Status and Trends of Piñon-Juniper Vegetation
in the western United States

Report to Defenders of Wildlife

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Introduction

In 1922, Walter Perry, forester of the Carson National Forest in New Mexico, wrote a report entitled “A Word for the Lowly Piñon”. He described piñon pine with these words, “The piñon tree (Pinus edulis) of our southwestern country is classed as an “inferior species”. It is, if one has in mind only the production of “clear” or “select” lumber… while it falls short as a lumber producer, it is not by any means valueless. In fact it has a very considerable value…” (Perry 1922). This forester was a man ahead of his time as he chronicled the cultural and ecological values imparted by widespread piñon-juniper ecosystems. The plight of this woodland did not decline with Perry’s words, and today the piñons and accompanying junipers are at times considered invaders of habitats (e.g. Miller et al. 2008, Munson et al. 2020) with characteristics that some feel are of greater value (grasses for forage, or shrublands for avian species, for example). Land managers have adopted this view, and as a result piñon-juniper woodlands have faced decades of clearing, chaining, reseeding to improve grass cover, and overgrazing (Redmond et al. 2014, Weisberg et al. 2018).

Recently, however, piñon-juniper has emerged as a vegetation type of conservation value and concern (Board et al. 2018, Rondeau et al. 2017). This change in perspective has developed both because many high-quality piñon-juniper woodlands have been recently lost or degraded (Macalady and Bugmann 2014), and because of the many ecosystem services provided by this woodland, including carbon sequestration (e.g. Barger et al. 2011a, Filippelli et al. 2020, Huang et al. 2010), soil and hydrologic stability (Williams et al. 2018), home to insects, birds, small mammals, and food and shelter for humans (Floyd 2003, Lanner 1981). For example, some 25 obligate bird species are associated with piñon-juniper woodlands, and at least some are declining, notably the piñon jay, the primary long-distance disperser of piñon seeds and a sensitive species listed by the New Mexico Bureau of Land Management (Boone et al. 2018, Johnson et al. 2017). Land managers trying to balance the needs of humans, native wildlife and ecosystems, and livestock have struggled with costs and benefits when considering values of piñon-juniper woodland, perhaps more so than any other ecosystem of the West (Hartsell et al. 2020, Romme et al. 2009). Recently, researchers have turned their attention to focus on the vulnerability of piñon-juniper woodlands (Floyd et al. 2021, Friggens et al. 2020, Rondeau et al. 2017).

The purpose of this report is to detail the history, condition, trends, and outlook of piñon-juniper systems in the western United States. This report will discuss first the taxonomy of the conifers that make up this woodland and point out that not all piñon-juniper woodlands are alike in species or ecosystem dynamics. The mobility of these woodlands (the expansion and contraction) will be discussed through the lens of prehistoric migrations into the western United States. This will be followed by a discussion of various types of fire regimes that characterize the woodlands and how those have changed in recent climates. The effects of land use such as cattle grazing, chaining, and fuel reduction will be discussed. Finally, the report covers recent climatic changes including drought and rising temperatures that have directly killed trees, reduced fecundity of populations, and precipitated widespread insect attacks.

Part 1—Natural processes

Ecological and taxonomic description

Piñon-juniper or juniper woodlands cover over 75 thousand square miles in the United States- including California, Arizona, Texas, New Mexico, Utah, Nevada, and Colorado (Lanner 1981), and juniper woodlands extend to eastern Oregon and

Washington. Piñon and juniper extend well into Mexico in the Sierra Madre Occidental and Sierra Madre Oriental and into Baja California Norte and Baja California Sur.

Piñon species exhibit hybridization and introgression, therefore their taxonomy has been challenging (Lanner and Phillips 1992). Piñon species of the Cembroid subfamily of pines include: *Pinus monophylla* var *monophylla*, single-needled piñon of the Great Basin and Utah; *Pinus californiaru*m (previously *Pinus monophylla* var *californiarum*) one-needled piñon of southern California; *Pinus edulis* var *edulis*, two-needled piñon of New Mexico, Colorado, Utah and northern Arizona; *Pinus fallax* (previously *Pinus edulis* var *fallax* and *Pinus monophylla* var *fallax)* one and two needled of the Mogollon Highlands in central Arizona, southern Arizona Sky Islands, and southeastern New Mexico; *Pinus discolor* (previously *Pinus cembroides* var *bicolor*, Felger et al. 2021), three-needled piñon of southern New Mexico, West Texas and southern Arizona); *Pinus cembroides* var *cembroides*, three needled piñon of southeast Arizona and Mexico*; Pinus quadrifolia*, four needled piñon of Baja California; *Pinus remota,* two or three needled piñon of southwest Texas and northeast Mexico; and *Pinus cembroides* var *laguna* of Baja CA Sur (Felger et al. 2021, Montes et al. 2019). However in this report, we focus only on piñon species of the United States-- *Pinus monophylla, Pinus edulis, Pinus fallax,* (distribution in Figure 1), *Pinus discolor* and *Pinus cembroides*.

Piñon-juniper woodlands are co-dominated by a species of piñon and one or more species of junipers. Juniper species include: *Juniperus osteosperma* in the Great Basin, the Colorado Plateau, and southern Rocky Mountains west of the Continental Divide; *Juniperus monosperma* in New Mexico, central Arizona, and the southern Rockies east of the Continental Divide; *Juniperus scopulorum* in the Colorado Plateau and in the southern Rockies; and *Juniperus deppeana* in Arizona south of the Mogollon Rim and in southern New Mexico and Mexico. While worthy of consideration, other piñon and juniper species will not be included here, and indeed the bulk of the research on challenges and threats to the woodlands comes from the *Pinus edulis-Juniperus monosperma* and *Juniperus osteosperma* or *Pinus monophylla-Juniperus osteosperma* systems.

Geographic movement after glaciation

Geographical movement of piñon and juniper at the modern woodland edge--expansion and contraction--appears to be a key consideration in many management decisions (Bates et al. 2019, Munson et al. 2020). The ebb and flow of conifers in and out of ecotones with grasslands or shrublands will be discussed in a section of this report below. However, in order to understand the fluxes in distribution occurring today, it is important to outline the migration patterns of piñon and juniper in prehistory, recognize how recently these woodlands have been occupying their current geographic areas, and understand that this movement still occurs today at ecotones.

Pinus monophylla is the only pine in the world known to have exclusively single needled fascicles, and this trait is shared, probably by pollen flow, into *P. fallax* and in *P. californiarum*, both of which have one and two needles. *Pinus edulis* has two needles, and *P. cembroides* three needles. Piñon needles are viewed as drought adaptations, with surface area to volume ratios, thick waxy covering, and stomatal placements that allow efficient use of limited precipitation. Piñons vary in their needle morphology and in the number of needles per fascicle, traits that have been used for taxonomy but are also interpreted as responses to precipitation. Single-needled piñons occupy areas with predominant winter precipitation and two-needled piñons occur in areas with summer monsoon precipitation, and the variable one and two needles in areas occur with extreme May to June drought (Cole et al. 2008).

