.

the alpine ecotones. On the PSI-AR, it is predominately found from about 8,100 to 11,100 ft (2,400 to 3,400 m) (ARP 2019; PRISM 2020; PSICC 2019; USGS 2020); it also occurs on the Pawnee National Grassland at about 5,200 ft (1,600 m) (Schoettle and Rochelle 2000). Limber pine grows on well-drained soils derived from a wide range of parent materials (Steele 1990).

Limber pine is most prevalent in subalpine forests of the Front Range, but it can be common in montane forests as well (table 1; figs. 1, 4). Limber pine rarely grows in pure stands (ARP 2019; PSICC 2019). It is most commonly found growing alongside ponderosa pine, Douglas-fir, lodgepole pine, quaking aspen, Rocky Mountain bristlecone pine, and Engelmann spruce (ARP 2019; PSICC 2019). Plant communities growing underneath limber pine tend to be sparse and dominated by shrubs, such as kinnikinnick (*Arctostaphylos uva-ursi*), common juniper (*Juniperus communis*), and currant (*Ribes* spp.) (Peet 1981). Limber pine is a long-lived seral species but can be a climax species on the most xeric of sites (Schoettle 2004; Steele 1990).

## *Ecology*

### *Reproductive Ecology*

Limber pine is a slow-growing species with delayed reproductive maturation (Schoettle 2004; Tomback et al. 2011). Forest-grown trees can produce their first seed-bearing cones at around 30 years of age but do not produce full cone crops until they are approximately 60 to 80 years old, or older on harsh sites (Schoettle, personal observation). Limber pine is a masting species with good cone crops occurring every 4 to 5 years, although some trees may produce some cones at other times. Along the Front Range, cones mature in the first half of September (Schoettle et al. 2019b). Hot, dry summers can accelerate cone maturation by up to a few weeks. Seeds lost to cone and seed insects can be extensive for limber pine in Colorado, especially for those seeds that mature following a mast year (Schoettle and Negrón 2001; Williams et al. 2020). We hypothesize that the elevated risk of insect damage to seeds following a masting event is due to an increase in predator populations.

Throughout the core range of limber pine, including the Front Range, Clark's nutcracker (*Nucifraga columbiana*) is the primary seed disperser, influencing population structure (Carsey and Tomback 1994; Schuster et al. 1989). Limber pine seeds are large and commonly wingless. The long-distance dispersal by nutcrackers facilitates the mixing of diverse seed sources for the colonization of sites following disturbance, resulting in low levels of genetic differentiation (i.e., structure) among populations across the landscape (Bower et al. 2011; Tomback et al. 2011). Nutcrackers are rare visitors to the Dave's Draw limber pine population on the Pawnee National Grassland and it is hypothesized that seed-caching rodents are the primary seed dispersers at grassland sites (Tomback et al. 2005). Once dispersed, seeds are readily consumed by not only their bird and rodent dispersers but by numerous other species as well (Tomback and Achuff 2010).

### *Ecology of Seedlings, Saplings, and Mature Trees*

Limber pine has many traits that confer drought tolerance (drought tolerance score of 4.7 out of 5.0; Niinemets and Valladares 2006). Limber pine has a strong stomatal response to vapor pressure deficit, which limits water loss under highly evaporative conditions and thereby conserves hydraulic function (Pataki et al. 2000; Reinhardt et al. 2011, 2015). The species also tends to have a high root-to-shoot ratio, a characteristic of drought-tolerant species (Borgman et al. 2014, 2015). In some habitats, it can access groundwater via a deep taproot, thereby decoupling its water supply from local precipitation patterns (Roberts et al. 2004).

Limber pine is considered shade-intolerant, receiving a shade tolerance score of 1.6 out of 5.0 (Niinemets and Valladares 2006; Steele 1990). However, sparse overstory canopy cover and nurse objects can improve seedling establishment and performance (Casper et al. 2016; Coop and Schoettle 2009); with climate warming, these conditions may be increasingly important (Schoettle et al. 2022a).

Fire has played a historical role in the metapopulation dynamics of limber pine in and surrounding the Front Range (Brown and Schoettle 2008) and elsewhere (Webster and Johnson 2000). Because of limber pine's broad elevational distribution in the Front Range, it likely experienced the full spectrum of fire regimes prior to the 1900s (Brown and Schoettle 2008; Veblen 1986). However, limber pine has bark that is thin, branches that do not readily self-prune, and a stature that is generally short, making it poorly adapted to survive even low-severity fire (Stevens et al. 2020). Although limber pine is an early seral species, postfire seedling establishment is typically slow. Individuals accumulate over decades, generating an uneven age stand structure (Brown and Schoettle 2008; Cleaver et al. 2016; Goeking and Windmuller-Campione 2021; Windmuller-Campione and Long 2016). Postfire seedling densities can vary across the landscape, with successful establishment in some areas of the Front Range and only sparse establishment in others (Coop and Schoettle 2009, 2011); this suggests that numerous factors, including climatic, seedbed, overstory, and understory conditions, all influence seedling establishment (Kueppers et al. 2017; Schoettle et al. 2022a).

Limber pine is highly susceptible to mortality from biotic agents such as white pine blister rust and mountain pine beetle. White pine blister rust is caused by the nonnative fungal pathogen *Cronartium ribicola* (fig. 16). The pathogen can infect all five-needle pines in North America, but to complete its life cycle it must use currant (*Ribes* spp.) or select other species as alternate hosts (Geils et al. 2010). Infections in mature trees build over a period of several years, initially causing reduced vigor and branch death, and if the infection reaches the tree bole, tree death (Burns et al. 2008). Infections in seedlings tend to progress more rapidly (Schoettle and Sniezko 2007). Mountain pine beetle is a native insect that attacks numerous North American pine species. Limber pine has very low constitutive chemical defenses against mountain pine beetle, making it highly susceptible to attack and mortality (Bentz et al. 2016; Gray et al. 2015). Mountain pine beetle kills limber pine trees by mass attack, with large trees preferentially affected.


**Figure 16a-b—**Fruiting canker of *Cronartium ribicola* on (a) a limber pine branch and (b) a bole of a Rocky Mountain bristlecone pine (*Pinus aristata*), is the nonnative fungal pathogen that causes the lethal disease white pine blister rust. The high level of mortality by white pine blister rust will reduce population size and therefore may reduce the adaptive capacity of the species to climate change (Schoettle et al 2022a.) USDA Forest Service photos by Anna Schoettle.

The sensitivity of limber pine to mountain pine beetle and other stressors is increased by limber pine dwarf mistletoe (*Arceuthobium cyanocarpum*), making it another forest health concern. Trees infested with dwarf mistletoe use more water and experience greater water stress and mortality than uninfected trees (Glatzel and Geils 2009; Kolb et al. 2016; Robinson and Geils 2006; Zweifel et al. 2012). Until the recent beetle epidemic, dwarf mistletoe was the second most damaging agent of limber pine behind blister rust in the central and southern Rocky Mountains (Cleaver et al. 2015; Kearns and Jacobi 2007; Taylor and Mathiasen 2002). Chapter 8 (Negrón 2024, this report) presents more information on these and other insects and diseases of limber pine.

### *Potential Direct Impacts of Climate Change*

Evidence and characterization of the impacts of climatic warming on limber pine suggest that mortality of mature trees is associated with long-term cumulative, rather than short-term acute, climatic stress (Kane and Kolb 2014; Millar et al. 2015). Sustained climatic stress is already increasing along the Front Range and contributing to increased limber pine mortality (Andrus et al. 2021; Smith et al. 2015). For example, at

Niwot Ridge in the northern Front Range, limber pine mean annualized mortality rates increased over a 31-year period of observation, coincident with increases in warmer and drier conditions (Smith et al. 2015). However, climate-associated mortality has been less for limber pine than some other co-occurring species (Andrus et al. 2021; Kane et al. 2014; Smith et al. 2015) and could portend an increased role of limber pine in a drier future (Schoettle et al. 2022a; Windmuller-Campione and Long 2016).

The bioclimatic envelope models of Crookston (2009) suggest a future overall loss in climatically suitable area for limber pine in the Front Range. Under a climate change scenario similar to the Hot scenario, climatically suitable area was predicted to decrease from 8.0 million ac (3.2 million ha) currently to 4.5 million ac (1.8 million ha) by 2060 and 1.7 million ac (0.7 million ha) by 2090 (box 1; table 3; fig. 17). Crookston's (2009) models also suggest a future shift in climatically suitable area to higher elevations.

While bioclimatic envelope models developed by Monahan et al. (2013) for limber pine in Rocky Mountain National Park did not show a clear trend in the amount of climatically suitable area through 2100, they did show a clear future upslope shift. These authors developed their models using an ensemble of 31 GCMs and two distinct training datasets: one collected locally in the Park, and one collected across limber pine's range.

A more suitable climate at higher elevations may promote the elevational advancement of limber pine seedling establishment and performance above the current alpine treeline (Moyes et al. 2013, 2015). Although restricted, limber pine regeneration above the current alpine treeline appears to be greater than for other species due to long-distance seed dispersal by Clark's nutcracker (e.g., Millar et al. 2015; Smithers et al. 2018), suggesting that its role in treeline dynamics may increase in the absence of insect, disease, and wildfire pressures (Sindewald et al. 2020).

