



Mixed Conifer Forests in the San Juan Mountain Region of Colorado, USA: The Status of Our Knowledge and Management Implications

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ROCKY MOUNTAIN
RESEARCH STATION



San Juan Headwaters
FOREST HEALTH PARTNERSHIP

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Cover photo credit: A cool dry mixed conifer forest in the San Juan Mountain region. Photo credit: Michael Remke.

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management efforts and research needs, with specific local information relating to the San Juan Mountain region. This synthesis was inspired by the 2010 Mixed-Conifer Forests in Southwest Colorado: A Summary of Existing Knowledge and Considerations for Restoration and Management (Pelz 2010) lead by CFRI and requested on behalf of the San Juan Public Lands Center and the Pagosa Ranger District in 2009, and serves as an update to the 2010 knowledge synthesis.

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CSU is founded as a land-grant institution, and we accept that our mission must encompass access to education and inclusion. And, significantly, that our founding came at a dire cost to Native Nations and peoples whose land this University was built upon. This acknowledgment is the education and inclusion we must practice in recognizing our institutional history, responsibility, and commitment.



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Executive Summary

The purpose of this knowledge synthesis is to compile and synthesize current and best available science for mixed conifer forest ecology and management to inform future management efforts and research needs, with specific local information relating to the San Juan Mountain region, USA. To compile and synthesize latest best available science relating to mixed conifer forests in this region, we draw on literature from the San Juan Mountain region, and utilize studies across Colorado, the southern Rocky Mountains, and the western United States. Whenever we derive information from outside of our focal area, we attempt to make insights from studies that are applicable to mixed conifer forest ecosystems in the San Juan Mountain region.

Broadly, mixed conifer forest types are defined as forests with more than two conifer species, and generally exist in elevation ranges between ponderosa pine and spruce-fir forests in the Rocky Mountains. These forest types have traditionally been defined as either Warm/Dry, Cool/Dry, or Cold/Wet (or similar variations). It is important to note that for any given site, multiple varieties of mixed conifer forests could exist within a stand or in adjacent stands. Therefore, we provide a brief description of the silvics of the common tree species found in the mixed conifer forests of the San Juan Mountain region. To account for commonly used definitions of mixed conifer forests in the literature, we first define each forest type and the primary factors associated with each forest type, and then for each forest type we provide more detailed information regarding common disturbances (e.g., fires, insects, and diseases), successional trajectories, impacts of climate change and compounding disturbances, and management implications. We also provide information detailing the degrees of confidence (e.g., low, moderate, or high) we have in successional trajectories, disturbances, compounding disturbances, climate change, or management implications based on the quality and availability of the scientific literature for that specific forest type and consideration.

A clear emergent theme across all mixed conifer forest types in the San Juan Mountain region is the dynamic nature of these forests, and that complexity must be embraced in our understanding of how these forests came to be over time and how these forests will respond to any single disturbance, compounded disturbances, or management actions, particularly in an era of changing temperature, drought, and disturbances. Given the diverse array of human values, micro- and macro-climatic gradients, soils, and topographic features relating to these forests, we suggest that they should be managed in ways which can promote this complexity. Importantly, additional perspective on local social and economic considerations is needed to guide the management decisions that may occur in these forests. At stand and project levels, managers of mixed conifer forests may benefit from incorporating and adopting principles of Ecological Forestry (EF), which may provide exciting opportunities for managers and stakeholders to embrace the complexity of these forests with curiosity and intention. Lastly, we suggest that without sustained research and monitoring efforts, the performance of active versus passive management strategies in these complex forests remains mostly unknown, limiting potential for future learning, investment, and application throughout the region.

Introduction

The purpose of this knowledge synthesis is to compile and synthesize current and best available science for mixed conifer forest ecology and management to inform future management efforts and research needs, with specific local information relating to the San Juan Mountain region, USA. Mixed conifer forests of the San Juan Mountain region cover ~880,000 ac across southern Colorado and northern New Mexico (LANDFIRE 2016). Mixed conifer forests make up 36% of forests in this region and are very important for multiple ecosystem services, including: supporting a wide variety of moss, lichen, fungal, garminoid, herbaceous, and shrub species; providing critical habitat for multiple wildlife species, in particular Canada Lynx; important watershed functioning and provision; carbon sequestration; and high-quality economic, recreation, aesthetic, cultural and spritual values. Despite the numerous benefits of mixed conifer forests in Colorado and across the world, the definitions of mixed conifer forests vary, and commonly used terms refer to forest types with different climatic characteristics. Simplified forest type delineations of mixed conifer forests create challenges in understanding the deeper ecology and management of these diverse forests. For this knowledge synthesis, we are focusing on mixed conifer forests of the southern Rocky Mountains, specifically those in southwestern Colorado and northern New Mexico in the San Juan Mountain region (Figure 1). Whenever possible, we draw on literature primarily from the San Juan Mountain region. We also use studies across Colorado, the southern Rocky Mountains, and the western United States but whenever we derive information from outside of our focal area, we attempt to make insights from studies that are applicable to mixed conifer forest ecosystems in the San Juan Mountain region. Broadly, mixed conifer forest types are defined as forests with more than two conifer species. Mixed conifer forests generally exist in elevation ranges between ponderosa pine and spruce-fir forests in the Rocky Mountains (Verkat 2013). These forest types have traditionally been defined as either Warm/Dry, Cool/Dry, or Cold/Wet (or similar variations (e.g., “Cold/Moist”)) in the scientific literature, particularly in North America (Pelz 2010; see definitions below). Various environmental factors shape all mixed

conifer forests including soils, topography, climate, and disturbance history. To account for commonly used definitions of mixed conifer forests in the literature, we first define each forest type and the primary factors associated with each forest type, and then for each forest type we provide more detailed information regarding common disturbances (including fires, insects, and diseases), successional trajectories, impacts of climate change, and management implications. It is important to note that for any given site, multiple varieties of mixed conifer forests could exist within a stand or in adjacent stands (Verkat 2013). Therefore, we provide a brief description of the silvics of the common tree species found in the mixed conifer forests of the San Juan Mountain region. The characteristics of stands adjacent to the stand of interest will influence and determine processes within a focal stand, thus understanding the factors influencing these stands is of critical importance (Parks et al., 2019, Meigs et al., 2020). Additionally, these factors exist on a continuum rather than in discrete categories, so stand conditions will likely be represented by a mix of categories outlined below for specific site conditions (Verkat 2013). For the purposes of this review, we will include a full continuum of mixed conifer types including, at the Warm/Dry end, pure ponderosa pine (*Pinus ponderosa*) forest, and, at the Cold/Wet end, spruce-fir (*Picea-Abies*) forests. Other species, such as Gambel oak (*Quercus gambelii*) and quaking aspen (*Populus tremuloides*) are sprouting species which are present to varying degrees in mixed conifer forest in the San Juan Mountain region and will be included in multiple mixed conifer types.

Determining Forest Type

Determining forest type is often considered an act of recognizing expected dominant or historical dominated tree species based on various site conditions, mostly related to climatic zones (Evans et al., 2017), though soils are likely equally important (Bowker et al., 2012). Mixed conifer forests exist as a spectrum of varying species compositions between pure ponderosa pine forests at the lower elevations and spruce-fir forests at the higher elevations (Verkat et al., 2013; Figure 2). These forest types are traditionally defined on relative climatic zones as Warm/Dry (hereafter WD), Cool/Moist (hereafter CM), and Cold/

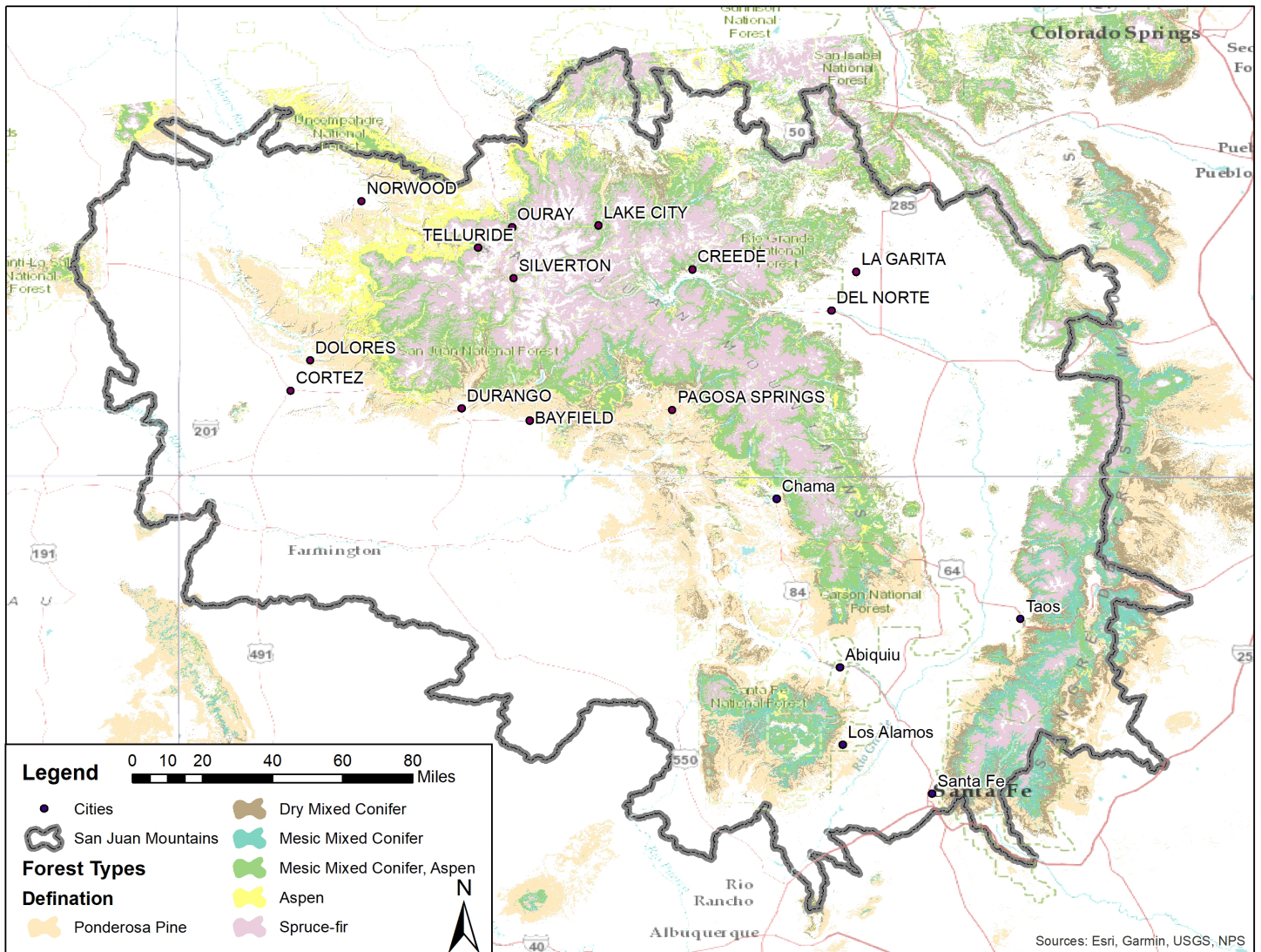


Figure 1: Map of the San Juan Mountain region, based on Hydrologic Unit 8 watersheds that include the San Juan River, Animas River, Rio Grande River, Dolores River, and Gunnison River. Forest types are based on LANDFIRE (2016); “Dry Mixed Conifer” most closely aligns with our definition of “Warm/Dry” forests, “Mesic Mixed Conifer and Mesic Mixed Conifer, Aspen” most closely align with our definition of “Cool/Dry” forests, and “Spruce-fir” mostly closely align with our definition of “Cold/Wet” forest, particularly at lower elevations as opposed to higher elevations where Engelmann spruce and subalpine fir are co-dominant with no other species present. This area encompasses southwest Colorado, northwest New Mexico, and small portions of northeast Arizona and southwest Utah, USA.

Wet (hereafter CW) mixed conifer forests (Evans et al., 2017). It is important to note these definitions can represent forest types across broad regions that vary widely in specific tree compositions and silvics. Often, mixed conifer forests are defined as Warm/Dry or Cold/Wet which represent opposite extreme ends of the continuum; we offer the additional Cold/Dry classification as an intermediate forest type to demonstrate more detailed perspective. Cool/Dry forests may be managed as Warm/Dry or Cold/Wet forests to better fit resource management plans based on site conditions. This discussion will focus

on mixed conifer forests in the San Juan Mountain region with a specific focus on northern New Mexico and southern Colorado.

Soils in this region are highly variable due to a wide array of geologic parent materials with growing conditions ranging from montmorillonite clays derived from shales to weathered igneous soils and grus with high nutrient content that are well drained. Soil characteristics vary across spatial scales on the scale of sub-meter to kilometers. On smaller spatial scales erosion and deposition patterns as

they relate to slope, aspect and topographic position are important drivers in soil characteristics whereas at larger spatial scales parent material is a strong driver. Soil conditions can exacerbate or mitigate stressors from climate to influence forest structure and patterns of mortality (Bowker et al., 2012) and soil biota from legacy trees post-disturbance can have strong implications on future tree regeneration (Simard et al., 2021, Remke et al., 2020).

Climatic zones in this region can vary by both large-scale and small scales. At larger scales, elevation and physical geographic features exert a strong influence on forest vegetation. From this perspective, lower elevations, southerly aspects, and locations further from mountainous topography or on the rain shadow

side of the mountains tend to be composed of WD mixed conifer forest types, whereas higher elevations and locations proximal to the windward (wet side) of mountainous topography drive species compositions towards CW mixed conifer forest types. These same factors can also influence the productivity and growth rate of forests where warmer and wetter sites may grow faster than colder, wetter sites. For example, in southern Colorado, mixed conifer forests near Pagosa Springs are much warmer and wetter than forests at similar elevations in the rain shadow northeast of the San Juan Mountain region; consequently, forests near Pagosa Springs tend to grow faster with higher regeneration rates than those near La Garita, CO where the local geography creates a rain shadow resulting in colder and drier conditions (Figure 1).

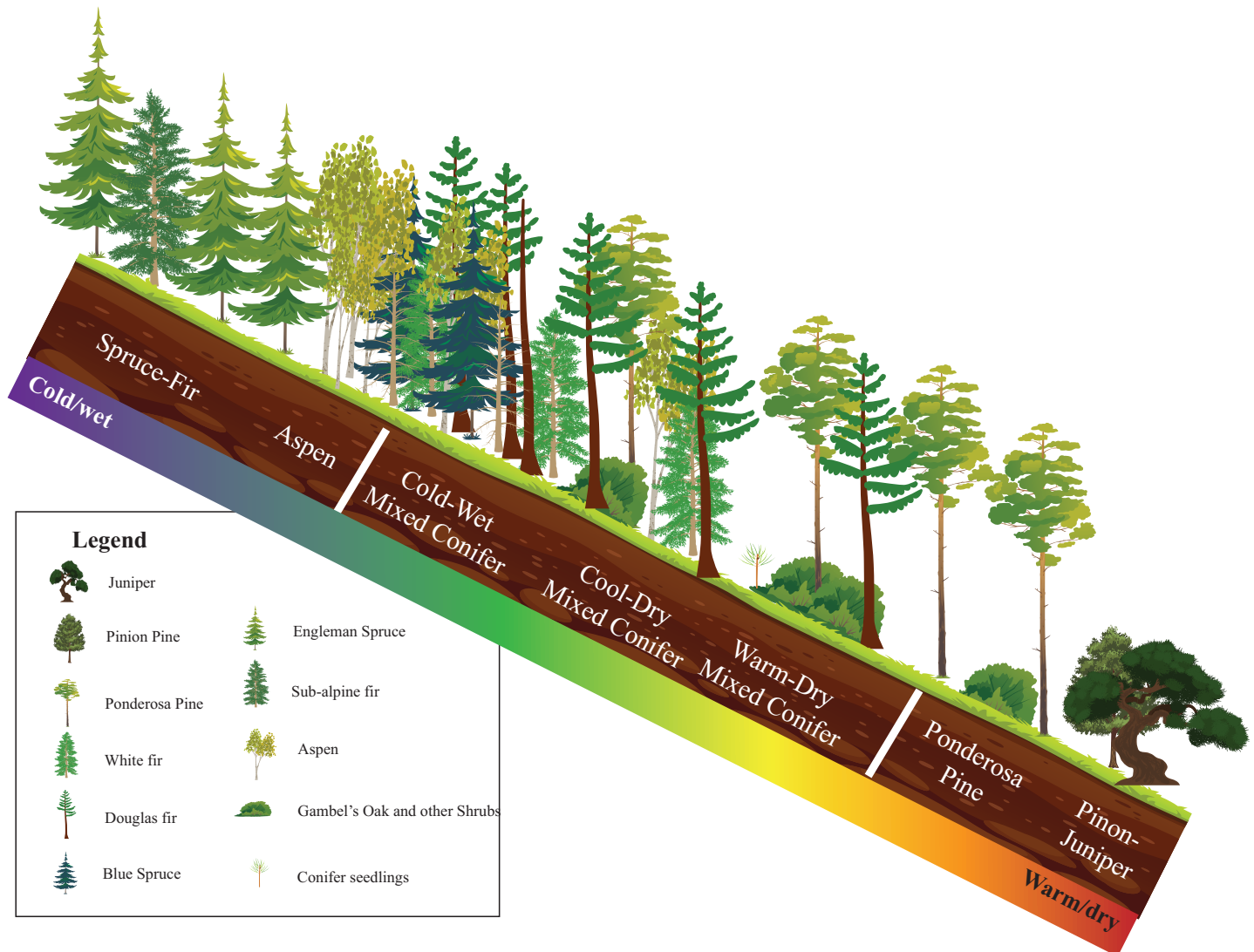



Figure 2: Graphical representation of forest types in the San Juan Mountain region represented on a hillslope where the lowest elevations are the warmest /driest sites and higher elevations are the coldest/wettest. Forest types not discussed in detail in this knowledge synthesis, such as pinon-juniper are still depicted for reference.