Through packrat midden analyses, Cole et al. (2013) have suggested that piñon needle morphology, stable for the last 40,000 years, provides a key to not only the changing distributions of piñons in response to glacial advances and retreats, but also may suggest modes of resiliency within the cembroid group. One key comes from the distribution of three piñons—*P. edulis, P. monophylla* and *P. fallax*—during the Wisconsin glaciation where each was pushed south yet grew on portions of their current southern ranges. For example, *P. fallax* occupied the current Sonoran desert areas. With warming and precipitation 120-150% of today's precipitation, about 11,700 years ago, piñons migrated northward 300-500 km to their current locations. The rate of those responses varied across the three piñon species- from 21 to 60 m/yr in *P. monophylla* to 43 m/yr in *P. edulis* (Cole et al. 2013). *Pinus fallax* once enjoyed a wide geographic range, but its northern migration resulted in a narrow, compressed range below the Mogollon Rim and into southwestern New Mexico, an area known as the Mogollon Highlands (Fleischner et al. 2017). Relatively slow migration is reflected at the northernmost edge of piñons today at Dutch John Mountain, Utah which was occupied by *J. osteosperma* for 8700 years. The drought of the 1200s prevented migration of piñons, which finally made their way into this northern area during wet decades of the 1300s. A relict stand at Owl Canyon, Colorado similarly reflects this northern migration (Gray et al. 2006). Nearby Dinosaur National Monument, Colorado, supports ancient piñons that are likely remnants of that wet time (Floyd et al. 2017, Hanna et al. 2018). Miller and Wigand (1994) discuss juniper migration following the drying and warming trends after the Holocene. Migrations after the Holocene into the Great Basin by *P. monophylla* and *J. osteoperma* are documented for specific mountain ranges and drainages (Miller et al. 1999). In short, piñon and juniper have been on the move for many centuries.

However, despite this ability of populations to respond to extreme climatic changes by migrating, such as occurred at the end of the Holocene, migration rates of piñon are too low to allow migration under predicted future climatic changes. Piñons will not be able to equilibrate to today's rates of changes, suggesting that contraction is likely (Cole et al. 2013). We are already seeing alarming death of piñons (e.g. Breshears et al. 2005, Shaw et al. 2005) and recently of junipers (Kannenberg et al. 2021).

Piñon-juniper woodland biodiversity

Piñon-juniper woodlands are rich in plant diversity. Lying between high deserts and ponderosa pine forests, they are capable of supporting understory plant species more common to the lower elevation desert and, in wet microsites, the upper elevation forests. Yet little has been published on the natural history of the widespread piñon-juniper woodlands. Piñon-juniper woodlands on the Kaiparowits plateau include 207 plant species of which 6 % are exotic (Floyd et al. 2008). Post-fire monitoring has documented plant diversity as well. For example, 210 plant species were recorded within one year of the 1996 fire in Mesa Verde National Park (van Riper and Stuart 1999). The National Park Service's Inventory and Monitoring program has documented hundreds of plant species in piñon-juniper woodlands in vegetation mapping projects (for example, in Dinosaur National Monument, Coles et al. 2008). We can glean some trends in biodiversity from management studies; for example Huffman et al. (2009) set up a series of thinning and burning demonstration sites and monitored the rich plant diversity across those sites.

The natural history of old-growth piñon-juniper woodland at Mesa Verde National Park, where livestock grazing has been absent for nearly a century, was summarized by naturalists who spent decades making observations of vascular plant diversity. Marilyn Colyer, Resource Manager, and associated researchers documented 256 vascular plant species in old-growth woodlands, several of which are endemic. In addition, a rich diversity of non-vascular plants and fungi (approximately 100 species of fungi, 165 known species of lichen, and 25 species of bryophytes) was recorded. There are 64 species of mammals and at least 113 species of birds. Soil microorganisms and over 10,000 insect species have been described in Mesa Verde's woodlands (see chapters in Floyd 2003). Piñon-juniper woodlands in Mesa Verde are rich in soil arthropods (Higgins et al. 2014).

Carbon sequestration

Terrestrial vegetation captures about one quarter of the man-made carbon dioxide each year; while tropical rain forests absorb carbon in a steady manner, semi-arid woodlands contribute to the temporal variability of global uptake (Ahlström et al. 2015). Carbon sequestration in these woodlands can be significant (Huang et al. 2010); one measure of carbon uptake, net primary productivity, in piñon-juniper woodlands increases with elevation and with greater woody cover (Barger et al. 2011, Filippelli et al. 2020, Huang et al. 2012). Piñon-juniper woodlands contain significant carbon in live and dead biomass as well as in soils; total woodland carbon of 104 tons/ha is lower than other western forest types, for example Douglas-fir forests with 245.9 total C tons/ha or ponderosa pine forests with total C 170.3 tons/ha. However, ponderosa pine area is only two thirds of the geographic extent of piñon juniper woodlands and Douglas-fir is less extensive as well (Heath et al. 2002). Therefore, considering the geographic extent and carbon uptake capacity, the contribution of piñon-juniper woodlands to carbon sequestration appears considerable.

Carbon sequestration was significantly reduced because of tree death in 2000-2005 as estimated by remotely sensed changes in above ground biomass and measured rates of carbon uptake; the loss of carbon uptake was 39 times greater than that attributed to wildfires or management activities (Huang et al. 2010).

Part 2: Recent challenges to piñon-juniper woodlands

Woodland dynamics: infill, contraction and expansion

Infill responses in older piñon-juniper woodlands: Ample evidence exists throughout the range of *P. edulis* and *P. monophylla*, and to a lesser extent *P. cembroides* and *P. fallax*, that these older stands benefitted from the wet decades of the 1900s, allowing a natural increase in the density of saplings and small trees in *P. edulis* stands whose seedlings require shade (Chambers 2001, Chambers et al. 1999, Floyd 1982, Floyd et al. 2004, Romme et al. 2009). For example Ffolliott and Gottfried (2002) documented a modest increase in *J. monosperma* stand density of 148 trees/ ha in 52 years near Flagstaff, Arizona. *Pinus monophylla* “infilling” was documented by Miller et al. (2008) and Weisberg et al. (2007). In *P. monophylla* stands in the Mt. Irish and Clover Mountains areas of the Great Basin, *P. monophylla* density doubled since the 1800s (Biondi and Bradley 2013). *Pinus cembroides* and *J. deppeana* increased in density in the Sky Islands of the Davis Mountains, Texas, by 422 trees/ha in a 115 year period, a rate deemed “not rapid” by the authors (Bataineh et al. 2020). Floyd (1986) compared stand structures of *P. edulis* and *P. cembroides* noting that in *P. edulis* stands, precipitation-enhanced establishment was followed by high mortality of the seedlings and saplings (even in wet decades), altering stand structures over the short term, while recruitment *in P. cembroides* stands was less volatile with lower seedling and sapling densities, but greater seedling. This study presents a caution: any snapshot of *P. edulis* stands is likely transitory and could be misleading (Floyd 1986).