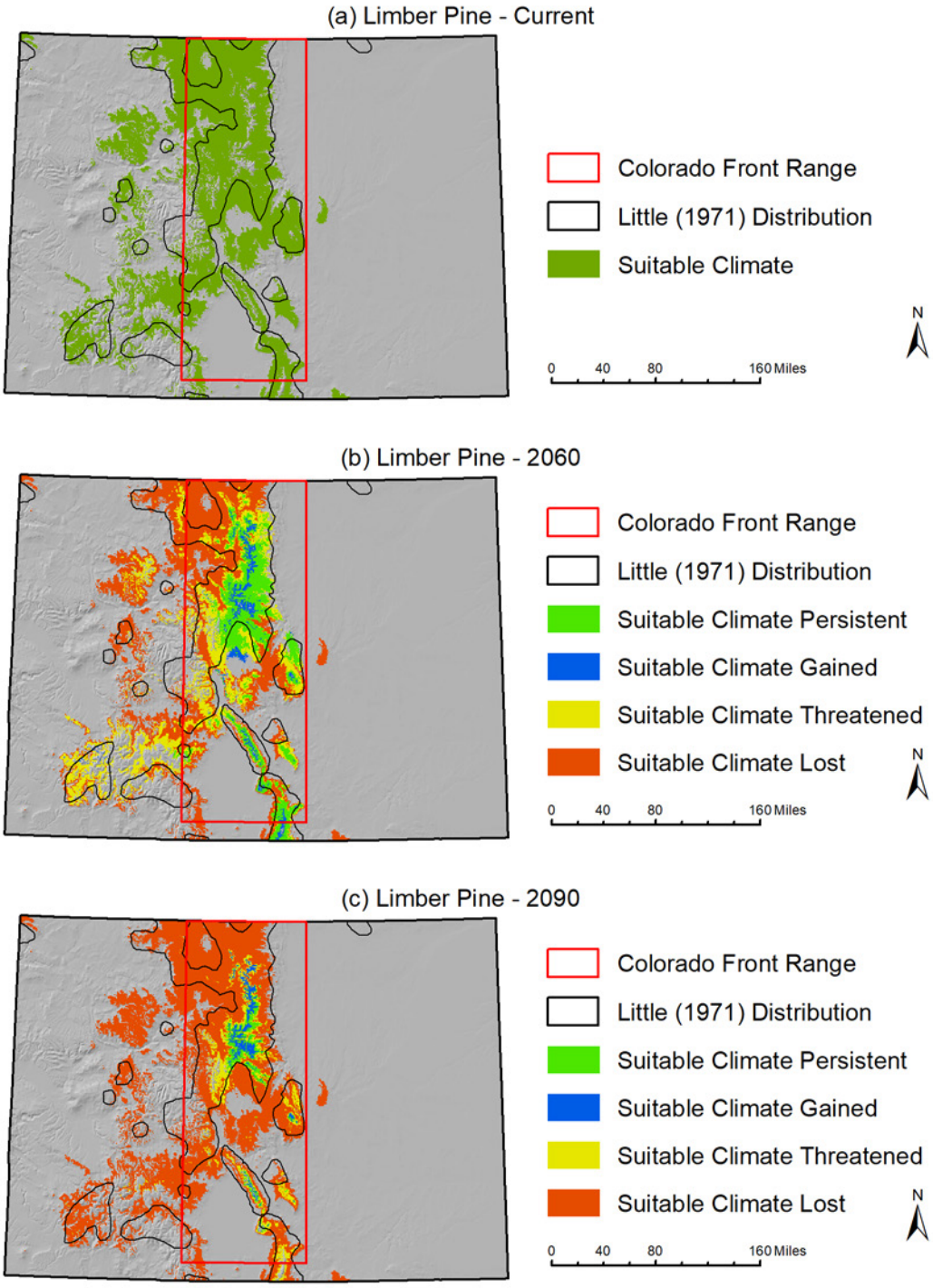



**Figure 17a-c—**The current and potential future suitable climate space of limber pine (Crookston 2009). Panel (a) depicts areas in Colorado where the current climate is suitable for the species. Panels (b) and (c) depict areas in Colorado where suitable climate in the future is predicted to be either lost, threatened, persistent, or gained under the HADCM3-A2 general circulation model (GCM), a GCM that crosswalks relatively well to the one representing our Hot future climate scenario. See box 1 for more information about how current and potential future climate suitability were determined. For all panels, the map of Little (1971) is used to represent the general current distribution of the species.

### *Potential Indirect Impacts of Climate Change*

#### *Wildfire*

Climate-driven increases in the size and severity of wildfires have been documented for many regions in the western United States and are predicted to continue (Abatzoglou and Williams 2016; Gergel et al. 2017; Higuera et al. 2021). In the central and southern Rocky Mountains, these current and future trends hold for both the montane and the subalpine forests where limber pine resides (Gergel et al. 2017; Higuera et al. 2021; Picotte et al. 2016; Wright and Roy 2022; Yue et al. 2013). Because limber pine is considered an early seral species, some fire is likely to benefit the species; however, increases in fire severity and frequency may tip the balance toward risking population extirpation from too much fire (Coop and Schoettle 2011; Keane et al. 2021).

#### *Insects and Diseases*

Repeated forest health monitoring assessments provide valuable condition trends for limber pine in the Rockies, revealing high mortality from white pine blister rust (Burns et al. 2023; Cleaver et al. 2015). In northern Colorado, Wyoming, and southeastern Montana, 73 percent of the stands have been invaded by blister rust with an average disease incidence of 26 percent, an increase of 6 percent over 8 to 9 years (Cleaver et al. 2015). Blister rust was first detected in northern Colorado in 1998 (Johnson and Jacobi 2000) and continues to spread southward (Schoettle et al. 2022a). A disjunct infection center in the Sangre de Cristo Mountains was found in 2003 (Blodgett and Sullivan 2004) and the incidence of blister rust on limber pine is currently over 50 percent in the area and has spread to the Wet Mountains (Burns 2006; Schoettle et al. 2022a). Disease severity continues to increase on limber pine (Burns et al. 2023). Risk analysis modeling using climate variables projected that 41 to 53 percent of limber pine habitat is at risk for blister rust in Colorado (Kearns et al. 2014). By 2030, limber pine is expected to experience a 40 percent reduction in basal area in the United States (Krist et al. 2014). In Alberta, Canada where blister rust has been impacting limber pine for more than half a century, limber pine is listed as endangered (Alberta 2014), and it is being considered for national listing as such under the Species at Risk Act.

The recent epidemic of mountain pine beetle has taken its toll on limber pine. This is likely the result of limber pine being a good host tree that fosters brood development (Cerezke 1995). High beetle-caused mortality has recently been observed on 75 percent of limber pine plots distributed across southern Montana, Wyoming, and northern Colorado, and on 18 percent of trees (Cleaver et al 2015). As of 2016–2017, mountain pine beetle continued to cause mortality of limber pine in northern Colorado though it has caused only minimal mortality in the Sangre de Cristo Mountains of southern Colorado (Burns et al. 2023). Climate warming is likely to expand the threat of mountain pine beetle to the higher-elevation five-needle pines, including limber pine (Fettig et al. 2022; Howe et al. 2021; Logan et al. 2010).

### *Capacity to Adapt to Climate Change*

Limber pine is facing multiple compounding factors that threaten the sustainability of populations and their evolutionary potential. The strong selection pressure of white pine blister rust alone is formidable, and adaptation to the disease is imperative to sustain or restore limber pine populations as it continues to spread. How white pine blister rust epidemiology will be affected by climate change is likely to be context-dependent and is therefore difficult to predict (Hennon et al. 2020; Schoettle et al. 2022a). This challenge is further complicated by pressures from other mortality factors that are each expected to further increase in a warming climate, most notably drought, mortality from mountain pine beetle, and wildfires of increasing frequency, size, and intensity (Schoettle et al. 2022a).

Because limber pine has not co-evolved with the nonnative fungal pathogen that causes white pine blister rust, it is highly susceptible to it. Fortunately, limber pine has some naturally occurring genetic resistance to the pathogen, providing the opportunity for adaptation. However, although limber pine has both heritable major gene resistance and quantitative resistance to white pine blister rust, the frequency of the more durable quantitative resistance appears to be very low (Schoettle et al. 2014, 2022b). The frequency of quantitative resistance traits may be too low to sustain viable limber pine populations when under high natural selection pressures without active management. A key limitation to projecting limber pine's population trajectories is the paucity of data on the frequency of quantitative resistance to white pine blister rust (Schoettle et al. 2022a). The high level of mortality by the rust will reduce population size and therefore may reduce the adaptive capacity of the species to climate change and other stressors (Schoettle et al. 2022a).

## Rocky Mountain Bristlecone Pine (*Pinus aristata*)

**Climate change vulnerability rating:** moderate to high

**Confidence in climate change vulnerability rating:** moderate information with moderate agreement

Drought is already a feature of Rocky Mountain bristlecone pine's environment, and the forecasted changes in climate may further intensify drought as a primary stressor. The relationships between cone production, seedling establishment, and climate suggest particular vulnerabilities to climate change. Rocky Mountain bristlecone pine currently shows only minor impacts from insects and diseases. However, the nonnative disease white pine blister rust is just beginning to spread into Rocky Mountain bristlecone pine's distribution; the species is susceptible to the disease and extensive mortality can be expected as the disease expands in area. The combination of low genetic diversity, moderate population isolation, a protracted and vulnerable regeneration dynamic, and added mortality by white pine blister rust will limit the adaptive capacity of this species to climate change.

### *Habitat*

Rocky Mountain bristlecone pine (hereafter RM bristlecone pine) is a long-lived five-needle pine with a very narrow distribution. Its disjunct populations grow in just three states: Colorado, Arizona, and New Mexico (NRCS 2020). Its core range is located in Colorado, and it achieves its greatest distribution in the Front Range, where it extends from Boulder County south to Las Animas County (ARP 2019; NRCS 2020; PSICC 2019). RM bristlecone pine is a major component of about 0.3 million ac (0.1 million ha) of forest on the PSI-AR (ARP 2019; PSICC 2019); these acres likely capture the bulk of the RM bristlecone pine in the Front Range. Great Basin bristlecone pine (*Pinus longaeva*), which grows in Utah, Nevada, and California, was distinguished from RM bristlecone pine in 1970 and the distributions of the two bristlecone species do not overlap.

RM bristlecone pine grows in cold, dry, and high-elevation environments. In PSI-AR Forests with a major component of RM bristlecone pine, long-term (1981 to 2010) mean annual temperature ranges from around 31 to 39 °F (-1 to 4 °C), while long-term mean annual precipitation ranges from around 15 to 38 in (39 to 96 cm) (ARP 2019; PRISM 2020; PSICC 2019). Precipitation peaks in late summer with the North American Monsoon (Schoettle et al. 2022a). Elevations range from around 9,400 to 11,800 ft (2,800 to 3,600 m) (ARP 2019; PSICC 2019; USGS 2020). Slopes on which the species is found tend to face southwest.