On a smaller or more local scale, topographic position has a strong effect on climatic zone and thus species composition (Figure 3). These local influences on climatic zone can occur on scales of site-to-within-stand specific variation. Here, wet sites will be found more commonly at valley bottoms and on more northerly aspects whereas drier sites will be more common on ridge tops and on south facing aspects. Soils also vary on small and larger scales and can be thought of as a factor that exacerbates or mitigates the climatic traits of a specific zone. For example, soils with more clay (Alfisols) tend to have a higher water holding content and thus can better retain moisture, whereas sandier soils (Andisols and Inceptisols) tend to drain faster and thus reduce available moisture (Bowker et al., 2012).

Lastly, it is important to note and understand that these forest types are found on the landscape on a continuum and are not discrete classifications, rather, the discrete classifications outlined here are to give a central point of comparison to initiate discussion and understanding of stand specific characteristics and desired conditions. This continuum can occur on small-to-large scales and thus the forest characteristics immediately surrounding a given stand will influence the dynamics within the stand of interest. As an example, a dry mixed conifer forest surrounded by wet mixed conifer may experience less frequent fire than dry forest types surrounded by adjacent dry forests (Verkat 2013). Forest characteristics in the present may also be the result of ecological processes and anthropogenic alterations

Table 1: Key characteristics of each mixed conifer forest type.



Warm/Dry	Cool/Dry	Cold/Wet
<p>Tree species composition: <i>Dominant:</i> Ponderosa pine <i>Codominant/subdominant:</i> Douglas-fir, white fir (primarily in understory)</p> <p>Common understory vegetation: <i>Shrub:</i> persistent Gambel oak and serviceberry <i>Forbs:</i> Spring Beauty, Blue eyed Mary, Bedstraw, Bastard toadflax <i>Graminoids:</i> Gyer's sedge, Kentucky bluegrass and squirrel tail, Idaho fescue</p>	<p>Tree species composition: <i>Dominant:</i> Douglas-fir <i>Subdominant:</i> White fir, limber pine, Southwestern white pine, ponderosa pine, aspen</p> <p>Common understory vegetation: <i>Shrub:</i> Gambel oak, serviceberry, snowberry, chokecherry, and Rocky Mountain maple. <i>Forbs:</i> Daisey species, larkspur <i>Graminoids:</i> Gyer's sedge</p>	<p>Tree species composition: <i>Dominant:</i> Blue spruce, Engelmann spruce, White fir, subalpine fir, limber pine <i>Subdominant:</i> aspen</p> <p>Common understory vegetation: <i>Shrub:</i> Gooseberry, elderberry, snowberry, Rocky Mountain maple, raspberry, and thimbleberry. <i>Forbs:</i> Monk's hood, columbine, calypso orchid, nodding sunflower, osha <i>Graminoids:</i> Gyer's sedge</p>
<p>Factors influencing vegetation development:</p> <ul style="list-style-type: none"> • Dry site growing conditions (e.g., low elevations, ridgetops, south slopes, well drained soils) • Frequent, low- and mixed-severity disturbance. These forests are more prone to - and supported by - frequent, low- and mixed-severity fire 	<p>Factors influencing vegetation development:</p> <ul style="list-style-type: none"> • Intermediate growing conditions (e.g., mid-elevations and mid-slopes, all aspects; soils or microsites that hold moisture better than adjacent dry sites, but receive more solar radiation than adjacent colder, wet sites) • Intermediate disturbance and mixed severity fire. These sites have longer times in between fires and thus have more fuel accumulation 	<p>Factors influencing vegetation development:</p> <ul style="list-style-type: none"> • Wet site growing conditions and areas of cold air (e.g., high elevations, valley bottoms, north slopes, and poorly drained soils) • Infrequent, typically high severity disturbances. These forests are prone to large scale insect disturbances and large, high severity fires with fire return intervals of 100-800 years

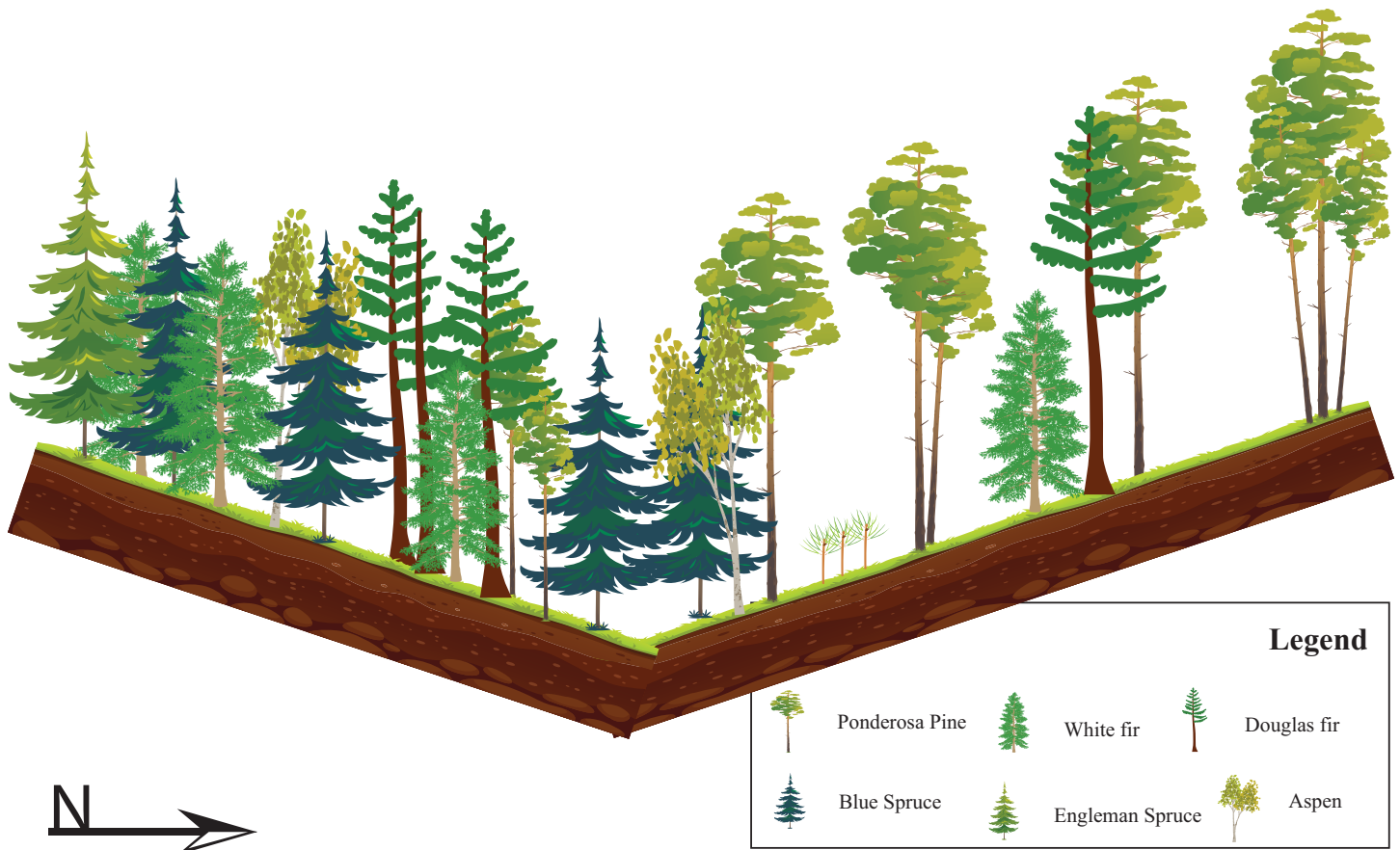


Figure 3: Translating mixed conifer forests from the idealized elevation gradient slope to a smaller scale example drainage with north and south facing slopes. This example of finer scale conditions illustrates an example of how mosaics of forest types are created over smaller areas.

rather than environmental characteristics alone. As an example, many WD mixed conifer forests have less Douglas-fir because of preferential logging and thus may more closely resemble pure ponderosa pine forests. A summary of environmental factors influencing dominant forest type classification is provided in Table 1.

Silvics of common tree species in San Juan Mountain region mixed conifer forests

Ponderosa pine (*Pinus ponderosa*) is widely distributed across western North America, growing on multiple soil types and topographies, generally found on drier sites in Warm/Dry mixed conifer forests (Oliver and Ryker, 1990). In the southern Rocky Mountains, ponderosa typically grows between 6,300-9,500 ft in elevation, but is highly influenced by aspect, topography, previous disturbances, soils, and moisture availability. Historical evidence illustrates that ponderosa pine had a frequent fire return

interval burning with low-moderate severity (Romme et al., 2009) with some small patches burning at high severity (Grissino-Mayer et al., 2004; Baker 2020). Ponderosa pine has many characteristics that make it a fire-tolerant species, including thick bark, shedding of its lower limbs, and having a high crown base (Fitzgerald 2005). Recent fires in the last ~30 years in ponderosa pine are believed to be larger and to burn more severely than historical fires, largely due to logging, grazing and fire-suppression which have created increased canopy connectivity with infilling of shade tolerant but fire-intolerant species (Fulé et al., 1997; Battaglia et al., 2018) such as Douglas-fir and white fir.

Douglas-fir (*Pseudotsuga menziesii*) has a large distribution across western North America, growing in a wide variety of climatic conditions, but preferring northern aspects at lower elevations and southern aspect at higher elevations, and soils that are well drained (Hermann and Lavendar

(1990). In the southern Rocky Mountains, Douglas-fir is most commonly found in Warm/Dry mixed conifer forests where it is co- or sub-dominant with ponderosa pine, or in Cool/Dry mixed conifer forests where it is the dominant tree species. Douglas-fir is a shade-tolerant but fire-intolerant species, where its presence in Warm/Dry mixed conifer forests can create conditions where fire can easily transfer from the forest floor into the forest canopy due to its triangular shape with low hanging branches (Tachajapong et al., 2008). The Douglas-fir tussock moth and Western Spruce Budworm are the most impactful insects to Douglas-fir trees of all sizes, both of which are currently active in the southern Rocky Mountains (Hermann and Lavendar 1990).

White fir (*Abies concolor*) grows in higher elevations of the Rocky Mountains in the western U.S. and is commonly found in all the mixed conifer forests in the San Juan Mountain region. White fir grows on a wide variety of soils, where productive stands are most dependent upon temperature and soil moisture availability. Like Douglas-fir, white fir is considered a shade-tolerant species, and is fire-intolerant when it is young, growing increasingly fire-tolerant as it increases in size and age. However, like Douglas-fir, when white fir is particularly abundant in Warm/Dry mixed conifer ecosystems, it can increase the risk of ground fire reaching into forest canopies and increases canopy connectivity, conditions which can create larger and more severe wildfires (Ritter et al., 2020). White fir can also be a dominant overstory tree in Cool/Dry mixed conifer systems. White fir is also impacted by many insects, most notably the Douglas-fir tussock moth and Western Spruce Budworm (Laacke, 1990).

Limber pine (*Pinus flexilis*) has a wide distribution across the Rocky Mountains growing in dry sites in all elevations in the San Juan Mountain region, where it is most frequently found on steep slopes and rocky ridges. Limber pine is most frequently found in the Cool/Dry mixed conifer type in the San Juan Mountain region, particularly on dry, rocky, and windy sites, but can also be found in the Warm/Dry and Cold/Wet mixed conifer types. Limber pine is impacted by numerous insects and diseases in addition to wildlife, which will eat its bark during winter months. Young limber pine is susceptible to

damage or mortality by wildfire, but mature limber pine is very resistant to damage from wildfire. Limber pine seeds are large and nutritious, making it an important food source for many wildlife species, including Clark's Nutcracker, which is largely responsible for the distribution of limber pine seeds (Steele 1990).

Southwestern white pine (*Pinus strobiformis*) is a five-needle pine species distributed across southwestern Colorado, New Mexico, Arizona, Texas, and Mexico, and is most commonly found in Cool/Dry mixed conifer forests of the San Juan Mountain region. Despite its wide distribution in the southern portion of North America, southwestern white pine is one of the least understood and understudied pines on the continent. In the San Juan Mountain region, southwestern white pine is rarely dominant, rather is part of a complex mixture of tree species dominated by Douglas-fir (Looney and Waring 2013). Interestingly, southwestern white pine is also known to hybridize with limber pine in the San Juan Mountain region (Menon et al., 2018).

Blue spruce (*Picea pungens*) has a relatively small distribution across the central Rocky Mountains, extending from higher elevations in eastern Idaho to Arizona and New Mexico; however, due to its unique blue color and triangular form, blue spruce is extensively planted as an ornamental tree. Blue spruce prefers cool and moist environments and is most commonly found in the Cold/Wet mixed conifer forests of the San Juan Mountain region where it frequently is located individually near stream sides. Like other fir and spruce species in the San Juan Mountain region, blue spruce is a shade-tolerant, fire-intolerant species which is also disturbed by numerous insects and diseases (Fechner 1990).

Engelmann spruce (*Picea engelmannii*) has a wide distribution across western North America, extending from Canada to New Mexico and Arizona where it is an important component of high elevation forests thriving during cool, short summers and long, cold winters with heavy snowpack. Engelmann spruce is often codominant with subalpine fir and is commonly found in the Cold/Wet mixed conifer forest type. Engelmann spruce is a shade-tolerant but fire-intolerant species, where it can grow easily

in competition in multi-aged or multi-storied forests or as a climax species but is highly vulnerable to fire where it will typically burn at moderate to high severity where most trees die due to the density of common stands (Alexandar and Shepperd 1990).

Subalpine fir (*Abies lasiocarpa*) has a wide distribution across the Rocky Mountains from northwestern Canada to Arizona and New Mexico and is an important component of high elevation forests where it is codominant with Engelmann Spruce in the Cold/Wet mixed conifer forest type. Subalpine fir is comprised of two varieties in the San Juan Mountain region: *Abies lasiocarpa* var. *lasiocarpa* and *Abies lasiocarpa* var. *arizonica* (corkbark fir; commonly identified for its white, cork-like bark). Like Engelmann spruce, subalpine fir is a shade-tolerant species that is highly susceptible to fire due to its low branches and thin bark; additionally subalpine fir is susceptible to insect outbreaks, most notably the western balsam bark beetle (*Dryocoetes confuses*) and the Western Spruce Budworm (*Choristoneura occidentalis*) (Alexandar et al., 1990).