Edge transitions and evidence for expansion: The jury is still out on whether piñon-juniper woodlands have expanded, contracted, or stayed just about the same in the last two centuries. Evidence for any of these trajectories come from 1) comparison of historical accounts and repeat photography in specific locations, 2) stand age studies, and 3) remote sensing. Few people have studied the piñon-juniper woodlands as deeply as Dr. Ronald Lanner, a forester who is Emeritus Professor of Forestry from Utah State University whose two books on the piñon pine (Lanner 1981) and the relationship of the pines and birds (Lanner 1996) chronicle the beauty and importance of these woodlands to western biota, including humans. In his commentary entitled "How did we get it so wrong?", Lanner admonishes forestry and range management for mistakes made in the Great Basin in eradicating stands of *P. monophylla* with little evidence of "expansion". In his words:

> "Eyewitness accounts of the 19th century forest, recently made accessible by digitization, paint a very different picture of its nature and extent, details of which are in a study by Lanner and Frazier (2011). The reports of federal explorers, Nevada state mineralogists, biologists C.H. Merriam and Frederick Coville, the dendrologists Franklin B. Hough and Charles S. Sargent, the naturalist John Muir, and a Nevada district attorney prosecuting timber trespass, describe dense pinyon-juniper forest where it is now regarded as an interloper. Then, as today, its stands encompassed tens of thousands of continuous acres from base to summit of mountain ranges all across Nevada within the present-day range of the type. No observer described savannas, even in the drier southern portions of the state. None of the many towns, mines, ranches, or smelters was reported short of structural wood, fuelwood, or charcoal until severe deforestation had been noted. At the scales of regional landscape, mountain range, and individual
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> Mining District, such adjectives as well-timbered, densely covered, thrifty growth, densely wooded, good supply, well-wooded, abundant, even inexhaustible were freely applied to this dryland coniferous forest. Muir climbed 10 ranges in central Nevada's pinyon juniper heartland and found them forested from base to summit, roughly, 5,000 –9,000 ft, as they remain today" (Lanner 2012).

John Muir, noteworthy naturalist, also documented expansive piñon-juniper woodlands in the Great Basin, around 1918. As quoted in Lanner and Frazier (2011):

> "Thus, Muir had first-hand knowledge of at least eleven Nevada mountain ranges, and ascended at least ten of them. Of the singleleaf pinyon, or nut pine, he generalized: "In the number of individual trees and extent of range this curious little conifer surpasses all the others combined. Nearly every mountain in the State is planted with it, from near the base to a height of from eight thousand to nine thousand feet above the sea. Some are covered from base to summit by this one species, with only a sparse growth of juniper on the lower slopes to break the continuity of these curious woods. ..Tens of thousands of acres occur in one continuous belt. Indeed, the entire State seems to be pretty evenly divided into mountain ranges covered with nut pines and plains covered with sage - now a swath of pines stretching from north to south, now a swath of sage; the one black, the other gray; one severely level, the other sweeping on complacently over ridge and valley and lofty crowning dome".

Similarly, historical accounts of the landscapes below the Mogollon Rim near Prescott, Arizona describe woodlands in extent and character similar to those today. Harley Shaw compiled historical accounts and repeat photography of the upper Verde region, surmising that while areas of infill and growth of trees are clear, "The picture that emerges of the general study area, for the mid-19th century, is one of a dry short grass prairie intermixed with stands of juniper. It may have been more savanna-like than it is now. Woodlands now seem denser, mainly on ridges in areas where they existed in 1854, but I see no evidence that they have greatly extended their range into the larger valleys, such as Big Chino. A few stands of extremely dense juniper were present in the 1850s…" (Shaw, 2006).

In contrast, on the San Carlos Apache reservation, using remote sensed imagery, three areas that were characterized as "savanna" in 1935 are now piñon-juniper and oak woodlands, apparently due to fire cessation and overgrazing (Middleton and Norman 2021). Extensive treatments using tree removal, herbicides, and mastication are converting these woodlands to more open, savanna habitats.

Successful recruitment during the cool wet decades of the early 1900s is reflected in expansion of the periphery of woodlands, however interpretation of this expansion depends on the scale of studies (Weisberg et al. 2007), and by a variety of definitions used by ecologists to describe characteristics of shrubland-woodland or grassland-woodland interfaces (e.g. Miller and Tausch 2001). Miller and Tausch describe “unprecedented” invasion of juniper and piñon, and “the most pronounced vegetation change in 130 years… in the Intermountain West”. Estimates range, but typically hover around, a ten-fold expansion in the past 140 years (Niemeyer et al. 2017).

These estimates are often based on studies with small-scale approaches and are highly dependent on landscape characteristics such as slope and elevation (Greenwood and Weisberg 2008). Also, rarely are definitions provided for the density or cover of a “woodland” or “forest” (but see Filippelli et al. 2020), making interpretations of “invasion” and “encroachment” difficult.

This report will separate key papers from Great Basin *P. monophylla-J. osteosperma* country from Colorado Plateau, Colorado and New Mexico papers which focus on *P. edulis* and *J. monosperma* or *J. osteosperma*. No mention could be found in the literature for expansion in the *P. fallax-J. deppeana, J. monosperma* woodlands of the Mogollon Highlands, nor of the southern Arizona and New Mexico *P.discolor* or *P. cembroides* populations.

Great Basin: Much of the early literature that drew attention to woody expansion was conducted in the Great Basin and Utah where single-needled piñon *P. monophylla* and *J. osteosperma* occur, and in eastern Oregon where *J. occidentalis* dominates with sagebrush steppe. While it would be difficult to review each of these studies here, a comprehensive review paper was provided by Miller et al. (2008) in which stands of the Intermountain West were reviewed. They document through studies of age-structure (comparing pre-settlement to post-settlement tree densities) that in the last two centuries stands have increased 140-635%. However, this "expansion" includes both areas that have thickened in the same footprint (infill) as well as areas that were previously unoccupied or had very low conifer densities. This review compares seven study populations from four ecological provinces in the Intermountain West and breaks the type of woodland-shrub dynamic into three phases with increasing tree dominance. The authors suggest that successful recruitment of piñon and juniper in the late 1800s through early in the 20th century is attributed to high precipitation, mild winters and abundant "seed disseminators" (Miller et al. 2008): "The most rapid period of expansion occurred between 1880 and 1920, which also coincided with the most rapid period of tree establishment. We were surprised by the consistent decline in expansion rates across all of the woodlands after 1950." This decline in the recruitment of piñon and juniper was attributed to changes in climate (drying) and reduced sagebrush habitats. In short, an ebb and flow, a dynamic at the interfaces of sagebrush and other shrublands, or grasslands, and piñon-juniper woodlands was documented (Miller et al. 2008). It is noteworthy that this work has been widely cited by 137 subsequent papers, many of which discuss expansion but rarely provide additional data.