RM bristlecone pine in the Front Range is almost exclusively restricted to the subalpine forest vegetation type (table 1; figs. 1, 4). Its most common tree associate is Engelmann spruce, but it also regularly grows with lodgepole pine, limber pine, aspen, and subalpine fir (ARP 2019; PSICC 2019). It can sometimes form pure stands, particularly

where harsh conditions put the site outside of the physiological tolerance of other tree species (ARP 2019; PSICC 2019). Ground cover is commonly dominated by rock, litter, and bare soil, with understory associates such as fescue (*Festuca* spp.), alpine clover (*Trifolium dasyphyllum*), and common juniper (*Juniperus communis*) generally of much lesser abundance (Johnston 1987; Schoettle and Coop 2017).

## *Ecology*

### *Reproductive Ecology*

RM bristlecone pine reproduces from seeds, which are relatively small and winged, as is typical of wind-dispersed conifers. Clark's nutcrackers, squirrels, and other animals cache seeds, but animals may predate on seeds to a greater degree than serve as agents of seed dispersal (Coop and Schoettle 2009). Cone production can occur by 40 years of age, but production of a full cone crop takes far longer; maturation rates likely vary with growing conditions. Good seed crops are produced every 2 to 3 years, with reproductive output greatest in high-elevation and low-density stands (Schoettle and Coop 2017). Potential climate drivers for cone production include negative associations with growing degree days and maximum summer temperatures, as well as the mean temperature of the coldest month (Schoettle and Coop 2017). At the level of individual trees, cone production is weakly related to tree basal area.

### *Ecology of Seedlings, Saplings, and Mature Trees*

RM bristlecone pine is limited by available habitat at the southern edge of its distribution, but it is unknown what limits it farther north into the abundant suitable habitat occupied by limber pine. Its northern range limit coincides with the reliable extent of the North American Monsoon, suggesting that seedling establishment may require late summer precipitation (Schoettle 2004). This hypothesis is further supported by the observation that RM bristlecone pine seedlings have a lower root:shoot ratio than limber pine, and prioritizing root growth provides limber pine with greater tolerance to inconsistent moisture availability during seedling establishment (Borgman et al. 2014).

While mature RM bristlecone pine trees are highly drought-tolerant (drought tolerance score of 4.9 out of 5.0; Niinemets and Valladares 2006), drought can still affect tree growth. Early studies have related antecedent moisture and temperature to growth in high-elevation stands of RM bristlecone pine. In recent decades, the severity of droughts in the southern Rocky Mountains and southwestern United States has increased (Allen et al. 2010; Williams et al. 2022) and this is evident in the radial growth patterns of RM bristlecone pine (Tintor and Woodhouse 2021). A large portion of interannual variability (52 percent) in annual ring growth of high-elevation RM bristlecone pines was attributed to June water stress (Tintor and Woodhouse 2021).

RM bristlecone pine is relatively shade-intolerant (shade tolerance score of 1.3 out of 5.0; Niinemets and Valladares 2006), and establishment is favored on exposed, rocky sites with relatively acidic, bare mineral soil, presumably due to competitive exclusion

on better sites (Baker 1992). However, young seedlings can also be found underneath nurse canopies of mature trees and beside other objects (Coop and Schoettle 2009).

RM bristlecone pine fire regimes can vary considerably with topography, elevation, and other environmental conditions. While a stand-replacing fire regime may be prevalent in some settings (Baker 1992), at least some stands may be best characterized by a low-severity fire regime. Fire-scarred RM bristlecone pines in open, low-density stands with grassy understories occur nearly throughout the range of the species, particularly where stands are adjacent to montane and subalpine grasslands (Coop and Schoettle 2011). Numerous fire histories have been reconstructed from RM bristlecone pines scarred by low-severity fires with mean fire intervals ranging from 7 to 103 years (mean of 40 years; Coop and Schoettle 2011). Stand density tends to increase with elevation, but fire behavior can be moderated in RM bristlecone pine stands by the lack of surface fuel continuity and widely spaced crowns. The regeneration response of RM bristlecone pine to fire appears to be the subject of some uncertainty. Baker (1992) concluded that bristlecone pine is a "long-lived pioneer that regenerates primarily after fire," while Brown and Schoettle (2008) found regeneration to be associated with long fire-free intervals, and Cocke and others (2005) reported nearly continuous regeneration in the Arizona populations. Consideration of the temporal and spatial scale of recovery can help reconcile these apparent contradictions. Open conditions that favor RM bristlecone pine seedling establishment may persist for decades to centuries after disturbance in these dry southern Rockies settings (Coop et al. 2010; Shankman and Daly 1988). Coop and Schoettle (2009) observed poor postfire regeneration three decades after two stand-replacing fires and RM bristlecone pine populations were low in burn interiors compared to unburned stands. However, seedling numbers were elevated near or beneath surviving trees, and total density was increased in partially burned patches. Seed availability and microsites that provide shelter strongly influence postfire RM bristlecone pine regeneration. On more favorable sites, regeneration densities of other species can be orders of magnitude greater than RM bristlecone pine due to the latter's relatively low fecundity, likely leading to its competitive exclusion over time (Moir and Ludwig 1979).

Both white pine blister rust and mountain pine beetle can cause significant mortality in RM bristlecone pine. White pine blister rust was first discovered on RM bristlecone pine in 2003 in the Sangre de Cristo Mountains of southern Colorado and is still spreading in the southern Rockies (fig. 16; Blodgett and Sullivan 2004; Burns 2006). The first detected RM bristlecone pine trees infected with blister rust were predominantly in moist, riparian areas, where the primary alternate host (*Ribes* spp.) is common and conditions are conducive to C. ribicola spore production. Infections are currently less common on the upland drier slopes (Burns 2006). RM bristlecone pine is susceptible to white pine blister rust, but early studies suggest that RM bristlecone pine has modest levels

of genetic resistance (Schoettle et al. 2022b); more studies are needed to understand the frequency and distribution of resistance traits. RM bristlecone pine has moderate constitutive defenses against mountain pine beetle, a native insect (Bentz et al. 2021). As with other pines, mountain pine beetle kills RM bristlecone by mass attack. More information on these and other insects and diseases is included in Chapter 8 (Negrón 2024, this report).

### *Potential Direct Impacts of Climate Change*

Drought is already a feature of RM bristlecone's environment. Drought and temperature-related mortality has not been widely documented for RM bristlecone pine. However, drought may be contributing to the substantial recent crown and branch dieback in individuals observed across much of the species' range (Schoettle and Coop 2017), and the forecasted changes in climate may intensify drought as a primary stressor in upcoming decades.

The bioclimatic envelope models of Crookston (2009) predicted that RM bristlecone pine's climatic niche may nearly vanish from the Front Range and the rest of Colorado by 2060 (table 3; fig. 18). Results indicated that 3.1 million ac (~1.3 million ha) in the Front Range are currently climatically suitable for bristlecone. However, under a future climate similar to the Hot climate scenario, approximately 87 percent of this area was predicted to be unsuitable by 2060, and an additional 6 percent was predicted to be only marginally suitable. Moreover, a negligible amount (< 0.1 million ac (< 0.1 million ha)) of currently unsuitable area was predicted to become suitable by 2060. However, when Malone et al. (2018b) developed range-wide bioclimatic envelope models that incorporated distinct RM bristlecone pine genetic lineages, the results presented a slightly more positive forecast; they projected a 74 percent decrease in the bristlecone pine suitable climate space by 2090.

The relationships of cone production to climate factors are suggestive of potential sensitivity to climate warming (Schoettle and Coop 2017). Likewise, the importance of the amount and timing of moisture to seedling establishment also suggests a vulnerability to increases in climate variability. A study in northern Arizona, well within the area of influence of the North American Monsoon, showed continuous recruitment of RM bristlecone pine (Cocke et al. 2005). These observations suggest that changes to the intensity and regularity of monsoonal precipitation may impact future RM bristlecone pine recruitment (Schoettle et al. 2022a). A lack of regeneration in some stands indicates that older trees can persist in suboptimal environments that are currently outside the conditions suitable for seedling establishment (Schoettle and Coop 2017).