Quaking aspen (*Populus tremuloides*) enjoys a wide variety of climates, soils, and topography, and has the largest distribution of all North American tree species. Quaking aspen (hereafter: aspen) is an important species for its aesthetic appeal and that it provides habitat for numerous birds, insects, and mammal species. Aspen is commonly found in the Cool/Dry and Cold/Wet mixed conifer forest types and in isolated pockets in Warm/Dry mixed conifer forests of the San Juan Mountain region where it grows in clonal clusters. While aspen can reproduce from seed, it commonly sprouts from connected root systems following disturbance; therefore, aspen is considered a fire-tolerant species as it readily recovers following fire and other disturbances, including numerous insect and disease pathogens (Perala et al., 1990).

Gambel oak (*Quercus gambelii*) is mountain shrub found in Utah, Colorado, southern Wyoming, New Mexico, and Arizona. It is most commonly found in the Warm/Dry and Cool/Dry mixed conifer forest types where it can be found as a shrub or tree growing in a wide variety of landscape conditions. Gambel oak reproduces from acorn production, and it also readily sprouts from root bases after disturbance,

such as herbivory, fire, human management, or other disturbance. As a result, Gambel oak is considered a fire-tolerant species; however, its role in fire behavior is quite complex depending on forest stand structure and density. Considering Gambel oak's diverse distribution across the southwestern US, little research has been conducted on Gambel oak ecology and management, prompting a need for increased scientific knowledge of Gambel oak ecology and management (Kaufmann et al., 2016).

Warm/Dry mixed conifer forest types

Forest Description: Warm/Dry mixed conifer forests tend to occupy warm and dry sites including south facing slopes, ridge tops, and lower elevation sites. Overstory species compositions are dominated by ponderosa pine and Douglas-fir (Figure 4). Many sites have a strong understory component of Gambel oak and other shrubs including serviceberry and chokecherry (Korb et al., 2007). Overstory trees are often found in groups and clumps with some individual trees and some large openings (Reynolds et al., 2013). These forests are often uneven-aged with groups of trees of even-aged trees where groups can vary in size from <0.1 acre to >75 acres (Reynolds et al., 2013). Forest conditions will vary greatly based on overall site conditions and management history where previous logging has a different influence than fire suppression alone. (Naficy et al., 2010, Rodman et al., 2017).

Successional trajectories: WD mixed conifer forests generally have a consistent dominance of overstory trees composed of ponderosa pine and Douglas-fir; however, changes in ecosystem processes from human related activities (i.e., grazing, logging, and fire suppression) have altered some successional dynamics (Fulé et al., 2009; Figure 5). The most prominent example of altered succession in these forests are the removal of the oldest, largest trees through historical logging and infilling and densification of fire-intolerant species such as white fir and Douglas-fir. Logging also often preferentially removed Douglas-fir from these forest types and created open canopy conditions that favors ponderosa pine recruitment. Generally, ponderosa pine recruitment occurred during periodic wet and fire free years favorable for seedling establishment



Figure 4: A photograph illustrating a Warm/Dry mixed conifer forest in the San Juan Mountain region. Ponderosa pine (foreground) and Douglas-fir (background) are present in the photograph (photo credit: Michael Remke).

and growth; however, other factors including bare mineral soil, lack of competition from other plants, and increased light in the forest understory are needed for successful regeneration, thus regeneration pulses generally occurs when there are canopy openings (Brown & Wu 2005). Less is known about Douglas-fir recruitment into the overstory in these forests, though it can be assumed these patterns are similar to ponderosa pine dynamics. White fir, however, establishes during fire-free periods in shady understory conditions and a long enough fire free period can result in white fir being recruited into the overstory as co-dominant (Tepley & Veblen 2015). Additional evidence suggests that fire free periods maintained by human activity by the Hemish peoples in the Jemez mountains facilitated type conversions from conifer dominated forests to persistent shrub fields (Roos & Guiterman 2021). Similarly, recent fire suppression combined with other less known factors has resulted in advanced shrub growth (e.g., Gambel oak) that vigorously sprouts following disturbance, including wildfire or mechanical

thinning and prescribed burning, and it is possible that oak dominance represents an intermediate successional stage in these forest types (van Auken et al., 2016, Korb et al., 2020). It's clear that these forests had highly variable structure with variable densities and cover of understory plant communities and that widespread oak cover, areas of high tree density, and variability have always been present in these forest types (Korb et al. 2013, Baker 2020).

Fire: WD mixed conifer forests in the southern Rocky Mountains have a complex relationship with fire. In some stands evidence demonstrates a frequent, low severity fire regime that occurs every 5-30 years (i.e., Romme et al. 2009, Fulé et al., 2013), however other localities and landscape perspectives suggest instances where mixed severity fire occurred every 30-100+ years (i.e. Baker 2018, Bigio et al., 2017, Grissino-Mayer et al., 2004). Fires in these forests varied in size and often burned across forest types with a mix of low-moderate severity and some large areas of high severity fire (Fulé et al., 2013, Tepley

& Veblen, 2015, Bigio et al., 2017, Baker 2018). Fire in these systems primarily occurred in summer when lightning strikes and dry conditions existed; however, during dry years fire occurred in virtually any month of the year (Grissino-Mayer et al., 2004, Baker 2018). Given fuel accumulation following wet, fire free periods, occasional mixed-severity fire occurred during subsequent droughts (Baker 2020). Additionally, particularly in northern New Mexico, fire has long been used as a tool to manage fuels near communities and protect developed areas. Ancestral Puebloan peoples utilized fire in different ways to burn and maintain fuels in different densities proximal to their communities, creating fire use zones (Roos et al., 2021), and these ideas have been transferred into fire and fuel management practices today via defensible space zones (Schoennagel et al., 2017). It should also be noted that fire suppression following European settlement has resulted in densification of all tree species and of the shrub component of these forests. It could be the case that a fire disturbance under current conditions could favor the formation of persistent shrub fields (i.e., Guiterman et al., 2018), or limited regeneration due to competition from shrubs and dry site conditions (Korb et al., 2020, Singleton et al., 2021). Some of these outcomes are likely linked to European settlement related fire suppression over the past century (Roos & Guiterman 2021).

Insects and Disease: WD mixed conifer forest types are host to many insects which at endemic levels cause isolated and periodic mortality (Negrón et al., 2020). These insects include roundheaded pine beetle, mountain pine beetle, Douglas-fir engraver, and Douglas-fir tussock moth. Frequent outbreaks of one or many of these insects can have more profound impacts on overstory trees resulting in widespread mortality, particularly when trees are already stressed by drought (Negrón et al., 2008). It is important to note mortality events exceeding 80% of overstory trees from insect attack are rare; however, when severe outbreak impacts 20-60% of overstory trees, heavy fuel accumulation from dead and down trees can contribute to fire with higher residence times and pose a greater risk to residual trees (Negrón et al., 2008, Clyatt et al., 2016). White fir is also host to a variety of insects and disease that include Western Spruce Budworm and annosous root rot (discussed

in greater depth later) that tend to naturally reduce the prevalence of white fir over time. These natural dynamics can cause variation in species dominance over time resulting in natural fluctuations in stand conditions (Verkat 2013).

Climate change is likely to have significant impacts on WD mixed conifer forests by either altering insect and disease disturbance (Loehman et al., 2017), fire behavior and regimes (Parks et al., 2018), or by creating conditions that are unfavorable for regeneration (Rodman et al., 2020a, b). It is possible that these change scenarios will interact to create scenarios where there is widespread loss of overstory trees combined with insufficient regeneration to maintain the forests that resemble current conditions (Chambers et al., 2016). It is likely that area burned by wildfire will continue to increase during dry conditions (Mueller et al., 2020) and this trend also corresponds to increasing areas of high severity fire (Singleton et al., 2019). These patterns are likely to result in conditions that are not favorable for regeneration of dry-adapted species in these forest types and thus could lead to type conversion (Rodman et al., 2020b, Parks et al., 2018, O'Connor et al., 2020). Reductions in overstory tree density from natural disturbances or management activities can reduce drought stress in remaining mature trees, thus enhancing climate resistance (Bottero et al., 2018). Conversely, some studies have demonstrated that regeneration during drought years is favored when residual canopy cover is higher due to shading effects that reduce drought stress (Kolb et al., 2019) and when in-tact associations with soil biota are preserved or restored (Remke et al., 2020). It's important to note that it is likely that deep soil water is maintained by winter snowpack whereas shallow soil moisture during the growing seasons is maintained by summer rain and that seedlings and mature trees likely utilize different sources of precipitation for water needs (Kerhoulas et al., 2012). Regional climate models for the southern Rocky Mountains generally predict warming trends with increasing lower elevation limits of snow that may result in shifts in the hydrologic niche for pine trees and alter available moisture, however the ecological response of these predictions is more uncertain (Rangwala et al., 2013).

Compounding disturbances in WD mixed conifer systems can result in an array of effects depending on the nature, extent, and severity of the initial and follow-up disturbances. In some ways, the frequent fire nature of these forests can be considered a system dependent on frequent, low-moderate intensity disturbances (Fulé et al., 2009). These low-moderate severity disturbances often maintained a more open forest structure, keeping sprouting shrubs to lower cover and extent, and promoting tree regeneration. It is important to note some components of the ecosystem, like residual old trees and soil biota, are minimally impacted by these frequent, low-moderate severity fires (Korb et al., 2004, Romme et al., 2009). However, it is important to distinguish those changes in fire regimes described above and climate change are likely to result in disturbances that are higher in severity and extent, and these disturbances can have compounding impacts. Some work has shown that repeated wildfire in dry-mixed conifer forests can result in type conversion from forested ecosystems

to grassland/savanna ecosystems, shrub fields, or alternative vegetation communities (Coop et al., 2015, Guiterman et al., 2018, Parks et al., 2018). Some mechanisms by which type conversions can occur are due to insufficient regeneration because of the mortality of potential seed sources (Korb et al., 2019, Rodman et al., 2020b), alteration of soil biota that removes mutualists that favor tree establishment (Owen et al., 2019), or alteration of microsites that favor tree regeneration (Owen et al., 2020). An additional consideration is that disturbance generally favors sprouting species and thus repeat disturbances may favor a conversion to sprouting species such as Gambel oak and aspen (Guiterman et al., 2018, Roos & Guiterman 2021, Andrus et al., 2021).

Management implications in WD mixed conifer systems are primarily focused on creating fire and drought resilient forests, utilizing best available historical structure and species composition data, climate projections, and the use of mechanical tools

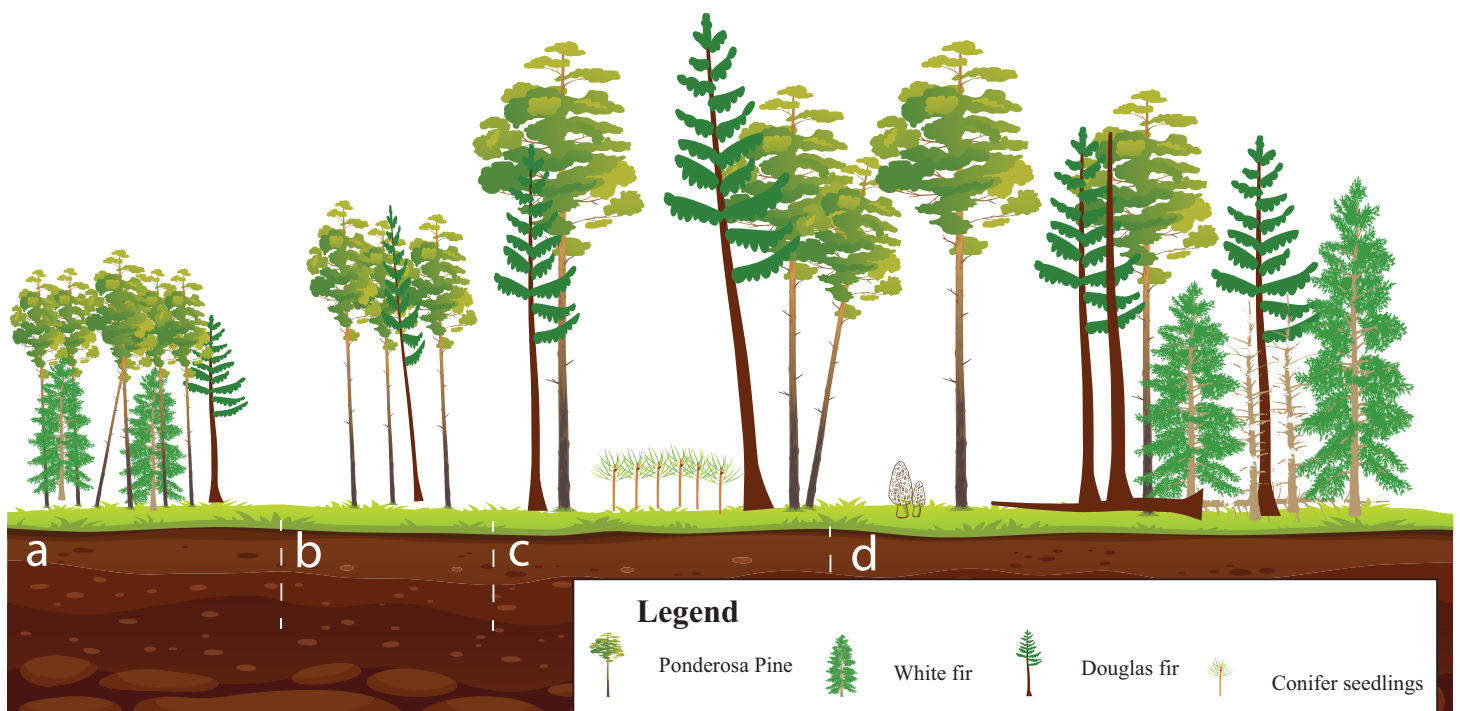


Figure 5: Vegetation developmental stages of Warm/Dry mixed conifer forests in the San Juan Mountain region. Each stage represents a unique vegetation development, and all these stages exist in a continuum and across mosaics within the region. Stages generally represent the following: a) management legacy stage where old and large trees are uncommon, and the understory is dense with standing live and dead shade-tolerant species. Preferential logging favored a species shift towards ponderosa pine. b) Mid-stand development following openings created from disturbance. This stage is best thought of as a group of regenerating trees reaching an older and large stage after recruiting in an opening. c) Late development forest with groups and clumps of trees of diverse species and age classes where recruitment is actively occurring in openings and there are areas with canopy connectivity. These spatial patterns are created and maintained by the heterogeneous influence of fire or other disturbances. d) The late development stage previously described carry forward into a forest structure with standing and felled down logs, old trees, and shade-tolerant trees in the understory. Spatial variability fosters variable responses to disturbance in this development stage.

or prescribed fire (Korb et al., 2012, Korb et al., 2020, North et al., 2021). It should be recognized that in some cases, management action can result in undesirable or unintended consequences such as a strong oak response (i.e., van Auken et al., 2016) and that thinning can accelerate drying in forest understory and thus may create an environment that is less favorable for regeneration (i.e., Kolb et al., 2019). It is clear the biggest benefit of historical forest structure is high spatial variability and un-even aged forest structure that facilitates resilience to various stressors (Palik et al., 2020). Work that enhances resilience to drought, fire, and insects by increasing spatial variability and retaining fire adapted individuals and species includes thinning of small-medium diameter trees and reintroducing prescribed or managed fire, which increases the probability that these forests will persist into an uncertain future (Bottero et al., 2017, Negrón et al., 2020, Stephens et al., 2020). In some

cases, retaining patches of small diameter trees or not treating areas within a project area can be used as a tool to help increase spatial variability (Palik et al., 2020). When disturbances do occur, creative augmentation strategies to restore ecosystems may be needed. The evidence that soil biota which provide mutualistic function and enhances seedling establishment are degraded, even 13 years after wildfire, suggests that restoring soil biota in artificial plantings may be a beneficial strategy to enhance restoration success (Owen et al., 2019, Remke et al., 2020). Additional research examining how soil water and understory shrub dynamics can help enhance management strategies that aim to cope with a changing climate and continued land use change could be useful (Nagel et al., 2017). Another challenge in WD mixed conifer forests is the continual growth of the Wildland Urban Interface (Radleoff et al., 2018), and thus management needs to consider community

Warm/Dry mixed conifer knowledge & degree of confidence

	High confidence	Moderate confidence	Low confidence
Successional trajectories	Spatial variability maintains diverse age groups across larger areas to provide resilience	Periodic recruitment of ponderosa pine	Sprouting shrubs may periodically establish as an intermediate successional trajectory
Fire	Frequent low-moderate severity surface fire historically	Occasional high severity burning in smaller patches historically; some recent fires reflect large (e.g., >1000 ac) high severity burn patches	
Insects/disease	Endemic populations of several beetle species result in periodic mortality	Mortality of trees is higher in drought stressed trees and trees with reduced growth rates 10 years prior to outbreak	Infrequent outbreaks of mountain pine beetle and round headed bark beetle can result in severe mortality events. Mortality events are episodic and rarely exceed 80% mortality
Climate change		<ul style="list-style-type: none"> Climate change is likely to increase burned area and burn severity from wildfire Reduced regeneration in disturbed areas Reduced plant growth, particularly in over-dense forest 	<ul style="list-style-type: none"> Increased risk of type conversions Increased drought resistance in less dense stands for overstory trees Increased susceptibility to drought for regeneration in less dense stands
Compound disturbances	Low-moderate severity disturbances favor desirable spatial variability	Repeated disturbances can favor type conversions, particularly following high severity wildfire and drought conditions	
Management implications	Restoring historical variability can enhance resilience to a variety of disturbances	Fire and climate refugia should be identified and protected from possible extreme events	Facilitating regeneration following artificial and natural disturbance can be difficult



Figure 6: A photograph illustrating a Cool/Dry mixed conifer forest in the San Juan Mountain region. Douglas-fir, white fir, and aspen are present in the photograph with multiple age classes and an increase in forest density and shrub growth (photo credit: Michael Remke).

values and actions which will enhance structure protection, maintenance of evacuation routes, and community resilience to fire in managing these forest types (Schoennagel et al., 2017, McWethy et al., 2019). Importantly, climate and fire refugia (e.g., individual to groups of isolated trees serving as a seed source) can be places where dry forest types persist (e.g., in drainages or ridge tops) for extended time periods despite repeated disturbances (McDowell et al., 2019, Krawchuck et al., 2020). These sites can be considered micro-sites that are protected from disturbance due to micro-topographic or climatic controlled buffers. In mixed conifer forests, these may exist in a mosaic of other forest types and should be identified and protected from significant alterations. During extreme droughts and fire years, these refugia may still be prone to disturbance, thus management may consider creating buffers around them to preserve them given the increasing possibilities of these events (Downing et al., 2020, Stevens et al., 2021). Lastly, since large and old trees have been removed from historical

logging, prioritizing the recruitment of new trees into large size classes and protecting existing large and old trees will enhance the resistance of these ecosystems to future disturbances (Baker 2021).