In contrast, at Mt. Irish and in the Clover Mountains, also Great Basin *P. monophylla* stands, pre-settlement piñons of greater than 400 years were documented, and like in *P. edulis* stands elsewhere (Floyd et al. 2004), these populations showed old growth characteristics with successful infill of saplings during the wet decades of the early 1900s. Like other *P. monophylla* stands (and unlike many areas of *P. edulis*), mortality later in the century was low, less than 10%, and successful establishment occurred in old growth stands but not into new areas (Biondi and Bradley 2013). Thus, these authors suggest that the drought of the 2000s has had less effect on *P. monophylla* than *P. edulis*, and that expansion into new geographic areas has not occurred. Similarly, changes in *P. monophylla* stands in the Simpson Park Mountains, Great Basin, have been characterized by both expansion and decline, but primarily as “infilling” rather than expansion into new geographic areas during the 30 yr period 1966-1995 (Weisberg et al. 2007).

More recent studies use remote sensing techniques to clarify the geographic locations and habitat types where expansion, or contraction, of woodlands is occurring. *Pinus monophylla-J.osteosperma* expanded overall by 33% in a 25 km^2 area in the Great Basin; however, much of that expansion took place in clearings among established stands, with lesser expansion (less than 11%) beyond the boundary. Further, the rate of expansion (or infill) was highly dependent on elevation, topography, and mesic conditions (Weisberg et al. 2007). Landsat has provided an opportunity to measure landscape changes at 30 m resolution. For example a “greenness index” was created across the Great Basin from satellite images showing that a 1986-2005 expansion occurred below 3000m elevation (due to increases in precipitation, rising carbon dioxide and its effect on plant water use efficiency, and grazing patterns), while in 2005 it occurred between 2200 and 2600 m (Bradley and Fleischman 2008). Remote sensing of biomass suggests that piñon-juniper woodlands, which are defined as “forested” if they have greater than 10% cover, are increasing in geographic extent by .46% per year (.39% between 2000-2016); 80% of increase in biomass is attributable to infilling of existing woodlands (Filippelli et al. 2020). Recently, other remote sensed data suggest that there has been little change across 75% of a 34,000- km^2 study area in the Great Basin, and that canopy was reduced in 12% (mostly low elevations and south slopes) and increased in 13% (mostly on hotter and drier sites), so virtually no net change occurred. These authors caution that “The dominant management paradigm for Great Basin pinyon-juniper woodlands - one of ‘landscape restoration from woodland expansion’ - needs to be broadened to achieve resilience of the overall landscape mosaic to climate change, fire regime shifts, and other stressors" (Weisberg et al. 2018).

Colorado Plateau: Manier et al. (2005) provide a comprehensive study of woody canopy changes on the Uncompaghre Plateau in western Colorado where *P.edulis-J. osterosperma* occur. In this study, analyses of aerial coverage show that between 1937-1994, spatial variability in coverage changes occurred, with contractions and expansions (for example piñon and juniper into sagebrush or grassland between the low elevations of 1800-2300 m). The net result however was little change in woody cover. The authors attribute this stability to human-caused changes which balance natural successional trends, and do not attribute changes strictly to wildfires (but see below).

At the northern edge of *P. monophylla- J. osteosperma* distribution at City of Rocks National Reserve in Idaho, a comparison of aerial coverage from 1950 to 2009 shows that while older piñon-juniper woodlands showed infilling during wet decades, no peripheral expansion has occurred. In fact, contraction of the extent of younger woodlands is evident, attributed to wildfires (Powell et al. 2013). We documented a similar wildfire-driven contraction of old-growth woodlands, which tend to rely on obligate seeding, by nearly 50% since 1994 in Mesa Verde National Park, while sprouting woodlands showed greater resiliency (Floyd et al. 2021). In Dinosaur National Monument, some expansion of piñon and juniper was documented at the historic ecotones, but there was overall contraction of woodlands in the past 90 years by 7% attributed to a shortening of the naturally long fire cycle due to climatic changes and land use history. While mountain shrublands also contracted, sagebrush expanded up to 26% (Arendt and Baker 2013).

Pinus cembroides-Juniperus deppeana oak woodlands: An increase in fire frequency and size has been documented in the past few decades in the Sky Islands of southern Arizona. One result of these fires has been a resilience of shrub components to the detriment of conifers, suggesting a type conversion to shrub fields and contraction of piñon and juniper (Minor et al. 2017). Similar conversion to oak shrublands from mixed conifer has been documented also in the Sky Islands region (Barton and Poulos 2018). As in shrub rich piñon-juniper woodlands on the Colorado Plateau, it is likely that the shrubs will replace what once was mixed conifer shrub systems due to climatic changes that are altering fire frequencies and post-fire revegetation patterns.

Pinus edulis-savanna type: In northern and central New Mexico, and parts of northern Arizona north of the Mogollon Rim, open piñon-juniper savanna develops from more frequent fire intervals than shrub-dominated or persistent woodlands (Romme et al. 2009, 2021). In these systems, fire-killed trees are in a dynamic with fire-resistant grasses, and lengthening of fire intervals (discussed below) has resulted in a favoring of the conifer component in recent times. For example, in New Mexico at Rowe Mesa, where woodlands include ponderosa pine as well as piñon and juniper, Margolis (2014) has shown through dendrochronologic methods that piñon and juniper have reached densities 600% higher than historical densities due to fire cessation (Margolis 2014, Malcolm et al. 2020). Similarly, in Wupatki National Monument where *J. monosperma* and grasslands coexist, new evidence suggests than juniper has expanded into grasslands recently as fire frequency has declined (Romme et al. 2021).

Possible effects of “invasion” include reduction in stream flow (Niemeyer et al. 2017), reduction of sagebrush habitat suitable for sage-grouse (e.g. Reinholt et al. 2020 and references within), reduction of range suitable for grazing (Jacobs 2011, Middleton and Norman 2021), soil erosion (Davenport et al. 1998), reduction of biodiversity (Miller and Tausch 2001), reduction in soil water available to other species (Roundy et al. 2014), and increased risk of stand replacing fire (see below).

Fire regimes in piñon-juniper woodlands

It is important to understand the fire history of piñon-juniper woodlands that has helped shape the woodland structures across the West, and to compare the different types of fire regimes that existed during the last several centuries (Romme et al. 2009). In this report, first the fire history is discussed for each woodland type, and then recent changes to the fire regime will be covered.

Fire history: Knowledge of historical and modern fire regimes and fire rotations is lacking in many piñon-juniper woodlands, but a growing body of knowledge is emerging. Fire rotation is defined as the expected time to burn a cumulative area equal to the extent of the landscape of interest (Baker, 2009). Some portions of the landscape typically burn more than once during a fire rotation, and other portions do not burn at all. In a comprehensive review of the literature, Baker and Shinneman (2004) critically evaluate whether stand-replacing high severity or low intensity surface fires occur in piñon-juniper woodlands. The management implications of these data are important—should there be evidence of "missed" surface fires as seen throughout ponderosa pine forests, then use of thinning and prescribed burning might indeed return these woodlands to their natural condition. They conclude that evidence for surface fires is lacking and that ".., national fire plans and assessments of the condition and health of piñon–juniper woodlands in the western United States are based on premature and likely incorrect conclusions about the natural fire regime in piñon–juniper woodlands. Local research is essential, at the present time, if effective, scientifically based restoration prescriptions are to be derived".