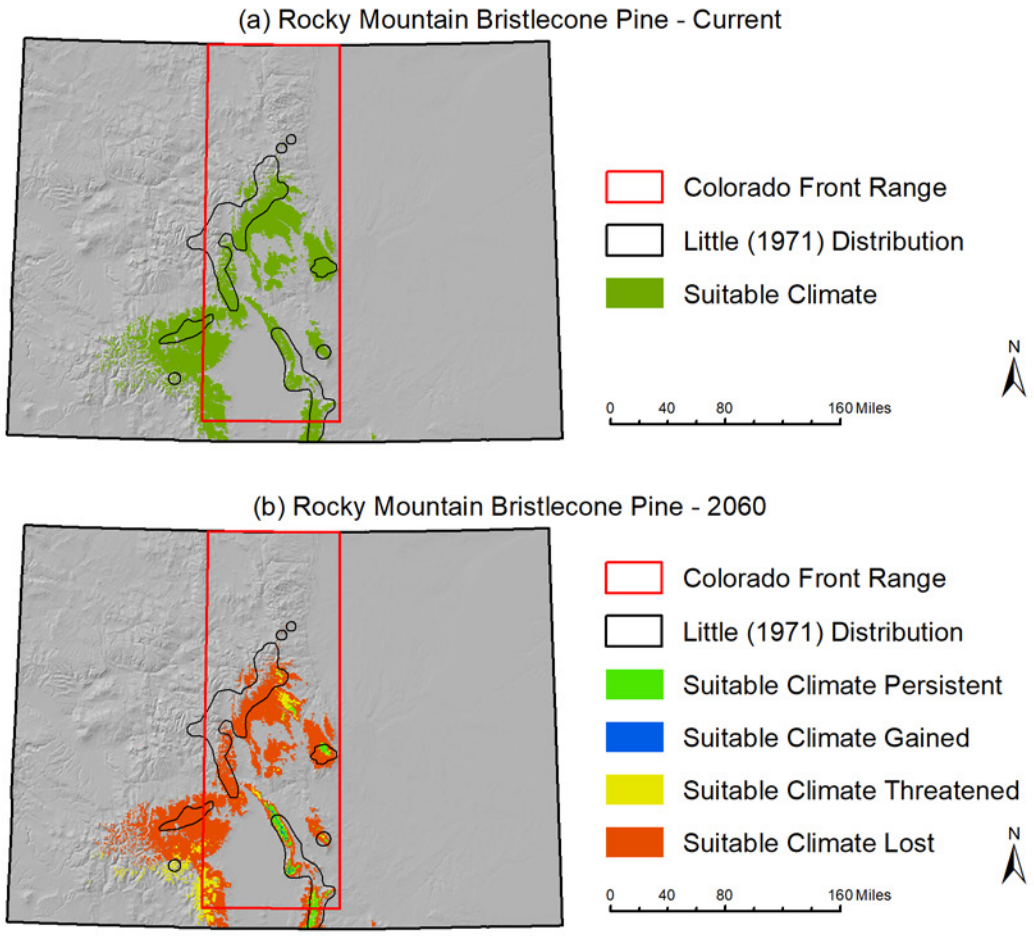



**Figure 18a-b—**The current and potential future suitable climate space of Rocky Mountain bristlecone pine (Crookston 2009). Panel (a) depicts areas in Colorado where the current climate is suitable for the species. Panel (b) depicts areas in Colorado where suitable climate in the future is predicted to be either lost, threatened, persistent, or gained in 2060 under the HADCM3-A2 general circulation model (GCM), a GCM that crosswalks relatively well to the one representing our Hot future climate scenario (2090 data are unavailable for this species). See box 1 for more information about how current and potential future climate suitability were determined. For all panels, the map of Little (1971) is used to represent the general current distribution of the species.

## *Potential Indirect Impacts of Climate Change*

### *Insects and Diseases*

During the recent epidemic, mountain pine beetle populations were far greater in northern than southern Colorado and therefore did not overlap with much of RM bristlecone pine's distribution (Bentz et al. 2021). Severe drought conditions on Telescope Peak in eastern California have enabled mountain pine beetle to overcome defenses in Great Basin bristlecone pine, resulting in high tree mortality (Bentz et al. 2022); however, it is unknown if a future drought in combination with a beetle epidemic will lead to a similar outcome for RM bristlecone pine.

### *Capacity to Adapt to Climate Change*

Individual RM bristlecone pine trees can attain lifespans of > 2,000 years, making them the oldest trees in Colorado (Brunstein and Yamaguchi 1992). This extreme longevity suggests that trees are able to tolerate considerable variations in climate. However, it is unclear what mechanisms enable trees to be so tolerant of climatic variability.

RM bristlecone pine has a very low genetic diversity, which increases its vulnerability to climate change (Schoettle et al. 2012b). While the overall genetic diversity is low, there is variation among populations that is likely a result of limited gene flow across distant mountaintop populations. This variation is correlated with site temperature and precipitation and suggests that the isolation has led to local adaptation (Schoettle et al. 2012b). The populations along the Front Range harbor the greatest genetic diversity and may serve as an important source of genetic variation to support adaptation in the future (Schoettle et al. 2012b). Mortality caused by white pine blister rust, and the direct and indirect effects of a changing climate may lead to a reduction of the already low overall genetic diversity through the loss of rare alleles or extirpation of small, isolated populations (Kim et al. 2003).

Evolutionary adaptation is most likely to occur under conditions where environmental change is gradual, the initial population size is large, generation time is short, and genetic variation is high (Aitken et al. 2008). Unfortunately, none of these conditions exist for RM bristlecone pine in Colorado. As discussed above, the habitat of RM bristlecone pine is rapidly changing, its populations are small and isolated, the species has delayed maturation and slow population turnover, and its genetic diversity is low. In total, the species is not positioned well for sustained evolutionary potential in a changing climate. RM bristlecone pine has tolerance to many individual stressors, but the novel combinations of the stressors coupled with the species' low genetic diversity and conservative life history strategy limit its capacity for rapid adaptation, making it vulnerable to irreversible impacts (Schoettle et al. 2022a). Proactive management, e.g., plantings and silvicultural treatments done before populations decline, to increase the abundance of younger cohorts with more diverse genetic combinations would improve RM bristlecone pine's adaptive capacity (Schoettle and Coop 2017; Schoettle and Sniezko 2007; Schoettle et al. 2012a,b; Schoettle et al. 2019b).

## Subalpine Fir (*Abies lasiocarpa* var. *lasiocarpa*)

**Climate change vulnerability rating:** moderate to high

**Confidence in climate change vulnerability rating:** Limited information with moderate agreement

Subalpine fir is highly sensitive to warm, dry conditions, and climate change is expected to directly compromise the survival of regenerating and mature trees. A Very Hot and Dry future climate scenario would be the most detrimental to subalpine fir survival in the Colorado Front Range; however, all scenarios would likely incite some level of mortality. Bioclimatic envelope models on par with the Hot future climate scenario suggest that by 2060, suitable climate space will be lost primarily in low elevations, with only marginal gains at higher elevations. In addition to these direct effects of warming, climate change will compromise subalpine fir indirectly by increasing the prevalence of fire and of an insect and disease disorder, subalpine fir decline. Very little information exists about subalpine fir's ability to respond plastically to changing environmental conditions, to evolve, and to migrate, but what is known suggests that it may have only some capacity to adapt through these mechanisms.

### *Habitat*

Subalpine fir is widely distributed in western North America. Its range extends from the Yukon to Arizona and New Mexico north to south, and from Alaska to Colorado west to east (Alexander et al. 1990; Little 1971; NRCS 2020). Subalpine fir is also widely distributed in the Front Range, dominating or co-dominating about 0.5 million ac (0.2 million ha) of forest on the PSI-AR alone (ARP 2019; Little 1971; NRCS 2020; PSICC 2019).

Subalpine fir occurs in areas in the Front Range where winters are long and cold and summers are short and cool. On the PSI-AR, the subalpine fir zone has long-term (1981 to 2010) mean annual precipitation values between ca. 21 and 39 in (54 and 98 cm), and long-term mean annual temperature values between ca. 32 and 38 °F (0 and 4 °C) (ARP 2019; PRISM 2020; PSICC 2019). Most precipitation falls as snow to form a deep winter snowpack. This zone ranges in elevation from ca. 9,100 to 11,700 ft (2,700 to 3,600 m) (ARP 2019; PSICC 2019; USGS 2020). Subalpine fir grows on a wide range of soil types (Alexander et al. 1990).

In the Front Range, subalpine fir is a key member of subalpine forests (table 1; figs. 1, 4). Subalpine fir rarely grows in pure stands (ARP 2019; PSICC 2019). It most commonly grows in stands with Engelmann spruce; it is also commonly found growing in stands with lodgepole pine and quaking aspen (ARP 2019; PSICC 2019). Understories in stands with a subalpine fir component vary in their composition but commonly include heartleaf arnica (*Arnica cordifolia*), gooseberry currant (*Ribes montigenum*), and blueberry (*Vaccinium* spp.) (Johnston 1987; Peet 1981). Subalpine fir can be either a very long-lived seral species or a climax species (Alexander et al. 1990).

## *Ecology*

### *Reproductive Ecology*

While subalpine fir can reproduce vegetatively by layering, particularly near treeline, its primary mode of reproduction is by seed (Alexander et al. 1990; Holtmeier and Broll 2017). Reproductive maturity in the Front Range can occur around 25 to 30 years of age under open conditions, but can be delayed by many decades under closed canopies (Andrus et al. 2020b). An appreciable amount of viable seed may only be produced a couple times a decade (Noble and Ronco 1978). Seeds are wind-dispersed, and most probably fall within about 264 ft (80 m) of parent trees (Noble and Ronco 1978). Seeds that have been collected and stored indoors can lose viability quickly if not kept under ideal conditions, and so the longevity of seeds in the soil seedbank is probably only a year or so (Edwards 2008).

### *Ecology of Seedlings, Saplings, and Mature Trees*

Consistent with its preference for habitats with cold winters, cool summers, and deep winter snowpacks, subalpine fir is relatively intolerant of drought. Niinemets and Valladares (2006) assigned it a drought tolerance score of 2.0 out of 5.0, a score lower than that of all major Front Range tree species in the subalpine zone except quaking aspen. Seedling establishment events in the Front Range, for example, can be less apt to occur in years with lower spring snowpacks and/or with warmer and drier summer conditions than average (Andrus et al. 2018; Hessl and Baker 1997). The generally slow growth of mature subalpine fir trees also can be slowed further by warmer and drier conditions, particularly at sites that are already on the warm, dry end of the climatic spectrum (Alexander et al. 1990; Villabla et al. 1994). Increases in the mortality of mature subalpine fir trees can likewise be driven by warmer and drier conditions (Andrus et al. 2021; Bigler et al. 2007; Reich et al. 2016).

Subalpine fir is well-adapted to shade. Its shade tolerance score is 4.8 out of 5.0, which is higher than the scores given to its major tree associates in the Front Range (Niinemets and Valladares 2006). Subalpine fir seedlings in particular can germinate and establish in deep forest environments with a high degree of shade and a thick forest floor (Knapp and Smith 1982). Seedlings and saplings can persist in the understory for decades and then quickly release following a low- to moderate-severity overstory disturbance event such as an insect outbreak, as was found at the Fraser Experimental Forest on the AR (Collins et al. 2011). However, more severe overstory disturbance events that dramatically reduce shade can cause declines in seedling and sapling growth (Collins et al. 2011).

The high-elevation forests supporting subalpine fir generally experience significant wildfire events only once every ca. 200 to 500 years or longer (Romme and Knight 1981; Schoennagel et al. 2004; Sibold et al. 2006). Often these events occur in association

with extreme region-wide droughts, as climatic conditions in high-elevation forests are otherwise usually insufficient to support wildfire (Higuera et al. 2014; Sibold and Veblen 2006; Sibold et al. 2006). If wildfire can be supported climatically, fire behavior tends to be extreme due to high fuel loads, and subalpine fir mortality tends to be high (Schoennagel et al. 2004; Sibold et al. 2006). However, even when fire behavior is less severe, subalpine fir mortality can still be high, as it lacks any notable fire-resistant traits (Stevens et al. 2020). Subalpine fir establishment after wildfire tends to be protracted, peaking one to many decades following the establishment of an initial cohort of more shade-intolerant tree species like lodgepole pine, quaking aspen, or Engelmann spruce (Aplet et al. 1988; Veblen 1986; Veblen et al. 1991a). That said, subalpine fir can still make up a notable proportion of the initial postfire cohort, depending on patterns of burn severity and adjacent forest composition (Aplet et al. 1988; Schapira et al. 2021; Veblen 1986).