Cool/Dry mixed conifer forest types

Forest Description: Cool/Dry mixed conifer forests tend to occupy cooler, shaded sites at lower elevations (i.e., 8,500-10,000 ft) in the San Juan Mountain region. As an example, CD mixed conifer forests may be present on north facing slopes adjacent to WD mixed conifer forests. Additionally, well drained soils at slightly higher elevations (i.e., 10,000-10,500 ft) or on mid-slope locations may favor CD mixed conifer forests. Overstories of mixed conifer forests are dominated by Douglas-fir with abundant ponderosa pine and white fir (Figure 6). Additionally, aspen may be present at some but not all sites. Understories of these forests are likely to have abundant white fir (Tepley & Veblen 2015). Like WD mixed conifer

sites, these forests have a strong understory shrub component, though species composition may be more diverse than WD sites, and may include Gambel oak, serviceberry, snowberry, choke cherry, and Rocky Mountain maple. Less is understood about spatial patterns in these forests; however, it is evident that spatial patterns are in part determined where small openings and gaps are formed from disturbance (Rodman et al., 2016). Given the diverse species composition of these forests, they are often uneven-aged.

Successional trajectories in CD mixed conifer forests primarily relate to disturbance history and scale of disturbance (Figure 7). In general, overstory composition of tree species that are relatively shade-intolerant (e.g., ponderosa pine) results in a tendency for these species to establish following disturbance while over time shade-tolerant species (e.g., white fir)

establish without disturbance (Rodman et al., 2016, Tepley & Veblen 2015). Little is discussed regarding successional patterns of these forests in the literature; however, disturbance is said to correlate strongly to climatic factors and thus it is likely that succession also strongly correlates to climatic factors (Schoennagel et al., 2005, Sherriff et al., 2014). Prolonged periods without disturbances such as fire are likely to result in an increased abundance of shade-tolerant species like white fir, while drier periods may shift dominance towards fire- and drought-tolerant species such as ponderosa pine (Tepley & Veblen 2015).

Fire: CD mixed conifer forests, with their high species diversity, tend to have a complex relationship with fire and various insects and diseases. Fire in these forests is less frequent (every 30-100 years) than fire in WD forests and primarily correlates to climate and fuel conditions (Romme et al., 2009, Verkat et al., 2013,

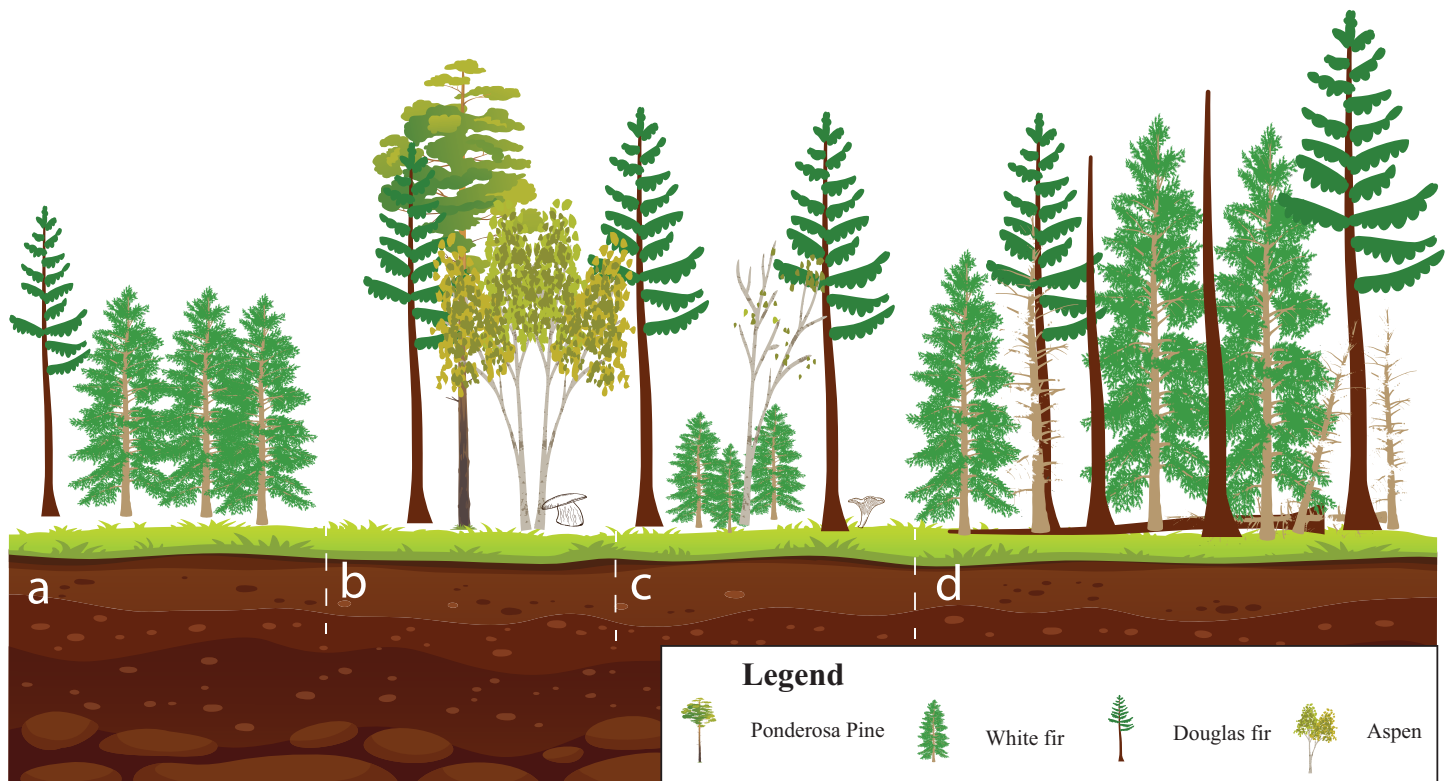


Figure 7: Vegetation developmental stages of Cold/Dry mixed conifer forests in the San Juan Mountain region. Each stage represents a unique vegetation development, and all these stages exist in a continuum and across mosaics within the land area. Stages generally represent the following: a) management legacy stage where old and large trees are uncommon, shade-tolerant species are more abundant, and residual dominants due to preferential removal of other species are present. b) Mid-stand development following openings created from disturbance. This stage has disturbance responding species such as aspen, and in a natural disturbance regime fire- and drought-tolerant overstory species remain. c) Late development forest with less disturbance promoted species and early development of shade-tolerant species. Note that early development species may remain on site in a deteriorated state with significant leaf drop and rot contributing to increases in soil organic material. d) The late development stage previously described carry forward into a forest structure with standing and felled down logs, old trees, and shade-tolerant trees in the understory. Spatial variability fosters variable responses to disturbance in this development stage.

Schoennagel et al., 2005, Baker 2018). In a landscape scale study, evidence of mixed severity fire existed across the entire study area suggested that mixed severity fire is a prominent feature of these forest types (Aoki et al., 2010). Importantly, mixed severity fire burns at varying intensities depending on fuel, topography, and fire weather (Yedinak et al., 2018). Thus, factors influencing fire behavior in CD mixed conifer forests are complex and vary greatly spatially, and create complex ecological feedbacks (McLauchlan et al., 2020). As an example, a wetter site in a CD mixed conifer forest could have existed for a longer time without fire, and thus have a greater abundance of fuels. Therefore, during a strong drought year this wet site would be more prone to high severity fire and the result may be a single patch of forest that burns at high severity, whereas an adjacent but slightly drier site may have had less fuel and may burned at moderate to low severity. High severity patches in CD mixed conifer forests are often believed to be 5-10 ha in size; however, some patches up to 74 ha in size may have existed and these patch sizes likely vary greatly depending on site conditions and forest structure pre-fire (Yocom-Kent 2015). Importantly, fire in these forests has in some cases been altered by fire suppression where up to three fire cycles have been missed, whereas in other components of these forests only one or two fire cycles have been missed. Consequently, the inherited challenge of understanding these forests is the complex mosaic that exist across the landscape, and it is evident that this complexity must be embraced (Yedinak et al., 2018). It is also likely that fire suppression has altered the spatial distribution of landscape heterogeneity in these forests by reducing the number of meadows and openings that mixed severity fire would have created and maintained (Stevens et al., 2021). Lastly, these forests are likely particularly vulnerable to climatic driven shifts in fire regimes and increasing fire frequency may result in transitions to more dominance by sprouting species and fire-resistant species (Abatzoglou et al., 2021; Hoecker and Turner 2022).

Insects and diseases in these forests are also complex and are related to species composition and climatic factors. One of the most prevalent insects in CD mixed conifer forests is Western Spruce Budworm (*Choristoneura freeman*, hereafter “spruce budworm”). Spruce budworm is a defoliator that

attacks the green needles of white fir, Douglas-fir, Engelmann spruce, blue spruce, and subalpine fir. Spruce budworm prefers shaded understory conditions, and several repeat defoliation events can cause physiological harm to trees by reducing tree leaf area for gas exchange and photosynthesis, sometimes resulting in tree mortality (Rocky Mountain Region, Forest Health Protection 2010). Outbreaks of spruce budworm have been shown to occur every 2-3 decades during warm/wet periods that can result in significant defoliation events (Ryerson et al., 2003). It is important to note that forests that have an abundance of trees susceptible to attack by spruce budworm, such as white fir, Douglas-fir, and blue spruce, will be more prone to outbreaks than forests that have less tree species which may be susceptible. A strong visual indicator of spruce budworm attack is branches draped with the lichen *Usnea* rather than green needles (Simard & Payette 2003). *Usnea* has long been used as an anti-microbial agent that effectively stops bleeding and has prevalence in cultural stories and uses in the Southwestern US, perhaps indicating a long-standing relationship with the prevalence of these types of insect attacks in forests (Ranković 2019). Common diseases in these forests include annosus root disease (*Heterobasidion annosum*). Annosus tends to primarily impact white-fir trees and is a common basidiomycete fungus, or fungus that produces a fruiting body. These fungi spread by spores from stumps of impacted trees and subsequently spread spores to small pockets of nearby trees (Garbelotto et al., 1997). Annosus kills its host and the sign of annosus is best visualized by concentric circles of dead fir.

Climate change has unknown implications for CD mixed conifer forests due to a lack of scientific information, though these forests have many potential trajectories depending on species composition and risk for high severity fire (i.e., topography). At the drier end of the spectrum of CD mixed conifer forests, it is likely that fire will become more frequent across this entire forest type. Potential for more extreme wildfire conditions because of warmer conditions and prolonged drought in the southwestern US are certainly possible (Westerling et al., 2016, Schoennagel et al., 2017, Biederman et al., 2021); however, some evidence also suggests that plant-drought interactions may limit fire under future scenarios because of limited fuel growth

(Hurteau et al., 2019). Warmer/drier conditions are also likely to influence regeneration conditions in CD mixed conifer forests, perhaps favoring dominance of sprouting species or species conversions (Parks et al., 2018, Rodman et al., 2020a, b). While many of these realities are uncertain, it is likely that climate change may increase the propensity of these forest types to compounding disturbances and/or conversion to drier community types such as species in the WD mixed conifer forest type.

Compounding disturbances in CD mixed conifer forest types can result in an array of results depending on the nature, extent, and severity of the initial and follow-up disturbances. Like potential compound disturbances in WD mixed conifer forest types, climate change and potential changes in disturbance regimes may result in larger or more severe impacts that may have cascading effects. Forest trajectories following potential compounded disturbances will depend on

the species composition present prior to disturbance and the scale and extent of each disturbance to how these forest types will respond. Importantly, some species, like aspen, may not be visually extant aboveground, but disturbance can prompt sprouting from belowground structures which could result in a shift to aspen dominance, particularly if repeat disturbances occur in short time periods (Andrus et al., 2021). Similarly, when Gambel oak is present, its sprouting response can result in oak dominance or influence species recovery (Harrington 1987).

Management implications in CD mixed conifer forests can be best approached by embracing complexity (Puettmann et al., 2009, Franklin et al., 2007, Martínez Pastur et al., 2020). Management activities should draw on information relating to current conditions and desired future conditions, and ideally would consider diverse factors including topographic position and alterations from previous

Cool/Dry mixed conifer knowledge & degree of confidence

	High confidence	Moderate confidence	Low confidence
Successional trajectories	Shade-tolerant species infill understory overtime	Post-disturbance communities consist of sprouting species or shade-intolerant species	
Fire		Infrequent (30-100 years) mixed severity fire driven by drought and abundance of fuels	High severity patches were historically small, with some larger patches
Insects/disease	Because of high species diversity, numerous native insects and diseases exist	Periodic Western Spruce Budworm outbreaks driven by warm/wet conditions	Annosus root disease is an important regulator in shade-tolerant species and infections worsen as susceptible species densities increase
Climate change		Drought and warmer conditions are likely to increase risk to extreme fire events	Drought is likely to alter regeneration dynamics and successional trajectories, perhaps resulting in type conversion and/or loss of forested areas
Compound disturbances	Low-moderate severity disturbances favor desirable spatial variability		Where present, sprouting species (e.g., aspen or Gambel oak) may become a dominant species following repeat disturbances
Management implications	Restoring historical variability can enhance resilience to a variety of disturbances	Embracing complexity is a critical component of managing these forests	Future desired conditions should consider current conditions and potential future conditions based on climate change and potential for disturbance

disturbances (or lack thereof). Proximity to communities or other highly valued resources may also drive specific management objectives when appropriate in these forest types (Gannon et al., 2019). Mimicking natural processes (i.e., mixed severity fire or spruce budworm) in these forest types would likely result in substantial wood product removal that could support economic markets while also maintaining ecological integrity of forest structure and function. This can include creating small patches of group selections to facilitate aspen sprouting and/or openings. These groups can mimic the openings that would have been created by mixed severity fire, spruce budworm, or other disturbances. Additionally, within the matrix of CD mixed conifers, removal of shade-tolerant species such as Douglas-fir and white fir can reduce wildfire risk and maintain residual overstory species with greater resistance to drought stress (Bottero et al., 2018). Using a combination of matrix thinning and group selection is ultimately likely to reduce the intensity of other insects and disease, like spruce budworm, by maintaining more species that are resistant to attack by spruce budworm and preserving more open forest understories that reduce the spread of spruce budworm. In other cases, where reducing fire risk is less of a priority, or geographies are difficult to reach due to topography and insufficient roads, no management action can be appropriate as ecological processes, such as annosus root disease, will naturally create openings and maintain reduced density of shade-tolerant species. Lastly, principles described for WD mixed conifer forests which promote the resistance, resilience, and transition of CD forests will promote the adaptability of these forests to any given potential disturbance, including climate change (Nagel et al., 2017).