In the western United States, historical fire rotations in "persistent" piñon-juniper woodlands (stands of various density and canopy cover found where local soils, climate, and disturbance regimes are favorable for piñon and juniper) (*sensu* Romme et al. 2009) are typically centuries long. Fire rotations in "persistent" stands have been reported from 230 to 340 yr in northern Arizona (Huffman et al. 2008, 2012) to 400 to 600 yr on the Colorado Plateau (Floyd et al., 2004, 2008; Romme et al., 2009; Baker and Shinneman 2004) to >1,000 yr in Colorado National Monument (Kennard and Moore, 2013) and 550 yr in Dinosaur National Monument (Floyd et al. 2017).

There are challenges in reconstructing past fires from current age structure, especially where historical fire perimeters cannot be detected precisely. Yet, patterns of stand ages in piñon-juniper are important to delineating fire history. Piñons and junipers are not fire tolerant and rarely form fire scars. Stands usually do not regenerate with an even-aged post-fire cohort but gradually fill in with trees over time spans ranging from decades to even a century, especially as noted above, during wet climatic periods (Huffman et al., 2012). Therefore, studies often determine the ages of the oldest living trees in a stand and assume that the last stand-replacing fire occurred before the establishment dates of those trees (Floyd et al. 2004, 2008, 2017, Huffman et al. 2008,Kennard and Moore 2013). It is impossible to know whether that fire occurred only a few years before the trees' establishment or decades earlier. Thus, estimates represent minimum stand ages. Despite having less precision using stand ages than is possible in other vegetation types, researchers are able to use piñon age data along with multiple lines of evidence—vegetation patterns, topographic position, fire scars or snags—to conservatively interpret fire rotation (Floyd et al. 2017).

Less is known about fire history in the two other types of piñon-juniper woodlands—piñon-juniper/savanna and wooded shrubland (Romme et al. 2009). In two New Mexico *P. edulis-J. monosperma-* savanna sites, mean fire intervals were re-constructed using 112 fire scars (rare in other piñon-juniper systems). Margolis (2014) documented that between 1547-1899, the mean fire interval was 7.8 years; recently, due to lack of recent fires, piñon and juniper density increased by 600 percent. In *Pinus cembroides*-oak woodlands in Big Bend and the Davis Mountains, Texas, frequent low intensity fires occurred with mean intervals of 11-36 years (point intervals 75-150 years) (Poulos et al. 2009). Fire history of *P. cembroides* woodlands show low severity fires occurred,but overall stand dynamics were driven by larger stand replacing fires in west Texas (Poulos et al. 2020). Wooded shrublands also have shorter fire return intervals, about 100-yr rotation, than persistent woodlands, about 400 yr rotation (Floyd et al. 2000, 2004).

Since the onset of drought conditions in the southwest in the late 1990s, fires have become larger and more frequent in all types of piñon juniper woodlands (Board et al. 2018).

Post-fire regeneration: Return of canopy trees after stand replacing wildfires in piñon-juniper woodlands is typically a very slow process, occurring over decades or centuries (Chambers 2001, Huffman et al. 2012, Koniak 1985, Poulos et al. 2020); for example, we have not observed new piñon or juniper trees becoming established in any of the places that burned within the past 30 years at Mesa Verde (Floyd et al. 2021). But we have seen considerable variation in post-fire response of the understory, notably in relation to species composition and physiognomic structure. Variation in post-fire understory characteristics are important not only for their own roles in community structure and function, but because the understory can either facilitate or hinder the process of tree re-establishment; for example, shrubs can function as "nurse plants" that create locally favorable microclimatic conditions for new tree seedlings, whereas heavy grass cover ofteninhibits tree seedling establishment (Chambers et al. 1999, Floyd 1982, Redmond et al. 2018, Schupp et al. 1999).

At Mesa Verde, two fundamental types of understory composition and structure in the piñon-juniper woodlands were distinguished: 1) stands having a large proportion (approximately 80%) of sprouting shrubs and forbs often resistant to drought, “sprouting woodlands”, and 2) stands in which many species (approximately 40%) regenerate after fire via seed germination rather than vegetative sprouting, “obligate seeding woodlands”. The responses after wildfires were compared (Floyd et al. 2021). Where shrubs are common communities stabilize soon after fires, however, they lack the piñon and juniper elements, and in the old growth stands that depend on obligate seeding species, climatic changes have caused novel plant communities dominated by invasive species (Floyd et al. 2021).

Invasive species

Throughout many types of piñon-juniper woodlands, non-native plant species have begun to replace natives after disturbances such as wildfires, in part due to nutrient spikes and death of trees, which create new spaces for non-native species. to invade. For example, in Dinosaur National Monument, modern piñon-juniper woodland fires have been invaded by *Bromus tectorum*, cheatgrass (Arendt and Baker 2013). At Mesa Verde National Park, where beginning in 1989 wildfires burned old-growth woodlands, *Carduus nutans*, musk thistle, and cheatgrass invasions were prolific, the density of weeds depending on soil texture type and nutrient status (Floyd et al. 2006). In Great Basin sites, cheatgrass invaded prescribed burn management sites most prolifically where there had been high tree cover and low perennial cover (Urza et al. 2019). In mid and low elevations where dry and warm conditions prevailed in the Great Basin, cheatgrass has invaded patches of woodland where trees have died and tree canopy reduced (Flake and Weisberg 2019a, 2019b, 2021).

The intrusion of fine fuels can likely cause future surface fires, preventing the slow recovery from fire by junipers and piñons (Chambers 2001). As a result, significant reductions in the extent of Great Basin, Colorado Plateau, and Arizona and New Mexico piñon-juniper woodlands, particularly the persistent type, is expected with warming and drying climates (Floyd et al. 2021). For example roughly 50% reduction of persistent woodlands has occurred in the last 30 years in Mesa Verde (Floyd et al. 2021). Long fire cycles are required for these woodlands to develop, and the presence of flashy, fine fuels will not likely allow such intervals to occur in the future. Indeed, Mesa Verde has seen re-burns of 1996 and 2000 fires, extending that period of possible recolonization by conifers. Similarly, using satellite data, Reinhardt et al. (2020) documented a 1.6% reduction in woodland area between 2011/2013 and 2015/2017 which effectively canceled out a similar amount of expansion. They attribute this to management treatments as well as wildfires. As in other ecosystems throughout the West, fires in piñon-juniper woodlands are becoming more frequent and larger in recent decades, although the characteristics of stand replacing wildfires is similar to that of historic fires (Floyd et al. 2004, 2021, Romme et al. 2009).