Subalpine fir decline, a complex but poorly understood disorder brought about by multiple interacting factors, is currently regarded as one of the most widespread causes of subalpine fir mortality in the Colorado Front Range (Harvey et al. 2021; Lalande et al. 2020; Reich et al. 2016). The western balsam bark beetle (*Dryocoetes confusus*), a native insect that preferentially kills older trees of low vigor, is typically a major contributor to subalpine fir decline (Harvey et al. 2021; Lalande et al. 2020). Beyond the western balsam bark beetle, contributors to the decline commonly include high stand density, drought, Armillaria (*Armillaria* spp.) root disease, and other insect and disease agents (Harvey et al. 2021; Lalande et al. 2020; Reich et al. 2016). A current, widespread decline event has been ongoing in the Front Range and across Colorado since the early 1990s; between 2008 and 2017, it killed subalpine fir trees across more than 1.8 million ac (0.7 million ha) (Harvey et al. 2021; Lalande et al. 2020; Reich et al. 2016). Surviving subalpine fir trees in the understory are commonly available to recruit into the overstory following subalpine fir decline, fostering resilience (Redmond and Kelsey 2018).

### *Potential Direct Impacts of Climate Change*

Climate change appears to have already caused increases in the mortality of mature subalpine fir trees in the northern Front Range (Andrus et al. 2021; Smith et al. 2015). Annual mortality rates due to climate-driven stress increased over a 37-year period (1982 to 2019), paralleling increases in summer climatic water deficit and the frequency of extremely warm (90th percentile) summer days. All four future climate scenarios would therefore be likely to cause additional increases in subalpine fir mortality rates, particularly the Very Hot and Dry scenario.

Climate change also has already driven reductions in the frequency of subalpine fir establishment events in the northern Front Range in recent years (Andrus et al. 2018). These reductions, observed over a 35-year period (1975 to 2010), were coincident with declining spring snowpacks and warmer and drier summer conditions. Further reductions in establishment events would therefore likely continue under all four future climate scenarios examined here, but would likely be the least severe under the Warm and Wet scenario and the most severe under the Very Hot and Dry scenario.

A bioclimatic envelope modeling study provides insight into how future climate change, and in particular the Hot future climate scenario, may lead to a net loss of suitable climate space for subalpine fir in the Front Range (Crookston 2009). Approximately 4.5 million ac (1.8 million ha) in the Front Range were estimated to be currently climatically suitable for this species (box 1; table 3; fig. 19). By 2060, only 3.4 million ac (1.4 million ha) were predicted to be climatically suitable, and by 2090, that number dropped to 1.3 million ac (0.5 million ha). Additionally, 23 percent (2060) and 71 percent (2090) of this suitable area was categorized as threatened, indicating that its climatic suitability was predicted to be marginal at best. Areas that were predicted to be climatically suitable for subalpine fir in 2060 and/or 2090 were typically at higher elevations relative to current climatically suitable areas.

### *Potential Indirect Impacts of Climate Change*

#### *Wildfire*

Climate change has already increased the frequency of drought in subalpine forests across the northern Front Range and surrounding area, leading to an increase in area burned that is unprecedented in the last 2,000 years (Higuera et al. 2021). Indeed, in just the last 20 years (2000 to 2020), the fire rotation interval for this landscape has shortened from every 204 to 315 years to 117 years (Higuera et al. 2021). The trend of increasing fire activity is likely to continue, especially under the Hot and the Very Hot and Dry climate scenarios (Heidari et al. 2021; Rangwala 2024, this report; Rocca et al. 2014; Temperli et al. 2015; Turner et al. 2022). Because subalpine fir is poorly adapted to survive even low-severity wildfire, continued increases in fire activity could drive major losses of the species (Stevens et al. 2020). Moreover, because subalpine fir can establish poorly in the first few decades after wildfire even under ideal climatic conditions, and because it is expected to have fewer establishment events under a warmer climate, these losses could be long-lasting (Andrus et al. 2018; Aplet et al. 1988; Davis et al. 2023; Veblen 1986; Veblen et al. 1991a).

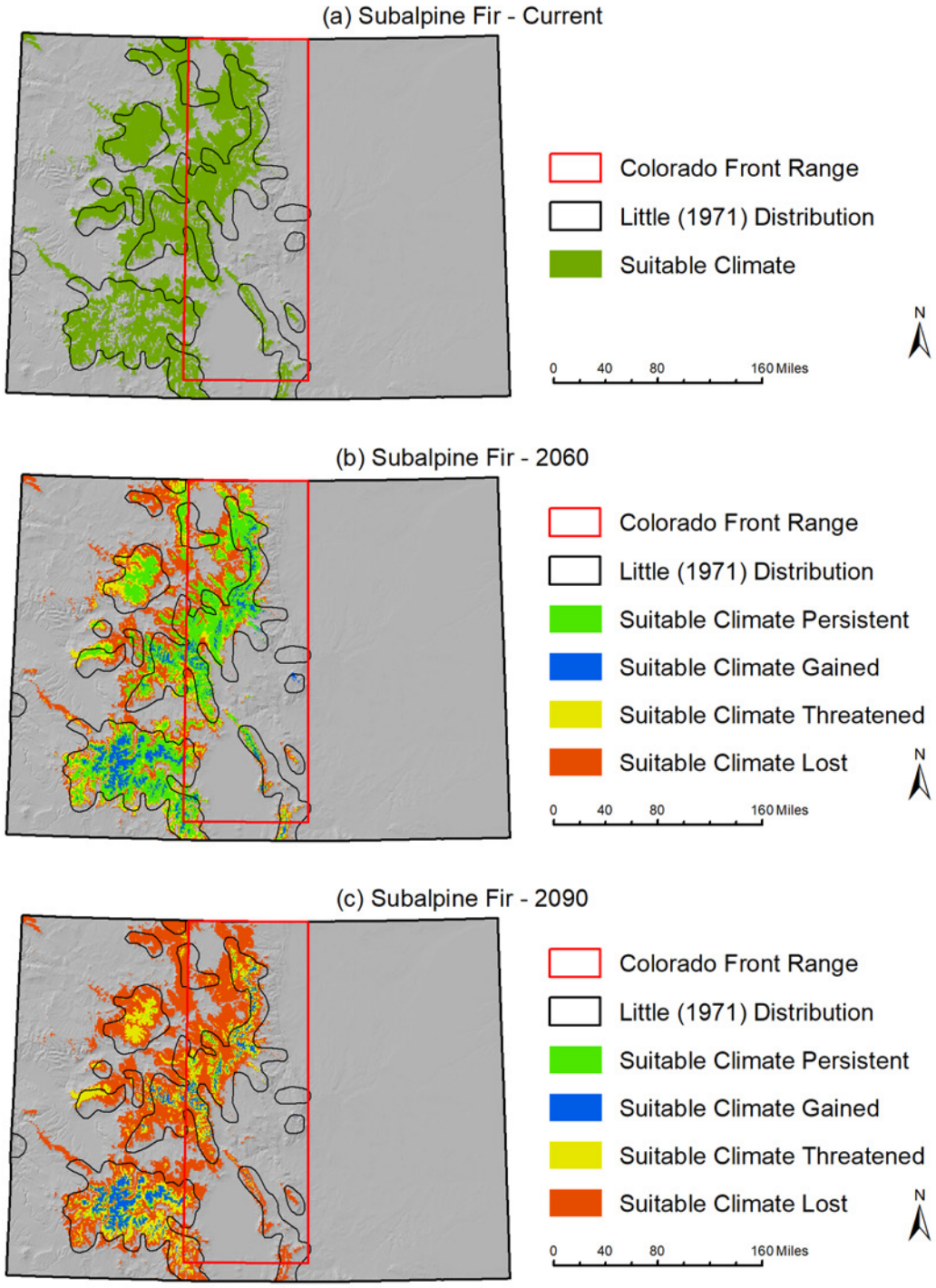



**Figure 19a-c—**The current and potential future suitable climate space of subalpine fir (Crookston 2009). Panel (a) depicts areas in Colorado where the current climate is suitable for the species. Panels (b) and (c) depict areas in Colorado where suitable climate in the future is predicted to be either lost, threatened, persistent, or gained under the HADCM3-A2 general circulation model (GCM), a GCM that crosswalks relatively well to the one representing our Hot future climate scenario. See box 1 for more information about how current and potential future climate suitability were determined. For all panels, the map of Little (1971) is used to represent the general current distribution of the species.

### *Insects and Diseases*

Severe drought appears to be a major driver of subalpine fir mortality attributed to subalpine fir decline; Harvey et al. (2021) showed that at the scale of the U.S. Rocky Mountains, the extent of subalpine fir decline increased during and following years with high Palmer Drought Severity Indices (i.e., extreme droughts). However, the role of warm, dry sites is less clear. Reich et al. (2016) found that in Colorado, the decline was concentrated in marginal portions of the Engelmann spruce-subalpine fir zone, where site conditions are relatively warm and dry relative to the core of the zone. Meanwhile, Harvey et al. (2021) found that in the Colorado Front Range, the decline was more prevalent in wetter sites, and speculated that this may be because wetter sites had greater subalpine fir abundance and therefore had more exposure to the decline's biotic components (e.g., western balsam bark beetles and *Armillaria* root disease) than their drier counterparts. Despite the uncertainty surrounding the role of site conditions, it is likely that subalpine fir mortality due to subalpine fir decline will become increasingly prevalent across the Front Range under a changing climate, particularly if climatic changes increase the frequency of extreme droughts, as the Hot, Very Hot and Wet, and Very Hot and Dry scenarios do.