Cold/Wet mixed conifer forest types

Forest Description: Cold/Wet mixed conifer forests are found at higher elevations (i.e., 9,500-11,000 ft), valley bottoms, and north facing slopes that tend to have a prolonged winter season with significant snowfall in the San Juan Mountain region. Dominant overstory species include Engelmann spruce, blue spruce, and subalpine fir (Figure 8). All these species are shade-tolerant and tend to need partial shading to establish and survive. Common understory tree species may include aspen, Douglas-fir, and white

fir and any of the previous mentioned overstory tree species. Common shrub species include gooseberry, snowberry, sumac, and common juniper. These forests can be even-aged to uneven-aged depending on successional class and spatial extent and are often intermixed with meadows and openings of various sizes.

Successional trajectories in CW mixed conifer forests are poorly understood (Pelz 2016). Key factors for future successional trajectories depend primarily on current species presence (Figure 9). When aspen is present, disturbance can prompt widespread aspen sprouting, which may become a dominant species until conifer regeneration advances over aspen canopies. Across much of the CW mixed conifer forests, aspen exists in small numbers where disturbance has been absent and is extremely abundant on slopes where fire (or other disturbance) has occurred (Tepley & Veblen 2015). Aspen is prone to diseases which limit its persistence on the landscape and ultimately favor conifer establishment and dominance. Additionally, conifer regeneration in aspen stands or in conifer stands without aspen is generally dependent on seed bank source and micro-site conditions created by residual overstory and/or dead and down trees (Pettit et al., 2019, Carlson et al., 2020). In some cases, particularly where relict overstory Douglas-fir trees exist, Douglas-fir regeneration may be common (Dye and Moir 1977). This suggests these forest successional trajectories are likely dynamic as climate fluctuates over time spans of centuries. It is also clear regeneration and forest processes occur slowly in these forest types due to short growing seasons and saturated soil following snow melt. Preserving micro-sites and shading from residual overstory trees (dead or alive) can be critical for facilitating forest succession, which in turn supports diverse wildlife species (Squires et al., 2020). Understory shrub layers in this forest type tend to be diverse and complicated. Ongoing research and monitoring in the shrub layers of these forests is needed to better understand understory responses to natural and artificial disturbance.

Fire dynamics in CW mixed conifer forests is most similar to those in the subalpine forests (dominated by subalpine fir and Engelmann spruce) than the other fire dynamics we have discussed, although



Figure 8: A photograph illustrating a Cold/Wet mixed conifer forest in the San Juan Mountain region. Subalpine fir and Engelmann spruce dominate this site; multiple trees have experienced mortality due to recent spruce beetle activity (photo credit: Michael Remke).

mixed severity fire is still relevant to these forest types. Generally, infrequent, stand-replacing fire occurred in these forest types every 300 years or more, and fire prone time periods in these forests occurred during periods of severe drought (Schoennagel et al., 2005, Harvey et al., 2021). These fires tended to be stand-replacing, killing >80% of trees and prompting significant regeneration events; however, due to spatial discontinuity in fuels and variation in weather and fire behavior based on slope and aspect, there were still elements of mixed severity fire in these mixed conifer forests.

Insects and disease in CW mixed conifer forests are most recognized for recent widespread spruce bark beetle (*Dendroctonus rufipennis*) outbreaks. These native insects tend to have more profound impacts on tree mortality when prolonged drought stresses mature trees (Hart et al., 2014). However, recent evidence indicates that these widespread

mortality events are more likely driven by warmer temperatures than by drought stress (Pettit et al., 2020). Thus, considerable debate still exists regarding whether widespread beetle outbreaks of similar extent and severity occurred previously in these forest types, though some studies suggest they likely did in lodgepole pine forests elsewhere in Colorado (Negrón 2020). Some studies of historical photographs demonstrate that many outbreaks of bark beetles occurred between 1850 and 1880, suggesting that periodic mortality events maybe an integral component of the CW mixed conifer forest disturbance regimes. Interestingly, insect outbreaks tend to only impact >90% of the canopy in relatively small (<60 acres) disconnected areas, where over the broader geography >10% of overstory trees remain intact (Rodman et al., 2021). Bark beetle impacts also tend to result in the subsequent increase in abundance of bark beetle predators, like three-toed woodpeckers (*Picoides dorsalis*), that then spread

to adjacent forests with endemic populations and help regulate beetle populations (Nappi et al., 2015, Kelly et al., 2019). This reflects similar patterns to other mixed conifer disturbance dynamics where complete canopy removal is rare and isolated to small geographies and that areas of high mortality benefit other organisms, particularly birds (Hutto et al., 2015). Given these realities, recent bark beetle related mortality in adjacent spruce-fir forests have been extensive and may be unprecedented in spatial scale (Hart et al., 2017). CW forests also experience spruce budworm infestations during warm/wet years on a decadal timescale similar to CD mixed conifer forests (Ryerson et al., 2003). Evidence also demonstrates that warmer temperatures, rather than drought alone, are contributing to spatial extent and severity of on-going outbreaks (Pettit et al., 2020).

Climate change is at the root of a tremendous amount of uncertainty concerning CW mixed conifer forests. Perhaps the most certain reality is that these high elevation forests are more prone to fire during warm Pacific decadal oscillations and the resultant droughts (Sherriff et al., 2014). Thus, it can be assumed that an increase in frequency and severity of drought brought by climate change could create scenarios where fire is

more likely in these forest types (Schoennagel et al., 2017). There are additional concerns about potential tree regeneration in these forest types, though the dynamics are not fully understood. Spruce and fir trees may be dependent on high moisture availability and shade to successfully regenerate, and thus prolonged drought may reduce seedling survival (Harvey et al., 2021). An additional consideration is that drier conditions may favor alternative species compositions, such as Douglas-fir, and in some instances at the drier end of spruce distribution, abundant Douglas-fir regeneration could occur, particularly when legacy Douglas-fir is present (Dye and Moir 1997). Additionally, as mentioned above, warmer temperatures during on-going drought may exacerbate disturbance such as beetle attack and/or individual tree mortality events (Field et al., 2020; Pettit et al., 2020) These uncertainties in part depend on the potential consequences of compounding disturbances in these forest types.

Compounding disturbances in these forest types can occur from beetle outbreaks followed by fire, or repeated fires. The timing of a fire can influence how fire behaves in beetle impacted forest. Whether trees still have green needles, brown needles, or

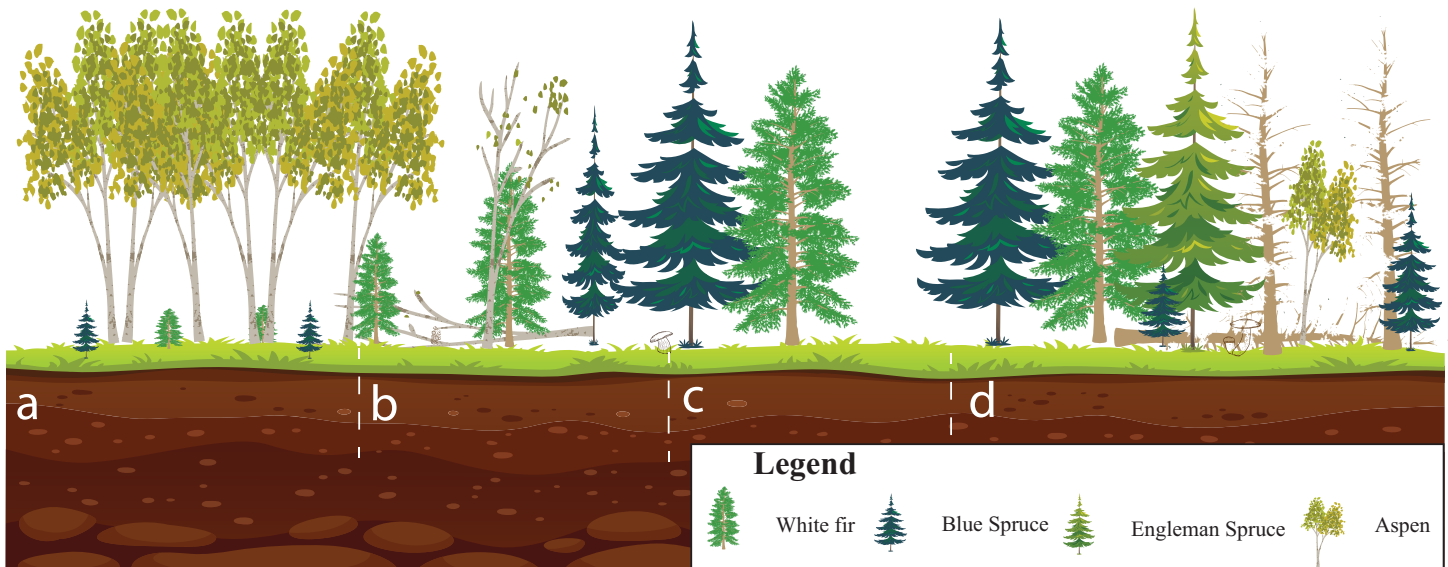


Figure 9: Vegetation developmental stages of Cold/Wet mixed conifer forests in the San Juan Mountain region. Each stage represents a unique vegetation development stage, and all these stages exist in a continuum and across mosaics within the land area. Stages generally represent the following: a) Post disturbance stage is dominated by aspen; in systems where sprouting species are absent this stage may be better represented by a meadow or opening. b) Coniferous transition where aspen begins to rot and fall over, and conifers advance into the understory and age into more mature trees. Diverse ages of conifers may exist. c) Late development forest with a mix of species and trees at a mature stage with variously sized openings. d) A diverse landscape of Cold/Wet mixed conifer forests with a variety of standing live and dead trees of various species, fallen logs, regeneration, and some sprouting species representing a mosaic of conditions.

have lost all their needles depends primarily on time since mortality, where trees that are still green are weakened, brown needle trees have recently died, and trees with no needles have been standing dead for extended time periods. Given these forests typically experience high severity fire, influence of beetle mortality on fire severity has been observed (Hart et al., 2015, Sieg et al., 2017). Fire conditions and behavior, including fire spread and flame length, can vary in the different phases of beetle mortality based on fuel moisture conditions, wind speed and surface fuel dynamics (Sieg et al., 2017). This variability in fire and fuel dynamics following beetle infestation is dependent upon various complex fuel and weather scenarios; a clear takeaway is that fire severity and probability do not automatically increase following beetle mortality, as these elevations often have abundant moisture that limits the likelihood of

fire. Another important aspect of compounding disturbance in these forests type is the potential for future dominance by aspen (Andrus et al., 2021).

Management implications in these CW mixed conifer forest differ from other mixed conifer forest types in that infrequent but severe disturbance and slow regeneration rates can make it difficult to know if actions represent a shift towards desired conditions. Management is also often limited in these forests due to water features, insufficient roads, and steep slopes. Common management practices include salvage logging following bark beetle outbreaks or wildfire. Salvage logging can be efficient for facilitating release of advanced regeneration when already present; however, when advanced regeneration is absent, salvage logging can limit seedling establishment by altering microsites in the understory (Leverkus

Cold/Wet mixed conifer knowledge & degree of confidence

	High confidence	Moderate confidence	Low confidence
Successional trajectories		Pre-disturbance conditions influence successional trajectories If aspen is present, aspen dominance followed by a transition to conifer	Tree regeneration may vary based on climatic conditions at the time of regeneration, sometimes favoring dry adapted species
Fire		Infrequent, stand-replacing fire every 300+ years	Mixed severity fire can occur based on variability in fuels, topography, or fire weather
Insects/disease		Episodic bark beetle outbreaks can occur during time periods of drought	Temperature may also be a factor influencing bark beetle outbreak, thus making recent outbreaks unprecedented compared to historical outbreaks
Climate change			Drier conditions could favor more extreme and frequent fire behavior; warmer conditions could facilitate regeneration of lower elevation species
Compound disturbances			Insect outbreaks alter and redistribute fuels that sometimes can alter fire behavior, but not burn severity
Management implications			Group selections that retain overstory trees can increase resilience to insect outbreaks; thinning to favor advanced regeneration can accelerate stand development

et al., 2021). Other management strategies can include group selection to increase spatial variation and facilitate meadow formation and advanced regeneration (Palik et al., 2020). Meadow formation can also be done in a way that maintains proper shading to slow snowmelt rates while also increasing snow accumulation by canopy removal (Musselman et al., 2015). Such strategies have been demonstrated to be effective in theory-based physical models; however, field quantification and validation of these models are needed to improve their predictive power if management is specifically interested in manipulating snow water through canopy removal. Lastly, management that increases solar radiation to the forest floor can reduce regenerative success which can compound to have negative feedback on wildlife use in these forests (Squires et al., 2020). As a result, it is imperative that management seeks to facilitate regenerative success and be cautious of managing in areas that lack regeneration. Additionally, group selections that mimic disturbance patterns and leave residual overstory trees can reduce the severity of spruce budworm impacts (Moise et al., 2019).

Summary

A clear emergent theme across all mixed conifer forest types is that complexity must be embraced in our understanding of how these forests came to be over time and how these forests will respond to any single disturbance, compounded disturbances, or management actions. This innate complexity will be unique across all local geographies and certainly vary significantly on even broader regional geography as the current and desired conditions of these forests depend on numerous climatic, geomorphic, and anthropogenic factors. Not only do these forests vary widely over space, but time and temporal scale is another critical perspective when understanding these forests. Another key takeaway that can be difficult to capture in the synthesis of our understanding of these individual and collective mixed conifer forest types is the dynamic nature of these forests. Cool climatic periods may correspond to fire-free driven shifts in species compositions towards more shade-tolerant and fire-intolerant species in all forest types, sometimes even creating shifts in what resembles Warm/Dry mixed conifer transitioning towards Cold/Dry mixed conifer forests

(Tepley & Veblen 2015). Similarly, warmer and drier periods may increase fire frequency in all forest types and shifts from Cold/Dry forests towards more fire-resistant species dominance that resembles Warm/Dry mixed conifer forests, or Cold/Wet mixed conifer to aspen dominated forests may be considered natural vegetation dynamics and type conversions in these forests (Verkat 2013). These ever-changing dynamics may include landscapes that were once ponderosa pine forests transitioning into natural state mixed conifer forests and vice versa.

Spending time in these diverse forests lends one to consider the perspective that no two stands are identical and that each forest stand is unique on its own and cannot always be easily compared to other forests. Thus, the point of this document is to outline key processes and knowledge gaps to help us better understand and appreciate these forest types and what factors we may consider when deciding whether, and how, to manage these forests. We would like to extend a perspective from the geomorphic sciences that proposes the idea of the 'Perfect Landscape' (Philips 2007), which suggests that no two geomorphic landforms, even if generally in the same family of landforms (i.e., Fault Block Mountains) are identical in nature and appearance because each unique landform is exposed to different environments prior to, during, and after its formation. We would like to offer that mixed conifer forests, and all forests are perfect forests, in that site conditions from a perspective of soils, climate, ecological processes and feedbacks, as well as interactions with human values and use of forested land areas result in truly unique stands and forests.

Management of mixed conifer forests in the San Juan Mountain region

Above, we summarized a broad swath of knowledge about mixed conifer forests using the spectrum of Warm/Dry to Cold/Wet forests to help guide a more nuanced and complex perspective for understanding disturbance dynamics and ecology in the San Juan Mountain region. Given the diverse array of human values, micro- and macro-climatic gradients, soils, and topographic features, these forests should be managed in ways which can promote this complexity. Importantly, additional perspective on



Figure 10: Cool/Dry mixed conifer forest following treatment at Pagosa Creek near Pagosa Springs, CO where fire resistant trees have been maintained and a small opening has been created. (photo credit: Michael Remke).

local social and economic considerations is needed to guide the management decisions that may occur in these forests.