Declining reproduction

In addition to novel fire frequency and sizes in these woodlands, changes in climate have also affected the fecundity of the remaining stands. The Cembroid group of pines require two (in one case three) growing seasons to mature a female cone. Masting of large patches is typical, although the locations of masting stands are not consistent in any year across the landscape. The evolutionary significance of masting has been well-studied; avian and other dispersal vectors become overwhelmed with the seeds, caching them in germinable sites, and in some cases, as with pinyon jays, failing to retrieve all the seed (Balda and Bateman 1971). This interrelationship is exhibited also by the fact that pinyon jay gonad development is stimulated by the presence of green piñon cones

(Ligon 1974, 1978). Masting occurs at 5-7 year intervals, and the large masting events have been attributed to low summer temperatures at cone initiation (Forcella 1981). Recently, Wion et al. (2019) have attributed masting events to preceeding years with low vapor pressure deficits and high precipitation, while low cone production occurs in drier years resulting in less masting. Masting has declined by 40% since 1974 in stands revisited in New Mexico; the authors attribute this drop to rising temperatures (Redmond et al. 2019). For these or other reasons as yet unknown, piñon cone production seems to be on the decline in recent decades (Wion et al. 2019).

Masting also occurs in juniper and oak as an inverse response to the same environmental cue, lagged late-summer/autumn temperatures during fruit primordia formation (1-yr lag for juniper and oak, 2-yr lag for piñon pine). Juniper masting increases with higher late winter precipitation, and piñon masting is reduced by higher summer temperatures (Parmenter et al. 2018). In short, cone production is declining with climate change and threatening the fecundity of piñon-juniper woodlands.

In addition, a significant threat to sustainability of these woodlands is a precipitous decline in seedling recruitment since the early 1990s, likely a result of lower cone and seed production. Comparing drought and pre-drought seedling densities using a series of historic plots at Mesa Verde, Floyd et al. (2015) documented a sharp drop in seedling densities after 1995. Similar declines have been recorded in piñon seedling densities in Colorado, caused by both reduced seedling density and high seedling mortality, while such an effect was not seen in juniper (Redmond et al. 2012).

Grazing

Cattle grazing has been shown to alter the integrity of piñon-juniper woodlands as it has most western ecosystems. Trampling, reduction of capacity for water infiltration, and destruction of the biological soil crusts are among the post-grazing factors that threaten piñon-juniper woodlands (Fleischner 1994, 2010). Such threats might conceivably be seen in the canopy, including the sustainability of recruitment to the woodland, or in integrity of understory and soil components. A general sense among managers suggests that infill and expansion of juniper into shrublands is in part due to grazing legacies (e.g. Burkhardt and Tisdale 1976, Miller et al. 2008, Middleton and Norman 2021), yet few studies directly test that assumption in different types of piñon-juniper woodlands that vary in understory components (Romme et al. 2009). Myriad data document a reduction in biotic crust cover, e.g. up to 80% in Grand Canyon National Park due to grazing, accompanied by a loss of grasses and forbs (Beymer and Klopetek 1992). In Grand Staircase-Escalante National Monument, both field and remote sensed data were used to compare grazed and ungrazed plots (Harris et al. 2003). Surprisingly, remote data showed photosynthetic biomass was higher and non-photosynthetic biomass and bare soil cover were lower in grazed than ungrazed areas. Field studies attributed this to a significant increase in shrubs and forbs in intercanopy spaces, accompanied by a one-third decline in grasses in grazed plots (Harris et al. 2003). Since shrubs may act as nurse plants for piñon establishment, the net effect could possibly be an increase in microsites for conifer establishment. In southeastern Utah, piñon recruitment was unaffected by grazing history (Barger et al. 2009). To date, few studies substantiate the roles of livestock grazing in recruitment of piñon and juniper (Hartsell et al. 2020).

Because cheatgrass invasion may be facilitated by grazing and warming climates (see section below), and cheatgrass is a fine continuous surface fuel, its presence in piñon-juniper woodlands may make fires more likely to spread, hence shorten the fire intervals. In addition, surface fires are typically not within the historic range of variability in piñon-juniper woodlands, with the possible exception of savanna type

(Margolis 2014, Romme et al. 2009). Such change to the native fire regime can have cascading effects on the sustainability of woodlands; frequent fires will reduce the likelihood that piñon and juniper can re-establish in the area (Floyd et al. 2021, but see Poulos et al. 2020).

Global Climate Changes: implications for piñon-juniper woodlands

Recent climate changes are a significant threat to the sustainability of piñon-juniper woodlands (Anderegg et al. 2013) particularly at the lower elevation edges of these populations. Climate changes increase insect populations, such as *Ips confusus,* the piñon engraver beetle that killed stressed piñons throughout the southwest in the early 2000s, averaging 6 % loss (e.g. Breshears et al. 2005, Clifford et al. 2013, Floyd et al. 2009, Kleinman et al. 2012, Gaylord et al. 2015, Shaw et al. 2005). But, many areas such as Mesa Verde National Park experienced greater than 30% mortality (Floyd et al. 2015), or as in northern New Mexico, some stands lost over 95% of their piñons (Breshears et al. 2005). Although this is a native beetle, warming temperatures allowed it to have many more generations than usual, causing the beetle to overwhelm the host piñon trees, especially those of the larger size classes (e.g. Clifford et al. 2011, Floyd et al. 2009).

In addition to insect-related mortality patterns, there are direct effects of recent climatic changes on piñon and juniper. Until the last year, piñon had appeared more susceptible to climate changes than junipers causing a shift in dominance toward junipers in some areas (Clifford et al. 2011, Floyd et al. 2009). But recently, death of junipers (*J. monosperma, J. osteosperma, J. deppeana*) is becoming very obvious (Kannenberg et al. 2021, personal observations). The direct effects are discussed below.

The West is experiencing decreased annual precipitation and shifts in monsoonal patterns, and these likely have different effects on piñons and junipers. Piñon and juniper utilize deep winter precipitation and more shallow summer monsoonal moisture differently. Junipers tend to continue to utilize available summer monsoonal water throughout the summer months, while piñon does not utilize it as well in midsummer when their roots are sensitive to hotter soil temperatures (Williams and Ehleringer 2000). Although commonly thought that junipers have more extensive roots and utilize deeper water sources than piñon, a recent study shows that piñon may have up to twice the root mass as juniper and similar root depths, and piñon had more fine root mass near its trunk and in shallow soils (Schwinning et al. 2020). More data are needed but it is clear that piñon and juniper have unique means of obtaining available water and that both seasonality of water and total amounts may affect these species differently, allowing for shifts in dominance of one species or the other.

Research suggests differential climate sensitivity exhibited across ages in *P. edulis* (Hanna et al. 2018). Macalady and Bugmann (2014) studied the growth of tree rings from *P. edulis* that survived the 1950s and 2000s droughts, comparing them with trees that died during those periods. They found that growth was 53% higher in trees which survived the droughts; if trees respond by increased growth during wet and cool years, this allows them to store carbon that could increase their chances of withstanding future droughts or insect attacks (Macalady and Bugmann 2014). Also *P. cembroides* in southern Arizona and in Mexico respond differently to high temperatures and drought throughout their latitudinal range, with a reduction in radial growth in the hottest and driest conditions (Herrera-Soto et al. 2018).