Subalpine fir may potentially benefit from climate-driven insect outbreaks that kill co-occurring tree species. Rodman et al. (2022a) compiled field data from 16 studies conducted in beetle-impacted subalpine forests across the southern Rockies and analyzed the data to characterize postoutbreak forest recovery. They found that subalpine fir was dominant in only about 10 percent of the plots prior to the outbreaks, but after the outbreaks it was dominant in about 28 percent of the plots. Moreover, growth simulations done with the Forest Vegetation Simulator predicted that subalpine fir would be dominant in about 32 percent of the plots in 30 years. Subalpine fir dominance may be able to be retained through climatic change in some of these expanded sites, particularly those that are in cooler, wetter environments.

### *Capacity to Adapt to Climate Change*

A rainfall exclusion study of established subalpine fir and Engelmann spruce seedlings near Mount Evans indicated that both species acclimate poorly to summer drought conditions (Goke and Martin 2022). Net photosynthesis declines were twice as severe for spruce compared to fir, yet neither species showed significant stomatal control in response to drought treatments (Goke and Martin 2022). The authors suggest that seedlings of these species prioritize carbon assimilation over drought mitigation, which may leave them vulnerable to future droughts (Goke and Martin 2022). Yet traits like water use efficiency and photosynthetic capacity vary among adult individuals across open and closed canopy forests, suggesting saplings and mature trees exhibit a higher degree of physiological plasticity than seedlings (Broderson et al. 2006; Carter and Smith 1988; Knapp and Smith 1981).

The limited genetics research on subalpine fir in the Front Range suggests that the species has some potential to adapt evolutionarily to climate change. Shea (1990) collected genetic material of both Engelmann spruce and subalpine fir from two adjacent stands at Niwot Ridge, finding that the overall genetic diversity of fir was comparable to that of spruce as well as to that found elsewhere for other conifer associates, such as lodgepole pine and Douglas-fir. Shea (1990) also indicated that fir's genetic diversity was much greater across space than across age classes, likely due to site-related selection pressures and relatively short pollen and seed dispersal distances that limit gene flow.

Subalpine fir's current distribution indicates that there is some opportunity for it to migrate within the Front Range in response to climate change. The southern limit of this species currently extends into New Mexico, which may enable it to withstand any latitudinal range shifts that might occur (Alexander and Shepperd 1990; Little 1971). Additionally, there are opportunities for gains in climatically suitable area above the current upper elevational limit, although these are considerably smaller than projected losses at the species' lower elevational limit (Crookston 2009). However, subalpine fir's relatively large seeds with short dispersal distances, low fecundity, and time to maturity make it unlikely to migrate in pace with climate change.

## Engelmann Spruce (*Picea engelmannii* var. *engelmannii*)

**Climate change vulnerability rating:** moderate to high

**Confidence in climate change vulnerability rating:** moderate information with moderate to high agreement

We expect Engelmann spruce in the Front Range to be moderately to highly vulnerable to climate change. Increases in temperature are predicted under all four future climate scenarios. Warmer temperatures and concomitant reductions in available moisture will likely directly drive losses in spruce abundance and decreases in spruce growth, except perhaps at the coolest, wettest sites, where increases in temperature may benefit spruce. More significantly, though, warmer temperatures will likely indirectly drive losses in spruce abundance by driving increases in area burned and in spruce beetle activity; indeed, such increases have already been documented, particularly in the northern Front Range. Engelmann spruce's ability to migrate in response to a changing climate will likely be restricted by limited upslope opportunities, relatively short seed dispersal distances, and long generation times. Thus, any potential future gains in spruce habitat will likely be outweighed by losses in warmer, drier sites and in areas experiencing wildfire and/or spruce beetle disturbances.

### *Habitat*

Engelmann spruce is a broadly distributed North American conifer. It ranges from British Columbia and Alberta south to Arizona and New Mexico, and from Washington, Oregon, and California east to Montana, Wyoming, and Colorado (Alexander and Shepperd 1990; Little 1971; NRCS 2020). Engelmann spruce is prominent in the Front Range (ARP 2019; Little 1971; NRCS 2020; PSICC 2019). It is a major component of forests on roughly 1.2 million ac (0.5 million ha) of the PSI-AR, as well as on many thousands of other acres, such as at Rocky Mountain National Park (ARP 2019; PSICC 2019).

Engelmann spruce occupies high-elevation areas with long, cold winters and short, cool summers. Long-term (1981 to 2010) mean annual precipitation in the PSI-AR Engelmann spruce zone, for example, ranges from about 17 to 39 in (44 to 98 cm), while long-term mean annual temperature ranges from about 32 to 40 °F (0 to 5 °C) (ARP 2019; PRISM 2020; PSICC 2019). Most precipitation falls as snow, with a winter snowpack typically persisting from October or November to May or June. Engelmann spruce on the PSI-AR generally occurs from approximately 9,100 to 11,700 ft in elevation (2,700 to 3,600 m) (ARP 2019; PSICC 2019; USGS 2020). It often defines the upper treeline at the highest elevations, particularly on mesic sites and north-facing slopes. Engelmann spruce grows on a variety of soil types, so long as they are moist (Alexander and Shepperd 1990).

Engelmann spruce in the Front Range is a key subalpine forest species (table 1; figs. 1, 4). While it can grow in pure stands, it is most commonly found growing alongside subalpine fir (ARP 2019; PSICC 2019). It is also commonly found growing with lodgepole

pine, quaking aspen, and Rocky Mountain bristlecone pine (ARP 2019; PSICC 2019). Herbaceous and shrubby species in the understory of Engelmann spruce dominated and co-dominated forests are varied, but can include heartleaf arnica (*Arnica cordifolia*), gooseberry currant (*Ribes montigenum*), and blueberry (*Vaccinium* spp.) (Johnston 1987; Peet 1981). Engelmann spruce can be extremely long-lived (> 800 years old) and can therefore function as either a seral or a climax species (Alexander and Shepperd 1990; Brown et al. 1995).

## *Ecology*

### *Reproductive Ecology*

Engelmann spruce regenerates primarily from seeds; layering is not thought to contribute significantly to regeneration except near treeline (Alexander and Shepperd 1990; Holtmeier and Broll 2017). Engelmann spruce seed production is episodic and appears to be at least partially controlled by climate. For example, yearly seed production at the Fraser Experimental Forest was highly variable over a 40-year time period, with intermediate levels of production occurring regularly and high levels occurring only infrequently (Buechling et al. 2016). High seed production during this period was shaped by climatic conditions across multiple years, including low spring snowfall (and putatively increased growing season length) a year before seed dispersal and high summer temperatures in the year of seed dispersal (Buechling et al. 2016). The small, winged seeds are wind-dispersed, and most fall within 300 ft (91 m) of parent trees, although some seeds can fall as far as 600 ft (183 m) from parent trees (Alexander and Edminster 1983). Seeds reaching the soil seedbank are readily lost due to predation and a short viability window (Johnson and Fryer 1996).

### *Ecology of Seedlings, Saplings, and Mature Trees*

Engelmann spruce is only somewhat drought tolerant. Niinemets and Valladares (2006) calculated its drought tolerance score as 2.6 out of 5.0. The roots of Engelmann spruce seedlings develop slowly, making them particularly susceptible to dry conditions (Noble 1973). Alexander (1984) found that adequate soil moisture was a leading determinant of survival for seedlings growing in a seed sowing experiment at the Fraser Experimental Forest. Andrus et al. (2018) found that broad-scale Engelmann spruce establishment events in the northern Front Range tended to occur in years when the spring snowpack water content was greater than average and/or when summers were cooler and wetter than average. Hill et al. (2019) showed that on the Gunnison National Forest, Colorado, later dates of last frost (indicative of cooler, wetter conditions in late spring and early summer) were correlated with greater Engelmann spruce seedling establishment, but that there was a tension between it and longer frost-free periods, which also increased establishment. Drought can also affect mature Engelmann spruce trees, yet the direction of the response is often site-specific. For example, Villalba et al. (1994) found that Engelmann spruce trees on xeric sites in the northern Front Range tended to put on wider annual growth rings in years with wetter growing seasons than with drier growing seasons. Additionally, at xeric sites, they found that the rings of Engelmann

spruce trees tended to be wider when growing season temperatures were cooler than when they were warmer (Villalba et al. 1994). However, at mesic to hydric sites, greater precipitation did not tend to strongly affect growth as water was not limiting, and cooler temperatures actually decreased growth (Villalba et al. 1994). Bigler et al. (2007) showed that Engelmann spruce trees in the northern Front Range have experienced episodes of drought-induced mortality over the last ~100 years, with slower-growing trees more susceptible than faster-growing trees.

Engelmann spruce is tolerant of shade. It has a shade tolerance score of 4.5 out of 5.0 (Niinemets and Valladares 2006), only slightly lower than that of its most common associate, subalpine fir. In fact, researchers working in the northern Front Range have demonstrated that for seedlings, some degree of shading strongly enhances survival and growth, and on southern aspects, it is essential (Knapp and Smith 1982; Noble and Alexander 1977). The benefits of shade appear to diminish as Engelmann spruce ages (Jacobs 2011).

The forests supporting Engelmann spruce are adapted to infrequent, extensive, high-severity wildfire events. Historically, such events typically occurred once every ~200 to 500 years or longer, often in association with extremely dry regional climatic conditions (Romme and Knight 1981; Sibold and Veblen 2006; Sibold et al. 2006). These conditions predisposed forests, which generally contained abundant fuels, to extreme fire behavior over large areas (Schoennagel et al. 2004; Sibold et al. 2006). Mortality from fire was typically high, as Engelmann spruce does not have many fire-adapted traits that promote survival (Stevens et al. 2020). After historical wildfires, Engelmann spruce was commonly a prominent member of the initial cohort of regenerating trees, although this cohort could take one or more decades to establish (Aplet et al. 1988; Veblen 1986; Veblen et al. 1991a).

Spruce beetles (*Dendroctonus rufipennis*) are the most significant insect and disease agent of Engelmann spruce in the Front Range. This native species has long caused widespread and severe mortality when beetle populations reach epidemic levels, particularly for large mature trees (Hart et al. 2014b; Rodman et al. 2022a; Veblen et al. 1991b). Epidemics appear to be triggered, at least in part, by warmer and/or drier climatic conditions (DeRose et al. 2013; Hart et al. 2014a, 2017). One such epidemic has recently occurred across Colorado, affecting an estimated ~1.0 million ac (~400,000 ha) between 2009 and 2018 (Derderian et al. 2016; Hart et al. 2017; Hicke et al. 2020). Chapter 8 contains additional information about spruce beetles and other insects and diseases affecting Engelmann spruce (Negrón 2024, this report).