Across large land areas, administrative boundaries restrict or constrain active management in these forests, including roadless, wilderness, and/or topographic limitations like steep slopes, rocky terrain, or sensitive hydrological features. These restrictions often leave a small portion of the total land area of these forests as suitable for active management. Despite this, land managers can incorporate these lightly or non-actively managed areas as part of a landscape mosaic to move towards broader-scale desired forest conditions. Unmanaged landscapes, such as wilderness areas, are subject to the processes that govern their ongoing development and trajectories and are relatively homogenous in this regard. By actively managing lands adjacent to these unmanaged areas with different goals, managers have opportunities to increase landscape heterogeneity

and complexity by utilizing a combination of both active and passive management approaches.

Land managers are commonly forced to accept the natural processes that govern these forests as a reality that shifts the context and objectives for managing mixed conifer forests. As an example, the 2002 Missionary Ridge Fire effectively removed a large forest area suitable for commercial timber production from the San Juan National Forest Plan (USFS 1992 and 2014). The fire created a broad but heterogeneous landscape of early seral conditions as well as other stages of development, but one that would be unlikely to produce significant forest product outputs for many decades. Since this fire produced large areas of young aspen and conifer forest, a desired vegetation condition of the San Juan National Forest Land Resource Management Plan (USFS 2014), this change, one outside the control of managers, accomplished some desired plan objectives despite limiting long-term forest product

production capacity. Managers should be aware that changes like this can occur very rapidly and thus should be ready to adapt active management goals and approaches both within and adjacent to burned areas to accomplish both landscape complexity and forest product production goals across landscapes. Because fire of all severities is a natural component to these ecosystems we encourage managers to consider the intentional use of fire (prescribed or managed fire) as a tool to achieve pyrosilvicultural goals and that unintentional landscape change brought about by naturally occurring mixed severity fire can be embraced (North et al., 2021). Simultaneously we also recognize that increases in human caused fires may result in undesired outcomes of fire and thus managers can work towards preventing human ignitions (Nagy et al., 2018).

The geographical distribution of mixed conifer forests and human infrastructure and values are also important considerations in managing these forest types. Forests adjacent to highly valued resources and assets (see Scott et al., 2013) may be managed with the goal of wildfire risk reduction with actions that include mechanical thinning of trees followed by managed or prescribed fire to reduce surface fuel loading (Cansler et al., 2021). Additionally, unplanned wildfire ignitions can result in desired outcomes across all mixed conifer forests depending on the specific circumstances (North et al., 2021). Additional geographic considerations include haul distance from project areas to mills that can process a diverse array of diameter and species compositions so that treatments are economically viable. In many cases, however, mixed conifer forests exist further away from communities and thus balancing these realities with ecological goals becomes a priority for delineating project areas. Lastly, temporal considerations of mixed conifer management are also important because repeat entries can help sustain local timber markets for longer time periods while still achieving desired ecological and social goals.

At stand and project levels, managers of mixed conifer forests may benefit from incorporating and adopting principles of Ecological Forestry (EF). EF approaches, common throughout productive forest regions, are applied within actively managed forests and use natural disturbance processes as a guide to restore and sustain complex structural and

compositional forest conditions (D'Amato et al., 2016). EF approaches consider and promote ecological values on landscapes where sustained forest product outputs are not only acceptable, but a desired goal of active management. EF considers the complexities of disturbance regimes and seeks to restore a diversity of stages of forest structure that these regimes produce, rather than aiming to facilitate and promote a single development stage. For the San Juan Mountain region, increased focus on the range of developmental stages common to historic mixed conifer forests is a way to both increase landscape complexity and develop silvicultural strategies that promote sustainable forest product goals over time. Management strategies can incorporate a mix of even-aged and uneven-aged silvicultural strategies to create complex landscapes of varying age, structures, and composition. At the stand scale, uneven-aged management using individual tree or group selection can promote stand to sub-stand scale complexity. At broader scales, using even-aged approaches to mimic stand-scale disturbances can promote fast growing, early seral species including aspen, or young conifer forests, and features such as meadows that can be missing in contemporary mixed conifer forests. Even-aged approaches can both create landscape complexity and efficiently produce forest product outputs (Parajuli et al., 2020). Combinations of even- and uneven-aged systems, along with intermediate harvests (i.e., thinning), can be combined to mimic the complexity sustained with active disturbance processes in mixed conifer forests. These efforts, along with natural disturbances (i.e., no action) due to fire, avalanche, or insect and disease, can concurrently promote heterogeneous and complex forested landscapes and meet desired economic goals. While much of our discussion focuses on timber management through silviculture, it should be noted that to achieve goals related to desired understory plant conditions, shifts in grazing management practice may also be required.

Managers should be aware that interventions could be ineffective or hinder desired outcomes and that no action may be desired. For example, salvage logging can release established advanced regeneration, but may also hinder new seedling establishment (Leverkus et al., 2021). Group selection may produce forest product outputs and generate conditions suitable for the establishment of young trees, but

harvested group areas may promote a persistent shrub layer, rather than a new cohort of young trees, limiting future forest succession and productivity (Korb et al., 2020). Further, efforts to both produce forest product outputs and generate forest complexity may still lead to uneconomical harvests, which ultimately may not be completed. Any management intervention is an artificial disturbance, and when combined with global climate change scenarios, may facilitate an unintended and/or undesirable transitions to alternative forest condition or structure. The potential for unintended consequences makes it essential that where management approaches are applied in mixed conifer forests to accomplish Ecological Forestry goals, the results be monitored and assessed. There is a large amount of subjectivity and uncertainty associated with management approaches to promote complexity in mixed conifer forests. Without sustained monitoring efforts, the performance of active versus passive management strategies in these forests remains mostly unknown, limiting potential for future investment and application throughout the region.

There is no one rigid set of desired conditions or goals appropriate for managing mixed conifer forests, only a broad range of acceptable and viable approaches that can maintain or enhance ecological integrity and ecosystem services. Management which aims to accomplish specific goals and objectives, such as protecting watersheds, reducing high severity wildfire risk, or preserving biodiversity, can also be in alignment with opportunities to be learned from management of these complex forests. The subjective nature of many management considerations in these forests leaves vast opportunities for creativity and innovation in management. Intentional consideration of economic outputs is an essential component of management prescriptions that has the potential to promote beneficial forest product industry and capacity and sustain appropriate management into the future. Ecological Forestry approaches provide exciting opportunities for managers and stakeholders to embrace the complexity of these forests with curiosity and intention. As we learn and understand forest responses to management efforts, we continue the centuries long human experiment of managing mixed conifer forests in the San Juan Mountain region and beyond.

Conclusion

Mixed conifer forests within the San Juan Mountain region vary greatly over spatial and temporal scales and possess a wide diversity of possible stand and landscape conditions. Larger geographies that include the central or northern Rocky Mountain regions begin to expand the species diversity found in mixed conifer forests. Additional species include lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*) and unique assemblages of understory plant communities. While it may seem that knowledge from the San Juan Mountain region is less relevant to geographies with different species compositions, the general categories and gradients described in this document remain relevant as the silvics of new species are introduced. With this complexity a helpful compass may be to consider the concepts of ecological stoichiometry and for any given site consider what resource is likely limiting forest growth and/or fire. For example at a dry site moisture may be limiting thus slowing plant growth and limiting fuel for fire, whereas at a wet site moisture may limit fire and if nutrients are also abundant, then abundant tree growth may reduce light in the understory and be the limiting factor for seedling establishment and growth. Understanding of the complexity of mixed conifer forests locally can help enhance understanding mixed conifer forests across broader regions.

Managing these complex forests is riddled with complex decisions that must include social values, economic considerations, as well as potential ecological outcomes. Management actions which promote or create diversity on the landscape may result in increased resilience and protection of ecosystem services. However, in some cases no management action can be seen as a tool or opportunity to help maintain or promote resilience. Management decisions in these forests can benefit from tools that increase both stand and landscape diversity, and can include creative combinations of standard silvicultural approaches. These principles ultimately borrow from Ecological Forestry practices pioneered by Jerry Franklin and others in mixed conifer forests of the Pacific Northwest, and offer a dynamic space for managers and stakeholders to try new approaches.

Literature cited

- Abatzoglou, J.T., Battisti, D.S., Williams, A.P., Hansen, W.D., Harvey, B.J., Kolden, C.A., 2021. Projected increases in western US forest fire despite growing fuel constraints. *Commun. Earth Environ.* 2. <https://doi.org/10.1038/s43247-021-00299-0>
- Alexander, R.R. and Shepperd, W.D., 1990. *Picea engelmanni* Parry ex. Engelm. Engelmann spruce. *Silvics of North America, Agriculture Handbook 654*, US Department of Agriculture, Forest Service, Washington, DC, USA (1990), 187-203. <https://www.fs.usda.gov/treearch/pubs/1547>
- Alexander, R.R., Shearer, R.C., Shepperd, W.D., 1990. *Abies lasiocarpa* (Hook.) Nutt. Subalpine fir. *Silvics of North America, Agriculture Handbook 654*, US Department of Agriculture, Forest Service, Washington, DC, USA (1990), 60-70. <https://www.fs.usda.gov/treearch/pubs/1547>
- Andrus, R., Hart, S., Veblen, T.T., 2021. Future dominance by quaking aspen expected following short-interval, compounded disturbance interaction. *Ecosphere*, 12(1), p.e03345 <https://doi.org/10.1002/ecs2.3345>
- Aoki, C.F., 2010. Fire History and serotiny in the Rocky Mountains of Colorado (Doctoral dissertation, Colorado State University). <https://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.987.2054&rep=rep1&type=pdf>
- Baker, W., 2018. Historical Fire Regimes in Ponderosa Pine and Mixed-Conifer Landscapes of the San Juan Mountains, Colorado, USA. *Fire* 1, 23. <https://doi.org/10.3390/fire1020023>
- Baker, W.L., 2020. Variable Forest Structure and Fire Reconstructed Across Historical Ponderosa Pine and Mixed Conifer Landscapes of the San Juan Mountains, CO. *Land* 9(1), p. 3 <https://doi.org/10.3390/land9010003>
- Baker, W.L., 2021. Restoration of forest resilience to fire from old trees is possible across a large Colorado dry-forest landscape by 2060, but only under the Paris 1.5°C goal. *Glob. Chang. Biol.* 1–22. <https://doi.org/10.1111/gcb.15714>
- Battaglia, M.A., Gannon, B., Brown, P.M., Fornwalt, P.J., Cheng, A.S. and Huckaby, L.S., 2018. Changes in forest structure since 1860 in ponderosa pine dominated forests in the Colorado and Wyoming Front Range, USA. *Forest Ecology and Management*, 422, pp.147-160. <https://doi.org/10.1016/j.foreco.2018.04.010>
- Bigio, E.R., Swetnam, T.W., Pearthree, P.A., 2017. Late Holocene fire-climate relationships of the western San Juan Mountains, Colorado. *Int. J. Wildl. Fire* 26, 944–962. <https://doi.org/10.1071/WF16204>
- Biederman, J.A., Dannenberg, M., Reed, S.C., States, U., Survey, G., Smith, W.K., 2021. Five Decades of Observed Daily Precipitation Reveal Longer and More Variable Drought Events Across Much of the Western United States Five Decades of Observed Daily Precipitation Reveal Longer and More Variable Drought Events Across Much of the Western Uni. <https://doi.org/10.1029/2020GL092293>
- Bottero, A., D'Amato, A.W., Palik, B.J., Bradford, J.B., Fraver, S., Battaglia, M.A., Asherin, L.A., 2017. Density-dependent vulnerability of forest ecosystems to drought. *J. Appl. Ecol.* 54, 1605–1614. <https://doi.org/10.1111/1365-2664.12847>
- Bose, A.K., Weiskittel, A., Kuehne, C., Wagner, R.G., Turnblom, E., Burkhart, H.E., 2018. Does commercial thinning improve stand-level growth of the three most commercially important softwood forest types in North America? *For. Ecol. Manage.* 409, 683–693. <https://doi.org/10.1016/j.foreco.2017.12.008>
- Bowker, M.A., Muñoz, A., Martinez, T., Lau, M.K., 2012. Rare drought-induced mortality of juniper is enhanced by edaphic stressors and influenced by stand density. *J. Arid Environ.* 76, 9–16. <https://doi.org/10.1016/j.jaridenv.2011.08.012>
- Brown, P.M., Wu, R., 2005. Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. *Ecology* 86, 3030–3038. <https://doi.org/10.1890/05-0034>
- Cansler, C.A., Kane, V.R., Hessburg, P.F., Kane, J.T., Jeronimo, S.M.A., Lutz, J.A., Povak, N.A., Churchill, D.J., Larson, A.J., 2021. Previous wildfires and management treatments moderate subsequent fire severity. *For. Ecol. Manage.* 119764. <https://doi.org/10.1016/j.foreco.2021.119764>
- Carlson, A.R., Sibold, J.S., Negrón, J.F., 2020. Canopy structure and below-canopy temperatures interact to shape seedling response to disturbance in a Rocky Mountain subalpine forest. *For. Ecol. Manage.* 472, 118234. <https://doi.org/10.1016/j.foreco.2020.118234>
- Chambers, M.E., Fornwalt, P.J., Malone, S.L., Battaglia, M.A., 2016. Patterns of conifer regeneration following high severity wildfire in ponderosa pine – dominated forests of the Colorado Front Range. *For. Ecol. Manage.* 378, 57–67. <https://doi.org/10.1016/j.foreco.2016.07.001>
- Clyatt, K.A., Crotteau, J.S., Schaedel, M.S., Wiggins, H.L., Kelley, H., Churchill, D.J., Larson, A.J., 2016. Historical spatial patterns and contemporary tree mortality in dry mixed-conifer forests. *For. Ecol. Manage.* 361, 23–37. <https://doi.org/10.1016/j.foreco.2015.10.049>
- Coop, J.D., Parks, S.A., McClernan, S.R., Holsinger, L.M., 2015. Influences of Prior Wildfires on Vegetation Response to Subsequent Fire in a Reburned Southwestern Landscape. *Ecol. Appl.* 26(2), p. 346-354. <https://doi.org/10.1890/15-0775.1>
- D'Amato, Anthony W., Palik, Brian J., Franklin, Jerry F. and Foster, David R., 2016. Exploring the Origins of Ecological Forestry in North America. *Journal of Forestry*. 115(2):126–127. <https://doi.org/10.5849/jof.16-013>
- Downing, W.M., Johnston, J.D., Krawchuk, M.A., Merschel, A.G., Rausch, J.H., 2020. Disjunct and decoupled? The persistence of a fire-sensitive conifer species in a historically frequent-fire landscape. *J. Nat. Conserv.* 55, 125828. <https://doi.org/10.1016/j.jnc.2020.125828>
- Dye, A.J. and Moir, W.H., 1977. Spruce-fir forest at its southern distribution in the Rocky Mountains, New Mexico. *American Midland Naturalist*, pp.133-146. <https://doi.org/10.2307/2424691>
- Evans, M.E., Falk, D.A., Arizpe, A., Swetnam, T.L., Babst, F., Holsinger, K.E., 2017. Fusing tree-ring and forest inventory data to infer influences on tree growth. *Ecosphere* 8(7). <https://doi.org/10.1002/ecs2.1889>
- Fechner, G. H., 1990. *Picea pungens* Engelm. blue spruce. *Silvics of North America, Agriculture Handbook 654*, US Department of Agriculture, Forest Service, Washington, DC, USA (1990), 238-249. <https://www.fs.usda.gov/treearch/pubs/1547>