Piñons have myriad adaptations that allow them to persist in arid conditions; they have needles rather than leaves with low surface area/volume, sunken stomata, thick waxy cuticle, and strong resistance to cavitation of xylem (air pockets in xylem rendering parts of the wood incapable of water flow), but even those are being stretched to the limit with recent climatic changes. A series of metrics have been developed to characterize tree death (Breshears et al. 2018, McDowell et al. 2008). The majority of trees die when precipitation drops below a threshold of 600 mm and vapor pressure deficits are greater than 1.7kPa (Clifford et al. 2013). A combination of carbon starvation, hydraulic failure (Plaut et al. 2012) and insect infestations caused piñon death (Gaylord et al. 2015).

Piñons differ from junipers in their responses to drought and temperature effects. For example, piñon stomata respond by closure when soil water potential becomes too low or when the atmosphere is too dry, a response called isohydry. On the other hand, juniper exhibits anisohydry, where stomata can remain open despite extreme drought stress. Since open stomata are required for carbon uptake and growth, closure due to drought has its costs in terms of growth and potentially resin production. Piñon uses and responds to variation in summer precipitation, while juniper does not, at least not as efficiently as piñon (West et al. 2007). Hence the threat of hotter droughts has played out differently on these two species. Piñon has in the recent past been more susceptible to hotter droughts, but junipers are showing uncharacteristic decline after the 2018 drought in southeastern Utah (Kannenberg et al. 2021) and more recently in southwestern Colorado, northeastern Arizona, and north of Flagstaff Arizona (personal observations). Recently remote sensing techniques have been applied to track extensive juniper death with some success, as these woodlands are difficult to assess due to small canopies (Campbell et al. 2020).

In earlier sections of this report, patterns of infilling and expansion of piñon and juniper were discussed. The 1800s and early 1900s were relatively wet, and woodlands increased in density or expanded into shrublands or grasslands. But, considering that the 2002-2005 drought caused a loss of 55% of tree cover, this has more than offset any gains in density, cover, or woodland extent that toccurred in the wet periods of the early 1900s (Clifford et al. 2011).

Part 3: Management implications

Restoration and treatments

As discussed above, piñon-juniper woodlands are often perceived to be unnaturally "encroaching" on other ecosystems, and as a result, it has become common practice for land managers to try to reduce its expansion at ecotones with sagebrush or grasslands, or reduce the woodland canopy (e.g. Lanner and Frazier 2011). Treatments have included chaining, thinning, burning and mastication. They are primarily aimed at reducing woodland canopy to prevent future fires (Coop et al. 2017, Huffman et al. 2009), increase hydrologic resources to other plants in the woodland (Rau et al. 2005), increase forage potential of the grassland/woodland ecotones (Bates et al. 2019, Redmond et al. 2013, Tausch and Tueller 1977), and habitat enhancement for specific wildlife (Boone et al. 2018, 2021). Such treatments often do not resemble restoration (sensu Huffman et al. 2009).

Ecological restoration would strive toward an ecological goal to move a woodland or forest closer to pre-settlement structure (Covington et al. 1997, Floyd and Romme 2012, Fulé et al. 2001, Huffman et al. 2009, Moore et al. 1999). Restoration of piñon-juniper woodlands to pre-settlement structures and processes is, in many ways, more difficult than in the surface-fire prone ponderosa pine forests. This is in part because in frequent stand replacing fires characterize much of the woodland (see fire section above) such that many hundreds of years may be required for a natural (high density, uneven aged) woodland to return. Thus, while thinning and surface burning treatments often can restore ponderosa pine forests to pre-settlement conditions (Moore et al. 1999), those techniques are not applicable to piñon-juniper woodlands if the goal is to return woodlands to the historical range of variability (HRV). Nonetheless, thinning and burning have been used to open piñon-juniper canopies in an effort to reduce natural stand replacing fires in the Wildland Urban Interface where saving structures and human life are major objectives (e.g. Huffman et al. 2009).

Unlike ponderosa pine restoration, "one size fits all" restoration models are rarely successful in piñon-juniper woodlands (Floyd and Romme 2012, Malcolm et al. 2020). Rather, the objectives must be clearly articulated. Floyd and Romme (2012) suggest that land managers must decide if restoration of structural vs. functional dynamics is the goal, and, if so, if passive vs. active and overstory vs. understory restoration is required, depending on the nature of the disturbance. For example, in Mesa Verde National Park in the late 1990s, managers determined that passive restoration of old-growth woodlands (to preserve their characteristics) and active restoration involving seeding of native grasses after the 1996 and 2000 fires (to prevent influx of weeds and erosion near archeological sites) were warranted (Floyd et al. 2006). Managers must articulate whether their actions are restorative (e.g. with a goal of maintaining HRV or a sustainable woodland) or are treatments meant to convert woodlands to other vegetation structures. Also, restoration and treatment that brought certain outcomes in the past may, under today's climate conditions, be less successful and encourage weeds.

Chaining effects: Chaining of woodlands, where heavy equipment such as bulldozers are used to push woody vegetation (generally once or twice, and followed by windrowing and seeding) was a common practice in the mid to late 20th century (Aro 1971, Coop et al. 2017, Ott et al. 2003, Tausch and Tueller 1977, 1994) but is still in use today in some fire mitigation treatments (Madsen et al. 2015, Munson et al. 2020, Redmond et al. 2013). While most of these widespread treatments did indeed increase perennial grass cover (notably the non-native *Agropyron cristatum* which was often seeded after chaining), ecological costs include reduced biodiversity, destruction of biotic crusts, shifts to juniper from piñon dominance, and rapid return of trees (Redmond et al. 2013). Sites that were chained and seeded were more successful at creating forage for deer if the sites had open canopies before treatment (Tausch and Tueller 1994). Chaining reduces habitat for breeding birds; there was reduced species diversity and population densities following chaining in piñon-juniper woodlands (O'Meara et al. 1981, Sedgwick and Ryder 1986). Chaining followed by seeding can reduce the hydrophobicity of soils under tree canopies and therefore is suggested as an effective strategy to improve hydrological conditions for forage species (Madsen et al. 2015). However, the reduction of biotic crust cover (which provides soil stability, nitrogen inputs, and erosion protection) by these treatments is rarely considered (but see Redmond et al. 2013).

Fuel reduction, thinning and burning, treatments: Recently, treatments have shifted to canopy fuel reductions, often to reduce fire risks. A thorough study was conducted by the Ecological Restoration Institute where experimental treatments of thinning, burning, and thinning+burning were compared by assessing canopy reductions, woodland structures, and the composition of understory shrubs and forbs (Huffman et al. 2009). This study showed the expected reduction in canopy and fuel structures with thinning; it also demonstrated that shrub understory was not significantly changed by thinning+burning treatments. The authors however cautioned that the new woodland structures may well be out of the HRV. They concluded that "Results suggest that managers face tradeoffs between altering stand structures and producing novel characteristics versus accomplishing fire mitigation goals" (Huffman et al. 2009).