### *Potential Direct Impacts of Climate Change*

Three field-based observational studies have already documented negative climate change effects on Engelmann spruce in the Front Range. The first of these studies, conducted by Andrus et al. (2018), examined the frequency of broad-scale Engelmann spruce establishment events in the northern Front Range, and how these events were

tied to climate. As mentioned above, they found that establishment events tended to occur in years when the spring snowpack water content was greater than average and/or when summers were cooler and wetter than average. They also found that in the recent half of the study period (1975 to 2010), a downward trend in the number of establishment events coincided with trends of declining snowpacks and increasing summer temperatures and moisture deficits. The other two studies, conducted by Andrus et al. (2021) and Smith et al. (2015), examined how background mortality rates of mature Engelmann spruce trees at Niwot Ridge correlated with climate variability. Their findings indicated that mortality rates increased over a 37-year period (1982 to 2019), particularly in old growth stands, and that increases in mortality rates coincided with warmer and drier climatic conditions.

A field-based experiment by Kueppers et al. (2017) provides insight into how a warmer future climate may limit Engelmann spruce regeneration in the Front Range. Working at forest, treeline, and alpine sites at Niwot Ridge, the authors looked at how warming treatments affected the recruitment of Engelmann spruce seedlings over a 4-year period. They found that warming treatments decreased first-year seedling recruitment at all sites, including the treeline and alpine sites. However, seedlings became less sensitive to warming as they matured over the next 3 years, possibly because many of the most heat-sensitive individuals had already been culled.

The bioclimatic envelope modeling done by Crookston (2009) suggests that the availability of suitable climate space for Engelmann spruce will decline dramatically in the Front Range under a future climate analogous to that of our Hot scenario. Model results indicated that currently, approximately 5.8 million ac (2.3 million ha) are climatically suitable for this species (box 1; table 3; fig. 20). By 2060, only 3.1 million ac (1.2 million ha) were predicted to be climatically suitable; by 2090, that number fell to only 1.7 million ac (687,000 ha). Moreover, 20 percent (2060) and 82 percent (2090) of these suitable acres were categorized as threatened, meaning that their climatic suitability was predicted to be marginal at best.

Gray and Hamann (2013) also used bioclimatic envelope modeling to predict that, across the U.S. Rocky Mountains, future suitable climate space for Engelmann spruce would move up in elevation. They used an ensemble of 18 GCMs, and thus their results may be most comparable to our middle-of-the-road Hot future climate scenario. Specifically, they predicted that relative to the suitable climate space of the 1961 to 1990 reference period, the 2050 climate space of Engelmann spruce will be approximately 548 ft (167 m) higher.

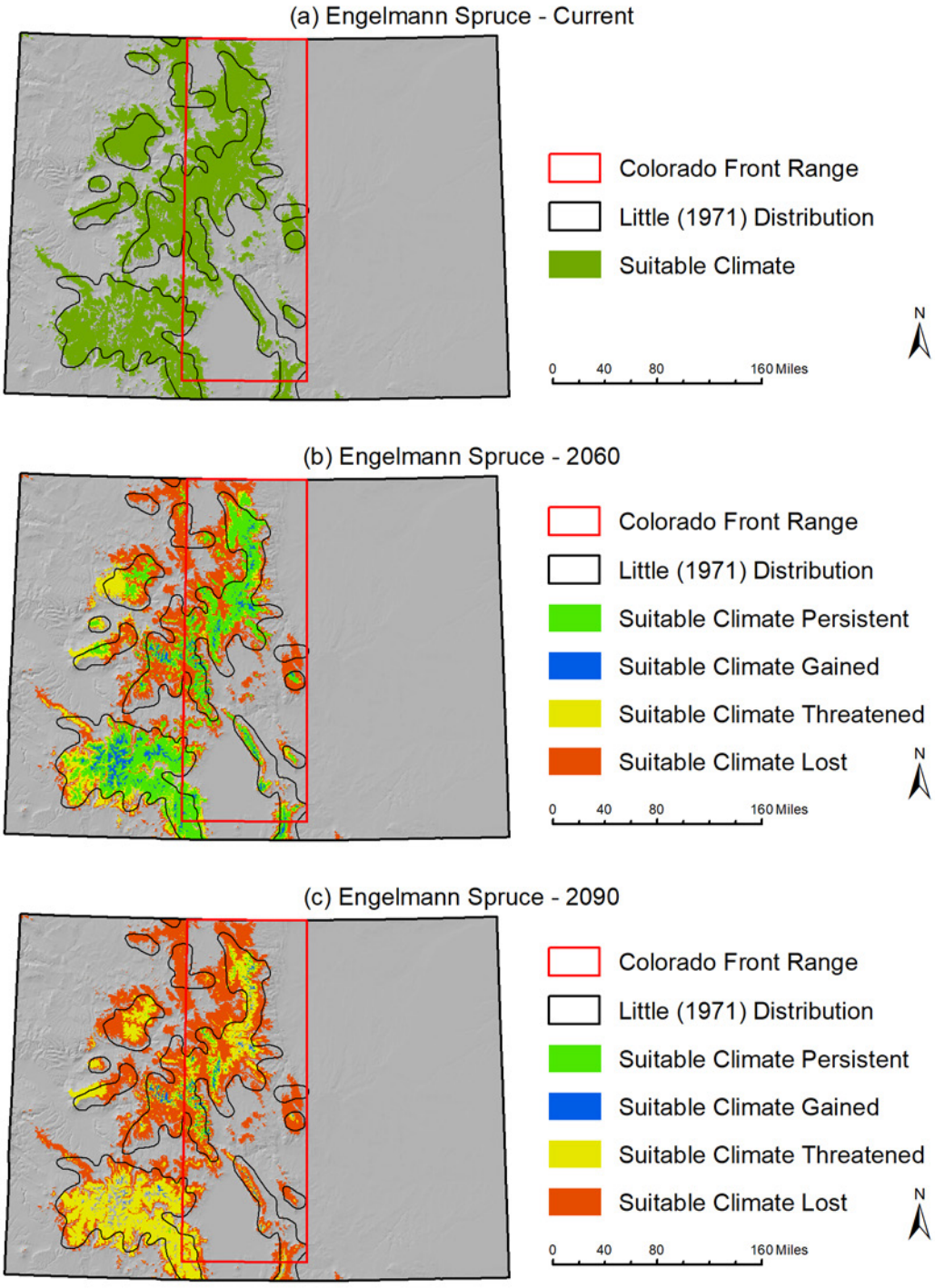



**Figure 20a-c—**The current and potential future suitable climate space of Engelmann spruce (Crookston 2009). Panel (a) depicts areas in Colorado where the current climate is suitable for the species. Panels (b) and (c) depict areas in Colorado where suitable climate in the future is predicted to be either lost, threatened, persistent, or gained under the HADCM3-A2 general circulation model (GCM), a GCM that crosswalks relatively well to the one representing our Hot future climate scenario. See box 1 for more information about how current and potential future climate suitability were determined. For all panels, the map of Little (1971) is used to represent the general current distribution of the species.

### *Potential Indirect Impacts of Climate Change*

#### *Wildfire*

Subalpine forests have naturally high fuel loads, and historically they tended to burn with stand-replacing severity every two or more centuries during extreme drought years (Higuera et al. 2014; Sibold and Veblen 2006; Sibold et al. 2006). Climate change is increasing the frequency of drought in subalpine forests, leading to an increase in annual area burned that is unprecedented in the last 2,000 years (table 2; Higuera et al. 2021). The record-setting 2020 wildfire season exemplified this: the drought-driven Cameron Peak, East Troublesome, and Williams Fork Fires together burned over 412,000 ac (167,000 ha) in the northern Front Range, often as crown fires that resulted in considerable Engelmann spruce mortality (table 2; Rodman et al. 2022b). Increases in area burned are likely to continue in the future, especially under the warmest and driest future climate scenarios (Heidari et al. 2021; Rocca et al. 2014; Temperli et al. 2015; Turner et al. 2022; Yue et al. 2013). Engelmann spruce is poorly equipped to survive even low-severity fire, and thus future increases in fire activity would be expected to drive considerable increases in mortality (Stevens et al. 2020).

Engelmann spruce is adapted to recover from its native stand-replacing wildfire regime through postfire seedling establishment (Aplet et al. 1988; Veblen 1986; Veblen et al. 1991a). While protracted seedling establishment following wildfires is not necessarily uncharacteristic for the species, a changing climate already appears to be slowing establishment rates (Andrus et al. 2018, Aplet et al. 1988; Davis et al. 2023; Veblen 1986; Veblen et al. 1991a). Future climatic changes over the next 10 to 30 years may further restrict seedling establishment, particularly at lower-elevation and south-facing sites (Davis et al. 2023).

#### *Insects and Diseases*

Recent spruce beetle outbreaks have caused substantial losses of mature, large-diameter spruce trees across the western United States, including on the PSI-AR (fig. 21; DeRose et al. 2013; Hart et al. 2017; Hicke et al. 2020; Rodman et al. 2022a). Warmer and/or drier conditions appear to have played an important role in fostering recent outbreaks. For example, Hart et al. (2017) found that in the southern Rocky Mountains, the initiation and spread of recent bark beetle outbreaks were positively associated with various measures of drought. Similarly, DeRose et al. (2013) found that across the Interior West, higher maximum summer and minimum winter temperatures were related to spruce beetle outbreak occurrences. Collectively, these authors posit that warmer, drier conditions may have increased beetle survival and reproduction, while simultaneously stressing trees and reducing their capacity to defend against beetle attacks. Moreover, analyses conducted with a range of GCMs suggested that continued warming and drying will exacerbate outbreaks, at least until host trees are depleted (DeRose et al. 2013; Foster et al. 2018; Temperli et al. 2015).