- Field, J.P., Law, D.J., Field, J.P., Breshears, D.D., Bradford, J.B., Law, D.J., Feng, X., 2020. Forest Management Under Megadrought: Urgent Needs at Finer Scale and Forest Management Under Megadrought: Urgent Needs at Finer Scale and Higher Intensity. <https://doi.org/10.3389/ffgc.2020.502669>
- Fitzgerald S., 2005. Fire ecology of ponderosa pine and the rebuilding of fire-resilient ponderosa pine ecosystems. In: Ritchie M. W., Maguire, D. A., Youngblood, A., technical coordinators. Proceedings of the Symposium on Ponderosa Pine: Issues, Trends, and Management, 2004 October 18-21, Klamath Falls, OR. General Technical Report PSW-GTR-198. US Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, California, USA.
- Franklin, J.F., Mitchell, R.J., Palik, B.J., 2007. Natural Disturbance and Stand Development Principles for Ecological Forestry. Gen. Tech. Rep. NRS-19. Newt. Square, PA U.S. Dep. Agric. For. Serv. North. Res. Station. 19, 44 p. <https://www.nrs.fs.fed.us/pubs/3293>
- Fulé, P.Z., Covington, W.W. and Moore, M.M., 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. *Ecological Applications*, 7(3), pp.895-908. [https://doi.org/10.1890/1051-0761\(1997\)007\[0895:DRCFEM\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1997)007[0895:DRCFEM]2.0.CO;2)
- Fulé, P.Z., Korb, J.E., Wu, R., 2009. Changes in forest structure of a mixed conifer forest, southwestern Colorado, USA. *For. Ecol. Manage.* 258, 1200–1210. <https://doi.org/10.1016/j.foreco.2009.06.015>
- Gannon, B.M., Wei, Y., MacDonald, L.H., Kampf, S.K., Jones, K.W., Cannon, J.B., Wolk, B.H., Cheng, A.S., Addington, R.N. and Thompson, M.P., 2019. Prioritizing fuels reduction for water supply protection. *International Journal of Wildland Fire*, 28(10), pp.785-803. <https://doi.org/10.1071/WF18182>
- Garbelotto, M., Slaughter, G., Popenuck, T., Cobb, F.W., Bruns, T.D., 1997. Secondary spread of *Heterobasidion annosum* in white fir root-disease centers. *Can. J. For. Res.* 27, 766–773. <https://doi.org/10.1139/x96-193>
- Grissino-Mayer, H.D., Romme, W.H., Floyd, M.L., Hanna, D.D., 2004. Climatic and human influences on fire regimes of the southern San Juan Mountains, Colorado, USA. *Ecology* 85, 1708–1724. <https://doi.org/10.1890/02-0425>
- Guiterman, C.H., Margolis, E.Q., Allen, C.D., Falk, D.A., Swetnam, T.W., 2018. Long-Term Persistence and Fire Resilience of Oak Shrubfields in Dry Conifer Forests of Northern New Mexico. *Ecosystems* 21, 943–959. <https://doi.org/10.1007/s10021-017-0192-2>
- Harrington, M.G., 1987. Phytotoxic potential of Gambel oak on ponderosa pine seed germination and initial growth (Vol. 277). US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, 1987.
- Hart, S.J., Veblen, T.T., Eisenhart, K.S., Jarvis, D. and Kulakowski, D., 2014. Drought induces spruce beetle (*Dendroctonus rufipennis*) outbreaks across northwestern Colorado. *Ecology*, 95(4), pp.930-939. <https://doi.org/10.1890/13-0230.1>
- Hart, S.J., Schoennagel, T., Veblen, T.T., Chapman, T.B., Franklin, J., 2015. Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. *Proc. Natl. Acad. Sci. U. S. A.* 112, 4375–4380. <https://doi.org/10.1073/pnas.1424037112>
- Hart, S.J., Veblen, T.T., Schneider, D. and Molotch, N.P., 2017. Summer and winter drought drive the initiation and spread of spruce beetle outbreak. *Ecology*, 98(10), pp.2698-2707. <https://doi.org/10.1002/ecy.1963>
- Harvey, B.J., Andrus, R.A., Battaglia, M.A., Negrón, J.F., Orrego, A., Veblen, T.T., 2021. Droughty times in mesic places: factors associated with forest mortality vary by scale in a temperate subalpine region. *Ecosphere* 3318. <https://doi.org/10.1002/ecs2.3318>
- Herman, R.K., and Lavendar, D.P., 1990. Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). *Silvics of North America*, Agriculture Handbook 654, US Department of Agriculture, Forest Service, Washington, DC, USA (1990), 527-540. <https://www.fs.usda.gov/treearch/pubs/1547>
- Hoecker, T.J., Turner, M.G., 2022. A short-interval reburn catalyzes departures from historical structure and composition in a mesic mixed-conifer forest. *For. Ecol. Manage.* 504, 119814. <https://doi.org/10.1016/j.foreco.2021.119814>
- Hurteau, M.D., Liang, S., Westerling, A.L., Wiedinmyer, C., 2019. Vegetation-fire feedback reduces projected area burned under climate change. *Sci. Rep.* 9, 1–6. <https://doi.org/10.1038/s41598-019-39284-1>
- Hutto, R.L., Bond, M.L. and DellaSala, D.A., 2015. Using bird ecology to learn about the benefits of severe fire. In *The ecological importance of mixed-severity fires* (pp. 55-88). Elsevier. <https://doi.org/10.1016/B978-0-12-802749-3.00003-7>
- Kaufmann, M.R., Huisjen, D.W., Kitchen, S., Babler, M., Abella, S.R., Gardiner, T.S., McAvoy, D., Howie, J. and Page, D.H., 2016. Gambel oak ecology and management in the southern rockies: the status of our knowledge. SRFSN Publication 2016-1. Fort Collins, CO: Colorado State University, Southern Rockies Fire Sciences Network. 16 p.
- Kelly, J.J., Latif, Q.S., Saab, V.A. and Veblen, T.T., 2019. Spruce Beetle outbreaks guide American Three-toed Woodpecker *Picoides dorsalis* occupancy patterns in subalpine forests. *Ibis*, 161(1), pp.172-183. <https://doi.org/10.1111/ibi.12596>
- Kerhoulas, L.P. and Kane, J.M., 2012. Sensitivity of ring growth and carbon allocation to climatic variation vary within ponderosa pine trees. *Tree Physiology*, 32(1), pp.14-23. <https://doi.org/10.1093/treephys/tpr112>
- Kolb, T., Dixit, A., Burney, O., 2019. Challenges and Opportunities for Maintaining Ponderosa Pine Forests in the Southwestern United States. *Tree Plant. Notes* 62, 104–112.
- Korb, J.E., Bombaci, S. and Siegel, R., 2014. The effect of sudden aspen decline on understory microclimate and vegetation in southwestern Colorado. *Canadian Journal of Forest Research*, 44(8), pp.914-921. <https://doi.org/10.1139/cjfr-2014-0087>
- Korb, J.E., Daniels, M.L., Laughlin, D.C., Fulé, P.Z., 2007. Understory Communities of Warm-Dry, Mixed-Conifer Forests in Southwestern Colorado. *Southwest. Nat.* 52, 493–503. [https://doi.org/10.1894/0038-4909\(2007\)52\[493:ucowmf\]2.0.co;2](https://doi.org/10.1894/0038-4909(2007)52[493:ucowmf]2.0.co;2)
- Korb, J.E., Fulé, P.Z., Stoddard, M.T., 2012. Forest restoration in a surface fire-dependent ecosystem: An example from a mixed conifer forest, southwestern Colorado, USA. *For. Ecol. Manage.* 269, 10–18. <https://doi.org/10.1016/j.foreco.2012.01.002>

- Korb, J.E., Fornwalt, P.J. and Stevens-Rumann, C.S., 2019. What drives ponderosa pine regeneration following wildfire in the western United States? *Forest Ecology and Management*, 454, p.117663. <https://doi.org/10.1016/j.foreco.2019.117663>
- Korb, J.E., Stoddard, M.T. and Huffman, D.W., 2020. Effectiveness of Restoration Treatments for Reducing Fuels and Increasing Understory Diversity in Shrubby Mixed-Conifer Forests of the Southern Rocky Mountains, USA. *Forests*, 11(5), p.508. <https://doi.org/10.3390/f11050508>
- Krawchuk, M.A., Meigs, G.W., Cartwright, J., Coop, J.D., Davis, R., Holz, A., Kolden, C., Meddens, A.J.H., 2020. Disturbance refugia within mosaics of fire, drought, and insect outbreaks enable forest persistence. *Front. Ecol. Environ.* <https://doi.org/10.1002/fee.2190>
- Krofcheck, D. J., Hurteau, M. D., Scheller, R. M., & Loudermilk, E. L., 2017. Restoring surface fire stabilizes forest carbon under extreme fire weather in the Sierra Nevada. *Ecosphere*, 8(1), e01663. <https://doi.org/10.1002/ecs2.1663>
- Laacke, R. J., 1990. *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. White fir. *Silvics of North America, Agriculture Handbook 654*, US Department of Agriculture, Forest Service, Washington, DC, USA (1990), 36-46. <https://www.fs.usda.gov/treearch/pubs/1547>
- LANDFIRE, 2016. Existing Vegetation Type Layer, LANDFIRE 1.1.0, U.S. Department of the Interior, Geological Survey, and U.S. Department of Agriculture. Accessed July 2021 at <http://landfire.cr.usgs.gov/viewer/>
- Leverkus, A.B., Buma, B., Wagenbrenner, J., Burton, P.J., Lingua, E., Marzano, R., Thorn, S., 2021. Tamm review: Does salvage logging mitigate subsequent forest disturbances? *For. Ecol. Manage.* 481, 118721. <https://doi.org/10.1016/j.foreco.2020.118721>
- Loehman, R.A., Keane, R.E., Holsinger, L.M. and Wu, Z., 2017. Interactions of landscape disturbances and climate change dictate ecological pattern and process: spatial modeling of wildfire, insect, and disease dynamics under future climates. *Landscape Ecology*, 32(7), pp.1447-1459. <https://doi.org/10.1007/s10980-016-0414-6>
- Looney, C.E., Waring, K.M., 2013. *Pinus strobiformis* (southwestern white pine) stand dynamics, regeneration, and disturbance ecology: A review. *For. Ecol. Manage.* 287, 90–102. <https://doi.org/10.1016/j.foreco.2012.09.020>
- Martínez Pastur, G.J., Vanha-Majamaa, I., Franklin, J.F., 2020. Ecological perspectives on variable retention forestry. *Ecol. Process.* 9. <https://doi.org/10.1186/s13717-020-0215-3>
- Menon, M., Bagley, J.C., Friedline, C.J., Whipple, A. V., Schoettle, A.W., Leal-Sàenz, A., Wehenkel, C., Molina-Freaner, F., Flores-Rentería, L., Gonzalez-Elizondo, M.S., Sniezko, R.A., Cushman, S.A., Waring, K.M., Eckert, A.J., 2018. The role of hybridization during ecological divergence of southwestern white pine (*Pinus strobiformis*) and limber pine (*P. flexilis*). *Mol. Ecol.* 27, 1245–1260. <https://doi.org/10.1111/mec.14505>
- McDowell, N.G., Grossiord, C., Adams, H.D., Pinzón-Navarro, S., Mackay, D.S., Breshears, D.D., Allen, C.D., Borrego, I., Dickman, L.T., Collins, A., Gaylord, M., McBranch, N., Pockman, W.T., Vilagrosa, A., Aukema, B., Goodsman, D., Xu, C., 2019. Mechanisms of a coniferous woodland persistence under drought and heat. *Environ. Res. Lett.* 14. <https://doi.org/10.1088/1748-9326/ab0921>
- McLauchlan, K.K., Higuera, P.E., Miesel, J., Rogers, B.M., Schweitzer, J., Shuman, J.K., Tepley, A.J., Varner, J.M., Veblen, T.T., Adalsteinsson, S.A., Balch, J.K., Baker, P., Batllori, E., Bigio, E., Brando, P., Cattau, M., Chipman, M.L., Coen, J., Crandall, R., Daniels, L., Enright, N., Gross, W.S., Harvey, B.J., Hatten, J.A., Hermann, S., Hewitt, R.E., Kobziar, L.N., Landesmann, J.B., Loranty, M.M., Maezumi, S.Y., Mearns, L., Moritz, M., Myers, J.A., Pausas, J.G., Pellegrini, A.F.A., Platt, W.J., Roozeboom, J., Safford, H., Santos, F., Scheller, R.M., Sherriff, R.L., Smith, K.G., Smith, M.D., Watts, A.C., 2020. Fire as a fundamental ecological process: Research advances and frontiers. *J. Ecol.* 108, 2047–2069. <https://doi.org/10.1111/1365-2745.13403>
- McWethy, D.B., Schoennagel, T., Higuera, P.E., Krawchuk, M., Harvey, B.J., Metcalf, E.C., Schultz, C., Miller, C., Metcalf, A.L., Buma, B., Virapongse, A., Kulig, J.C., Stedman, R.C., Ratajczak, Z., Nelson, C.R., Kolden, C., 2019. Rethinking resilience to wildfire. *Nat. Sustain.* 2, 797–804. <https://doi.org/10.1038/s41893-019-0353-8>
- Meigs, G.W., Dunn, C.J., Parks, S., Krawchuk, M.A., 2020. Influence of topography and fuels on fire refugia probability under varying fire weather in forests of the US Pacific Northwest. *Can. J. For. Res.* <https://doi.org/10.1139/cjfr-2019-0406>
- Moise, E.R.D., Lavigne, M.B., Johns, R.C., 2019. Density has more influence than drought on spruce budworm (*Choristoneura fumiferana*) performance under outbreak conditions. *For. Ecol. Manage.* 433, 170–175. <https://doi.org/10.1016/j.foreco.2018.10.031>
- Mueller, S.E., Thode, A.E., Margolis, E.Q., Yocom, L.L., Young, J.D., Iniguez, J.M., 2020. Climate relationships with increasing wildfire in the southwestern US from 1984 to 2015. *For. Ecol. Manage.* 460, 117861. <https://doi.org/10.1016/j.foreco.2019.117861>
- Musselman, K.N., Pomeroy, J.W., Link, T.E., 2015. Variability in shortwave irradiance caused by forest gaps: Measurements, modelling, and implications for snow energetics. *Agric. For. Meteorol.* 207, 69–82. <https://doi.org/10.1016/j.agrformet.2015.03.014>
- Naficy, C., Sala, A., Keeling, E.G., Graham, J., DeLuca, T.H., 2010. Interactive effects of historical logging and fire exclusion on ponderosa pine forest structure in the northern Rockies. *Ecol. Appl.* 20, 1851–1864. <https://doi.org/10.1890/09-0217.1>
- Nagel, L.M., Palik, B.J., Battaglia, M.A., D'Amato, A.W., Guldin, J.M., Swanston, C.W., Janowiak, M.K., Powers, M.P., Joyce, L.A., Millar, C.I., Peterson, D.L., Ganio, L.M., Kirschbaum, C., Roske, M.R., 2017. Adaptive Silviculture for Climate Change: A National Experiment in Manager-Scientist Partnerships to Apply an Adaptation Framework. *J. For.* 115, 167–178. <https://doi.org/10.5849/jof.16-039>
- Nagy, R., Fusco, E., Bradley, B., Abatzoglou, J.T. and Balch, J., 2018. Human-related ignitions increase the number of large wildfires across US ecoregions. *Fire*, 1(1), p.4. <https://doi.org/10.3390/fire1010004>
- Nappi, A., Drapeau, P. and Leduc, A., 2015. How important is dead wood for woodpeckers foraging in eastern North American boreal forests? *Forest Ecology and Management*, 346, pp.10-21. <https://doi.org/10.1016/j.foreco.2015.02.028>