These trade-offs are receiving attention in the most recent literature. For example, thinning treatments reduce habitat availability for suites of obligate bird species in Colorado (Magee et al. 2019). Three fuel reduction treatments—hydro-ax, chaining, and roller-chop—were followed by reduction in the use of habitats by birds, but no effect was seen on habitat use by small mammals (Bombaci et al. 2017). However, in another study, thinning negatively affected mammals (Gallo et al. 2016). Thinning treatments have negative impact on the sensitive obligate pinyon jay (Boone et al. 2018). Pinyon jays conduct different behaviors in different structured woodlands but tend to do many activities at the woodland/shrubland ecotone. Since thinning treatments often occur at the ecotone, they may make the pinyon jays especially vulnerable (Boone et al. 2021).

Prescribed fires may accompany thinning (Huffman et al. 2009, Bates et al. 2019) and this is generally effective in increasing perennial grass and forb cover but also promotes invasive annual grasses such as cheatgrass. Both mastication (see below) and use of prescribed burning increase the invasion of exotic grasses, notably cheatgrass (Urza et al.2019, Coop et al. 2017, Havrilla et al. 2017). More specifically, cheatgrass was most successful where *P. monophylla* cover was greatest before fire and where native perennial cover was lowest. Seeding native species reduced cheatgrass (Urza et al. 2019), similar to responses to aerial seeding after natural wildfires (Floyd et al. 2006).

Many tree removal treatments are carried out with the hypothesis that tree reduction will increase water availability to other plants, making soil water more available and hydraulic conductivity of the remaining plants increase (Ashcroft et al. 2017, Roundy et al. 2020). In the Great Basin *P. monophylla* treatments, “wet days” (hours/ day when hourly average soil water matric potential >_1.5 MPa), and “wet degree days” (hourly soil temperatures >0°C when soil is wet/24 hr) were increased by fuel reduction treatments.

However, other experimental evidence suggests the opposite may occur and that removal of trees through death or treatments will reduce soil water availability and actually worsen hydraulic conditions for the remaining trees (Morillas et al. 2017). In this experimental approach, piñon trees were girdled to simulate insect mortality. Evapotranspiration from canopy declined during dry years 2011 and 2012, but this decline was offset by a significant increase in evapotranspiration from the ground and reduced sap flow in trees. This study suggests that death of piñons "may trigger feedback mechanisms that leave piñon-juniper woodlands drier relative to undisturbed sites and potentially more vulnerable to drought" (Morillas et al. 2017). The authors suggest such a feedback mechanism should be considered when fuel reduction treatments are proposed.

Fuel reduction treatments are sometimes used to decrease erosion of woodlands. For example, erosion during precipitation events was reduced after fuel reduction treatments in northern New Mexico (Ashcroft et al. 2017).

Mastication treatments: Mastication has gained popularity in recent decades (Wozniak et al. 2020) although it costs more per acre than other treatments (Munson et al. 2020). In this technique, canopy trees are chopped and returned as smaller pieces to the surface. Mastication has been shown effective in reducing canopy cover (for example in fire mitigation treatments), but increases surface fuels and allows for long term, persistent changes to the environment which include the invasion of exotic species. A 10-year study suggests that following mastication, tree density increases by 10% in the first 1-6 years, shrubs increased by 40 % in 10 years, and in general, surface fuels increased significantly within 10 years (Wozniak et al. 2020). In Colorado, Faist et al. (2015) hypothesized that mastication would alter soil moisture, available nutrients, and create a physical barrier to seed infiltration and therefore decrease the seed bank. They found that in piñon-juniper treatments, the seed bank was not affected and forb cover was similar in treated and controls.

A thorough study compared short and long term consequences of three types of fuel reduction treatments-- mastication, lop and pile burn, and lop and broadcast burn-- in *P. edulis-J. osteosperma* treatments (Havrilla et al. 2017). Pre-treatment data were compared with up to six years of post-treatment growth. Herbaceous cover was slow to return, but by year six perennial cover increased seven-fold. Similarly, a delay was seen in invasive annual grasses, but by year six cheatgrass cover in mastication treatments was highest at 30% cover. As noted elsewhere, seeding treatments increased diversity and competed with cheatgrass.

Climate and treatments: While we have some information on the short-term effects of treatments in *P. edulis-J. spp.* and *P. monophylla-J. osteosperma* woodlands, little is known about long term effects and less is known about how climate will affect these treatments (Hartsell et al. 2020). Several papers caution against the continuation of widespread treatments until those long-term and future consequences can be determined (e.g. Floyd et al. 2021, Huffman et al. 2009, Redmond et al. 2013), and attention is needed especially in edge populations where climate effects might be greater and might suggest future responses to treatments in the core populations (Hartsell et al. 2020).

Summary

Piñon-juniper woodlands are widespread and taxonomically varied but share attributes of high biodiversity, supporting myriad plants and animals, and contributing significantly in ecosystem services. While this ecosystem has been challenged by historical management actions that seek to convert it to rangelands, recently the conservation values have become more important to managers and ecologists alike. The woodlands are facing new challenges from climate changes and human activities (Friggens et al. 2020). In preparing this review, it became clear that we have accumulated a considerable body of information about two of the piñon-juniper woodland types

(*P.edulis-J. spp*, and *P. monophylla-J. osteosperma*), and that we know very little about the rest of this widespread ecosystem. Even within the two best-known systems, significant gaps remain, as articulated by a recent review of the literature (Hartsell et al. 2020):

> "Despite the large amount of research on pinyon-juniper communities, our review suggests that important geographic and topical gaps in the literature remain. The lack of research in certain geographic areas, topics, and species is particularly challenging given the potential variability in species response to land management and climate change across the multitude of landscapeswhere these communities occur. There are a limited number of grazing studies, which was surprising considering that grazing is a widespread land use in pinyon-juniper communities. Understandingthe impacts of climate change and management, such as thinning and grazing, may require research at the edges of the species geographic and climate distribution because the leading edge may show effects of a changing climate before the core of a species distribution" (Hartsell et al. 2020).

Piñon-juniper woodlands in the western United States face myriad threats to their ecological integrity. Anthropogenic climate change and human intervention can be seen as a driver of these threats, whether directly or indirectly. Threats to piñon-juniper woodlands include:

1. Direct effects of drought, changes in precipitation patterns, and rising temperatures on tree death
2. Widespread tree death due to insect proliferation or pathogens
3. Reduced fecundity due to lowered cone production and changes in masting behavior
4. Increased fire frequency and larger fire sizes
5. Invasive species
6. Alteration to native woodland structures due to management treatments

Finally, managers and ecologists must consider the cascading effects of these threats on wildlife and human populations which have relied on piñon-juniper woodlands for shelter, food, soil and water stability, and beauty for many thousands of years.

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Figure 1. Distribution range of one- and two-needled piñon pines in the western United States (used by permission, Cole et al. 2008).