**Figure 21—**Recent spruce beetle outbreaks have killed a large number of Engelmann spruce trees in the Front Range, including these trees near the Long Draw Road on the Roosevelt National Forest. Warm and/or dry conditions appear to have played an important role in fostering these outbreaks (DeRose et al. 2013; Hart et al. 2017). Continued warming and/or drying will likely exacerbate outbreaks, at least until host trees are depleted (DeRose et al. 2013; Foster et al. 2018; Temperli et al. 2015). USDA Forest Service photo by Paula Fornwalt.

Following the mortality of mature Engelmann spruce trees due to spruce beetle, spruce recovery is most commonly facilitated by subcanopy trees that established prior to the outbreak (Andrus et al. 2020a; Redmond and Kelsey 2018; Rodman et al. 2022a; Veblen et al. 1991b). In contrast to wildfire, it is uncommon for a stand previously dominated or co-dominated by spruce to be completely devoid of preoutbreak spruce trees (Andrus et al. 2020a; Rodman et al. 2022a; Veblen et al. 1991b). The vulnerability of these surviving trees, and of any newly establishing trees, to climate change would likely be similar to that of undisturbed stands (Andrus et al. 2018; Crookston 2009; Gray and Hamann 2013; Kueppers et al. 2017).

### *Capacity to Adapt to Climate Change*

Research on Engelmann spruce plasticity, while limited, suggests that seedlings have little innate ability to tolerate climate change. Goke and Martin (2022) conducted a two-year rainfall exclusion study of established Engelmann spruce seedlings near Mount Evans, and their findings indicated that spruce seedlings acclimated poorly to simulated drought conditions. Relative to ambient conditions, spruce seedlings exposed to simulated drought exhibited net photosynthesis declines of 78 percent, and they showed little ability to close stomates to increase water use efficiency (Goke and Martin 2022). However, larger spruce seedlings showed better stomatal control than smaller seedlings, suggesting that individuals may be able to better respond to drought as they grow (Brodersen et al. 2006; Goke and Martin 2022; Knapp and Smith 1981).

The genetic diversity of Engelmann spruce may afford it some opportunity to evolutionarily adapt in situ to climate change. Shea (1990) found a fair amount of genetic diversity across individuals at Niwot Ridge, for example. That said, Shea (1990) also found that for individuals in very close proximity (around 177 ft [54 m]), genetic diversity was much more limited, and is probably an artifact of local selection pressures and limited gene flow due to short pollen and seed dispersal distances.

Engelmann spruce may also have some ability to withstand climate change in the Front Range through migration. The species is broadly distributed, which could potentially allow for latitudinal and elevational migration within the current Engelmann spruce zone (Rehfeldt 2004). Elevational migration above the current Engelmann spruce zone is also possible, although it will likely be highly constrained by topography (Crookston 2009; Gray and Hamann 2013). Moreover, the migration of Engelmann spruce both latitudinally and elevationally is likely to be hampered by a variety of factors, including seed dispersal distances and the time required to reach reproductive maturity; thus, migration rates are unlikely to keep pace with climate change (Alexander and Edminster 1983; Alexander and Shepperd 1990).

# Conclusions

## Take-Home Trends

In writing this chapter, we aimed to provide land managers with detailed assessments of the vulnerability of nine major tree species in the Front Range to climate change. A summary of our assessments is presented in table 4.

**Table 4—**The climate change vulnerability rating assigned in this assessment of nine major tree species in the Colorado Front Range, along with the confidence in that rating.

| Species | Vulnerability rating | Confidence in vulnerability rating |
|---|---|---|
| Twoneedle pinyon | Moderate | Limited information with moderate agreement |
| Ponderosa pine | Moderate | Moderate information with high agreement |
| Douglas-fir | Moderate | Moderate information with high agreement |
| Lodgepole pine | Moderate to high | Moderate information with moderate agreement |
| Quaking aspen | Moderate | Moderate information with moderate agreement |
| Limber pine | High | Moderate information with moderate agreement |
| Rocky Mountain bristlecone pine | Moderate to high | Moderate information with moderate agreement |
| Subalpine fir | Moderate to high | Limited information with moderate agreement |
| Engelmann spruce | Moderate to high | Moderate information with moderate to high agreement |

As our confidence ratings suggest, a major trend that emerged is that the vulnerability of all tree species is somewhat uncertain due to unknown patterns and rates of future climate change, as well as due to research gaps and conflicting research findings. Thus, though our vulnerability assessments were grounded in the available relevant literature, we view them more as educated guesses than as definitive evaluations. Some species were particularly understudied. For example, very little research has been done on twoneedle pinyon in the Front Range, one of the few species that may stand to benefit under climate change. However, even for more well-studied species such as ponderosa pine and Engelmann spruce, our confidence in the overall vulnerability rating was never particularly high. Additional research for each of the nine tree species would help boost this confidence.

Differences in vulnerability ratings across tree species indicate that lower-elevation species such as twoneedle pinyon, ponderosa pine, and Douglas-fir may be somewhat less vulnerable to climate change than higher-elevation species like Engelmann spruce, subalpine fir, and Rocky Mountain bristlecone pine. Other vulnerability assessments have arrived at similar conclusions, including those done for the northern Rocky Mountains of Idaho, Montana, and Wyoming, and for the Pacific Northwest of Washington and Oregon (Devine et al. 2012; Hansen and Phillips 2015; Keane et al. 2018). In part, this trend may be because lower-elevation species tend to have more opportunities for upslope migration, and because they tend to be more adapted to frequent disturbance, especially wildfire.

A final trend worth noting is that climate change appears poised to impact tree species more through indirect mechanisms than direct ones. In particular, climate change × wildfire interactions have the potential to cause significant mortality across large areas of each species' range, and for most species, to drive major declines in subsequent tree establishment. Insects and disease are also expected to interact with climate change to cause significant negative impacts for many species.

## Adaptation Strategies

It was beyond the scope of this chapter to translate our assessments into adaptation strategies that managers could implement to reduce ongoing and anticipated negative climate change impacts to Front Range forests and woodlands (Peterson et al. 2011). This is clearly a critical next step. Fortunately, many managers are already conducting activities that should help buffer forests and woodlands from climate change effects. For example, tree thinning treatments are occurring across the ponderosa pine and Douglas-fir zones to reduce high-severity wildfire risk stemming from overly dense forest conditions and ongoing and future climate warming (Barrett et al. 2021; Briggs et al. 2017; Cannon et al. 2018). Not only should these treatments mitigate wildfire risk, they should improve the vigor of the remaining trees and decrease their potential for mortality due to drought (Bradford et al. 2022). Similarly, planting treatments are ongoing in the ponderosa pine and Douglas-fir zones in areas where these species are not naturally re-establishing after high-severity wildfire (Guiterman et al. 2022; Marshall et al. 2023). In box 2, we highlight an adaptation strategy that is being implemented to conserve limber pine and RM bristlecone pine in the face of white pine blister rust, climate change, and other stressors. We hope that the content presented in this chapter can aid managers as they develop additional adaptation strategies to help Front Range forests and woodlands weather changing climatic conditions.

**Box 2**

## Adapting limber pine and Rocky Mountain bristlecone pine to promote their persistence in the face of white pine blister rust, climate change, and other stressors

*Cronartium ribicola*, the nonnative fungal pathogen that causes the lethal disease white pine blister rust, was first discovered in Colorado in 1998 on limber pine on the Roosevelt NF and in 2003 on Rocky Mountain bristlecone pine (along with limber pine) on the San Isabel NF and the Great Sand Dunes National Park and Preserve. Since then, the pathogen has continued to spread. It is estimated that more than half of the limber and Rocky Mountain bristlecone pine habitat in Colorado regularly has climatic conditions suitable for blister rust invasion and the other portions may also become infected as the pathogen becomes more common on the landscape (Howell et al. 2006; Kearns et al. 2014). The life cycle of *C. ribicola* requires two hosts: a five-needle white pine and an alternate host, most commonly *Ribes* spp. (McDonald et al. 2006). Infections are shed annually by the deciduous alternate hosts and are perennial on the pine hosts and accumulate over the life of the tree (Geils et al. 2010). The airborne spores of the pathogen produced on the alternate host enter the tree via needles and the fungus colonizes the branches and grows into the tree bole (fig. 16). The resultant cankers kill branches and eventually the tree. White pine blister rust infects and kills trees of all ages and threatens population sustainability. Branch mortality reduces seed production, reducing regeneration capacity well before tree mortality. Regeneration capacity is further reduced by seedling mortality.

The compounding effects of blister rust, as well as mountain pine beetle, Ips beetle, and dwarf mistletoe, in a warming climate threaten the persistence of limber pine and Rocky Mountain bristlecone pine and their ecosystems. These same stressors have impacted whitebark pine in the northern U.S. Rockies to such an extent that the species was listed as Threatened under the Endangered Species Act in fall 2022 (USFWS 2022). The proportion of dead limber pine lags behind that observed in whitebark pine by approximately a decade, suggesting that limber pine populations may be following a similar trajectory as whitebark pine (Goeking and Windmuller-Campione 2021). Limber pine is already proposed for listing under the Canadian Species at Risk Act (COSEWIC 2014; Government of Canada 2012).

Active management is recommended in the southern U.S. Rockies to accelerate adaptation to white pine blister rust and prevent limber pine and Rocky Mountain bristlecone pine from following the same trajectory as whitebark pine or limber pine to the north (Burns et al. 2008; Schoettle et al. 2019a). Paramount to this effort is increasing the number of trees with genetic resistance to blister rust in forest stands through seedling planting and protecting resistant seed trees from mortality by other stressors (e.g., mountain pine beetle and fire). Although blister rust and these pines have not co-evolved, low levels of genetic resistance to the pathogen naturally occur in both species (Schoettle et al. 2011, 2014, 2022b). However, more work is needed to identify trees and populations with genetic resistance. Including limber pine and bristlecone pine in postdisturbance planting mixes with other species (e.g., Engelmann spruce) would help forest recovery on the harsher portions of the treatment area and provide trees in the area that will spread genetic resistance traits in pollen and seed to nearby pines and forests. Because these pine species mature so slowly, proactively establishing trees with blister rust resistance in healthy stands in anticipation of blister rust invasion is also recommended to accelerate the increase and spread of disease-resistant genes (Schoettle et al. 2019b, 2022a).

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