- Negrón, J.F., Allen, K., Cook, B., Withrow, J.R., 2008. Susceptibility of ponderosa pine, *Pinus ponderosa* (Dougl. ex Laws.), to mountain pine beetle, *Dendroctonus ponderosae* Hopkins, attack in uneven-aged stands in the Black Hills of South Dakota and Wyoming USA. *For. Ecol. Manage.* 254, 327–334. <https://doi.org/10.1016/j.foreco.2007.08.018>
- Negrón, J.F., Huckaby, L., 2020. Reconstructing historical outbreaks of mountain pine beetle in lodgepole pine forests in the Colorado Front Range. *For. Ecol. Manage.* 473. <https://doi.org/10.1016/j.foreco.2020.118270>
- Negrón, J.F., 2020. Within-stand distribution of tree mortality caused by mountain pine beetle, *Dendroctonus ponderosae* Hopkins. *Insects*, 11(2), p.112. <https://doi.org/10.3390/insects11020112>
- North, M.P., York, R.A., Collins, B.M., Hurteau, M.D., Jones, G.M., Knapp, E.E., Kobziar, L., McCann, H., Meyer, M.D., Stephens, S.L., Tompkins, R.E., Tubbesing, C.L., 2021. Pyrosilviculture Needed for Landscape Resilience of Dry Western United States Forests. *J. For.* 1–25. <https://doi.org/10.1093/jofore/fvab026>
- O'Connor, C.D., Falk, D.A., Garfin, G.M., 2020. Projected Climate-Fire Interactions Drive Forest to Shrubland Transition on an Arizona Sky Island. *Frontiers in Environmental Science*, 8, 1–17. <https://doi.org/10.3389/fenvs.2020.00137>
- Oliver, W.W., and Ryker, R.A., 1990. *Pinus ponderosa* Dougl. ex Laws. Ponderosa pine. *Silvics of North America, Agriculture Handbook 654*, US Department of Agriculture, Forest Service, Washington, DC, USA (1990), pp. 413-424. <https://www.fs.usda.gov/treeearch/pubs/1547>
- Owen, S.M., Patterson, A.M., Gehring, C.A., Sieg, C.H., Baggett, L.S. and Fulé, P.Z., 2019. Large, high-severity burn patches limit fungal recovery 13 years after wildfire in a ponderosa pine forest. *Soil Biology and Biochemistry*, 139, p.107616. <https://doi.org/10.1016/j.soilbio.2019.107616>
- Owen, S.M., Sieg, C.H., Owen, S.M., Sieg, C.H., Fulé, P.Z., Gehring, C.A., Baggett, L., 2020. Persistent effects of fire severity on ponderosa pine regeneration niches and seedling growth. *Forest Ecology and Management*. 477, 118502. <https://doi.org/10.1016/j.foreco.2020.118502>
- Palik, B.J., D'Amato, A.W., Franklin, J.F. and Johnson, K.N., 2020. *Ecological silviculture: foundations and applications*. Waveland Press.
- Parajuli, M., Hiesl, P., Smidt, M., and Mitchel, D., 2020. Factors influencing productivity and cost in the whole tree harvesting system. *Clemson (SC): Clemson Cooperative Extension, Land-Grant Press by Clemson Extension*; 2020 Jul. LGP 1079. <https://lgpress.clemson.edu/publication/factors-influencing-productivity-and-cost-in-the-whole-tree-harvesting-system/>
- Parks, S.A., Holsinger, L.M., Panunto, M.H., Jolly, W.M., Dobrowski, S.Z. and Dillon, G.K., 2018. High-severity fire: evaluating its key drivers and mapping its probability across western US forests. *Environmental research letters*, 13(4), p.044037. <https://doi.org/10.1088/1748-9326/aab791>
- Parks, S.A., Dobrowski, S.Z., Shaw, J.D., Miller, C., 2019. Living on the edge: trailing edge forests at risk of fire-facilitated conversion to non-forest. *Ecosphere* 10, e02651. <https://doi.org/10.1002/ecs2.2651>
- Perala, D.A., Burns, R.M., & Honkala, B., 1990. *Populus tremuloides* Michx. quaking aspen. *Silvics of North America, Agriculture Handbook 654*, US Department of Agriculture, Forest Service, Washington, DC, USA (1990), 555-569. https://www.srs.fs.usda.gov/pubs/misc/ag_654/volume_2/vol2_table_of_contents.htm
- Pelz, K.A., 2010. Mixed-conifer forests in Southwest Colorado: A summary of existing knowledge and considerations for restoration and management. Colorado Forest Restoration Institute, Colorado State University. https://cfri.colostate.edu/wp-content/uploads/sites/22/2018/03/2010_MixedConiferKnowledgeSynthesis.pdf
- Pelz, K.A., 2016. Engelmann spruce regeneration following natural disturbances and forest management: a literature and expert-knowledge review focused on southwestern Colorado. Colorado Forest Restoration Institute, Colorado State University. <https://cfri.colostate.edu/wp-content/uploads/sites/22/2017/10/2016-CFRI-Spruce-Regeneration-in-SW-Colorado-compressed.pdf>
- Pettit, J.M., Burton, J.I., DeRose, R.J., Long, J.N. and Voelker, S.L., 2019. Epidemic spruce beetle outbreak changes drivers of Engelmann spruce regeneration. *Ecosphere*, 10(11), p.e02912. <https://doi.org/10.1002/ecs2.2912>
- Pettit, J.M., Voelker, S.L., DeRose, R.J., Burton, J.I., 2020. Spruce beetle outbreak was not driven by drought stress: Evidence from a tree-ring iso-demographic approach indicates temperatures were more important. *Glob. Chang. Biol.* 26, 5829–5843. <https://doi.org/10.1111/gcb.15274>
- Phillips, J.D., 2007. The perfect landscape. *Geomorphology*, 84(3-4), pp.159-169. <https://doi.org/10.1016/j.geomorph.2006.01.039>
- Puettmann, K.J., D'Amato, A.W., Kohnle, U. and Bausch, J., 2009. Individual-tree growth dynamics of mature *Abies alba* during repeated irregular group shelterwood (Femelschlag) cuttings. *Canadian journal of forest research*, 39(12), pp.2437-2449. <https://doi.org/10.1139/X09-158>
- Puettmann, K.J., Tappeiner, J.C., 2014. Multi-scale assessments highlight silvicultural opportunities to increase species diversity and spatial variability in forests. *Forestry* 87, 1–10. <https://doi.org/10.1093/forestry/cpt050>
- Ranković, B., 2019. *Lichen Secondary Compounds. Bioactive Properties and Pharmaceutical Potential*. Springer Publishing.
- Radeloff, V.C., Hesters, D.P., Anu Kramer, H., Mockrin, M.H., Alexandre, P.M., Bar-Massada, A., Butsic, V., Hawbaker, T.J., Martinuzzi, S., Syphard, A.D., Stewart, S.I., 2018. Rapid growth of the US wildland-urban interface raises wildfire risk. *Proc. Natl. Acad. Sci. U. S. A.* 115, 3314–3319. <https://doi.org/10.1073/pnas.1718850115>
- Rangwala, I., Sinsky, E. and Miller, J.R., 2013. Amplified warming projections for high altitude regions of the northern hemisphere mid-latitudes from CMIP5 models. *Environmental Research Letters*, 8(2), p.024040. <https://doi.org/10.1088/1748-9326/8/2/024040>
- Remke, M.J., Hoang, T., Kolb, T., Gehring, C., Johnson, N.C., Bowker, M.A., 2020. Familiar soil conditions help *Pinus ponderosa* seedlings cope with warming and drying climate 1–11. <https://doi.org/10.1111/rec.13144>

- Reynolds, R.T., Sánchez Meador, A.J., Youtz, J.A., Nicolet, T., Matonis, M.S., Jackson, P.L., Delorenzo, D.G., Graves, A.D., Richard, T., Meador, S., Andrew, J., James, A., Megan, S., Patrick, L., Donald, G., Andrew, D., 2013. Restoring composition and structure in Southwestern frequent-fire forests: a science based framework for improving ecosystem resiliency. RMRS GTR-310. Gen. Tech. Rep. PSW-GTR-220 86. https://www.fs.fed.us/rm/pubs/rmrs_gtr310.pdf
- Ritter, S.M., Hoffman, C.M., Battaglia, M.A., Stevens-Rumann, C.S., Mell, W.E., 2020. Fine-scale fire patterns mediate forest structure in frequent-fire ecosystems. *Ecosphere* 11. <https://doi.org/10.1002/ecs2.3177>
- Rocky Mountain Region, Forest Health Protection, 2010. Field Guide to diseases & insects of the Rocky Mountain Region. Gen. Tech. Rep. RMRS-GTR-241 Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 336p.
- Rodman, K.C., Sánchez Meador, A.J., Huffman, D.W. and Waring, K.M., 2016. Reference conditions and historical fine-scale spatial dynamics in a dry mixed-conifer forest, Arizona, USA. *Forest Science*, 62(3), pp.268-280. <https://doi.org/10.5849/forsci.15-136>
- Rodman, K.C., Sánchez Meador, A.J., Moore, M.M., Huffman, D.W., 2017. Reference conditions are influenced by the physical template and vary by forest type: A synthesis of *Pinus ponderosa*-dominated sites in the southwestern United States. *For. Ecol. Manage.* 404, 316–329. <https://doi.org/10.1016/j.foreco.2017.09.012>
- Rodman, K.C., Veblen, T.T., Battaglia, M.A., Chambers, M.E., Fornwalt, P.J., Holden, Z.A., Kolb, T.E., Ouzts, J.R., Rother, M.T., 2020a. A changing climate is snuffing out post-fire recovery in montane forests. *Glob. Ecol. Biogeogr.* <https://doi.org/10.1111/geb.13174>
- Rodman, K.C., Veblen, T.T., Chapman, T.B., Rother, M.T., Wion, A.P., Redmond, M.D., 2020b. Limitations to recovery following wildfire in dry forests of southern Colorado and northern New Mexico, USA. *Ecol. Appl.* 30, 1–20. <https://doi.org/10.1002/eap.2001>
- Rodman, K.C., Andrus, R.A., Veblen, T.T. and Hart, S.J., 2021. Disturbance detection in landsat time series is influenced by tree mortality agent and severity, not by prior disturbance. *Remote Sensing of Environment*, 254, p.112244. <https://doi.org/10.1016/j.rse.2020.112244>
- Romme, W.H., Floyd, M.L., Hanna, D., Bartlett, E., Crist, M., Green, D., Grissino-Mayer, H., Lindsey, J., McGarigal, K. and Redders, J., 2009. Historical Range of Variability and Current Landscape Condition Analysis: South Central Highlands Section. Southwestern Colorado & Northwestern New Mexico, pp.9-12. http://sanjuanheadwaters.org/wp-content/uploads/2018/01/Historical_Range_of_Variability_and_Current_Landsc.pdf
- Roos, C.I., Guiterman, C.H., 2021. Dating the origins of persistent oak shrubfields in northern New Mexico using soil charcoal and dendrochronology. <https://doi.org/10.1177/09596836211003255>
- Ryerson, D.E., Swetnam, T.W., Lynch, A.M., 2003. A tree-ring reconstruction of western spruce budworm outbreaks in the San Juan Mountains, Colorado, U.S.A. *Can. J. For. Res.* 33, 1010–1028. <https://doi.org/10.1139/x03-026>
- Schoennagel, T., Veblen, T.T., Romme, W.H., Sibold, J.S., Cook, E.R., 2005. ENSO and PDO variability affect drought-induced fire occurrence in rocky mountain subalpine forests. *Ecol. Appl.* 15, 2000–2014. <https://doi.org/10.1890/04-1579>
- Schoennagel, T., Balch, J.K., Brenkert-Smith, H., Dennison, P.E., Harvey, B.J., Krawchuk, M.A., Mietkiewicz, N., Morgan, P., Moritz, M.A., Rasker, R., Turner, M.G., Whitlock, C., 2017. Adapt to more wildfire in western North American forests as climate changes. *Proc. Natl. Acad. Sci. U. S. A.* 114, 4582–4590. <https://doi.org/10.1073/pnas.1617464114>
- Scott, J.H., Thompson, M.P., Calkin, D.E., 2013. A wildfire risk assessment framework for land and resource management. USDA For. Serv. - Gen. Tech. Rep. RMRS-GTR. <https://doi.org/10.2737/rmrs-gtr-315>
- Sherriff, R.L., Platt, R. V., Veblen, T.T., Schoennagel, T.L., Gartner, M.H., 2014. Historical, observed, and modeled wildfire severity in montane forests of the Colorado front range. *PLoS One* 9. <https://doi.org/10.1371/journal.pone.0106971>
- Sieg, C.H., Linn, R.R., Pimont, F., Hoffman, C.M., McMillin, J.D., Winterkamp, J., Baggett, L.S., 2017. Fires following bark beetles: Factors controlling severity and disturbance interactions in ponderosa pine. *Fire Ecol.* 13, 1–23. <https://doi.org/10.4996/fireecology.130300123>
- Singleton, M.P., Thode, A.E., Sánchez Meador, A.J., Iniguez, J.M., 2019. Increasing trends in high-severity fire in the southwestern USA from 1984 to 2015. *For. Ecol. Manage.* 433, 709–719. <https://doi.org/10.1016/j.foreco.2018.11.039>
- Simard, M. and Payette, S., 2003. Accurate dating of spruce budworm infestation using tree growth anomalies. *Ecoscience*, 10(2), pp.204-216. <https://doi.org/10.1080/11956860.2003.11682768>
- Simard, S.W., Roach, W.J., Beaugard, J., Burkart, J., Cook, D., Law, D., Murphy-Steed, A., Schacter, T., Zickmantel, A., Armstrong, G., Fraser, K.M., Hart, L., Heath, O.R.J., Jones, L., Sachs, N.S., Sachs, H.R., Snyder, E.N., Tien, M., Timmermans, J., 2021. Partial Retention of Legacy Trees Protect Mycorrhizal Inoculum Potential, Biodiversity, and Soil Resources While Promoting Natural Regeneration of Interior Douglas-Fir. *Front. For. Glob. Chang.* 3, 1–18. <https://doi.org/10.3389/ffgc.2020.620436>
- Squires, J.R., Holbrook, J.D., Olson, L.E., Ivan, J.S., Ghormley, R.W., Lawrence, R.L., 2020. A specialized forest carnivore navigates landscape-level disturbance: Canada lynx in spruce-beetle impacted forests. *For. Ecol. Manage.* 475, 118400. <https://doi.org/10.1016/j.foreco.2020.118400>
- Stephens, S.L., Westerling, A.L.R., Hurteau, M.D., Peery, M.Z., Schultz, C.A., Thompson, S., 2020. Fire and climate change: conserving seasonally dry forests is still possible. *Front. Ecol. Environ.* 18, 354–360. <https://doi.org/10.1002/fee.2218>
- Stevens, J.T., Haffey, C.M., Coop, J.D., Fornwalt, P.J., Yocom, L., Allen, C.D., Bradley, A., Burney, O.T., Carril, D., Chambers, M.E., and Chapman, T.B., Haire, S.L., Hurteau, M.D., Iniguez, J.M., Margolis, E.Q., Marks, C., Marshall, L.A.E., Rodman, K.C., Stevens-Rumann, C.S., Thode, A.E., Walker, J.J., 2021. Tamm Review: Postfire landscape management in frequent-fire conifer forests of the southwestern United States. *Forest Ecology and Management*, 502, p.119678. <https://doi.org/10.1016/j.foreco.2021.119678>
- Steele, R., 1990. *Pinus flexilis* James limber pine. *Silvics of North America, Agriculture Handbook 654*, US Department of Agriculture, Forest Service, Washington, DC, USA, 348-354. <https://www.fs.usda.gov/treearch/pubs/1547>

- Tepley, A.J., Veblen, T.T., 2015. Spatiotemporal fire dynamics in mixed-conifer and aspen forests in the San Juan Mountains of southwestern Colorado, USA. *Ecol. Monogr.* 85, 583–603. <https://doi.org/10.1890/14-1496.1>
- Tachajapong, W., Lozano, J., Mahalingam, S., Zhou, X., Weise, D.R., 2008. An investigation of crown fuel bulk density effects on the dynamics of crown fire initiation in Shrublands. *Combust. Sci. Technol.* 180, 593–615. <https://doi.org/10.1080/00102200701838800>
- USFS. 1992. Final supplemental environmental impact statement for the amendment of the land and resource management plan, San Juan National Forest. USDA Forest Service. Durango, CO.
- USFS. 2014. San Juan National Forest and Tres Rio BLM Field Office Land Resource Management Plan, San Juan National Forest. USDA Forest Service. Durango, CO.
- van Auken, O.W., Bush, J.K., 2017. Succession in *Quercus gambelii* (Gambel's Oak) Woodlands. *Am. J. Plant Sci.* 08, 96–112. <https://doi.org/10.4236/ajps.2017.82008>
- Verkat, J., 2013. *Vegetation Dynamics on the Mountains and Plateaus of the American Southwest*. Springer Publishing.
- Westerling, A.L., Brown, T.J., Schoennagel, T., Swetnam, T.W., Turner, M.G., Veblen, T.T., 2016. Climate and wildfire in western US forests. *For. Conserv. Anthr. Sci. Policy, Pract.* 43–55. <https://doi.org/10.5876/9781607324591.c003>
- Yedinak, K.M., Strand, E.K., Hiers, J.K., Varner, J.M., 2018. Embracing complexity to advance the science of wildland fire behavior. *Fire* 1, 1–8. <https://doi.org/10.3390/fire1020020>
- Yocom-Kent, L.L., Fulé, P.Z., Bunn, W.A., Gdula, E.G., 2015. Historical high-severity fire patches in mixed-conifer forests. *Can. J. For. Res.* 45, 1587–1596. <https://doi.org/10.1139/cjfr-2015-0128>



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