North American Pinyon–Juniper Woodlands: Ecological Composition, Dynamics, and Future Trends

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Abstract

Pinyon and juniper woodland is a major biome type centered on the Basin and Range and Colorado Plateau physiographic regions of interior western North America. It covers over 40 million ha from western Oregon in the northwest United States, eastward to Wyoming and southward to northern Chihuahua in Mexico, then westward to Baja California. Climatically, these woodlands lie within both the warm and cold temperate zones of North America but at the wetter and cooler portion of the semiarid realm where precipitation seldom exceeds 400 mm. This biome occupies a unique environmental envelope within North America, and with it comes a diverse complement of plant and animal species with the center of their ranges within its confines, and a wide variety of vegetation communities. The communities are characterized by low-statured woodlands and forests dominated by pinyon (nut pines) in combination with juniper trees. At lower elevations junipers tend to prevail and typically form very open-canopied woodlands of scattered trees in a shrubland or grassland matrix (shrubby woodlands and grassy woodlands or savannas, respectively). With increasing elevation, pinyons become more prevalent and co-dominate with junipers to form moderate-canopied woodlands and closed-canopied forests. Fire is integral to the dynamics of these woodlands ranging from high-frequency, low-intensity surface fires in grassy woodlands to low-frequency, high severity canopy fires in the forest communities. Across their domain, pinyon–juniper woodlands have been economically important in the lives of the people of western North America for millennia, from the harvesting of pinyon nuts and hunting to fuel wood gathering and livestock grazing. But now, given a growing human population in the region, increased landscape fragmentation, and potential climate change impacts, particularly on water availability, this biome is on the cusp of a transformation not yet seen in its history.

Introduction

Pinyon and juniper woodland is a major biome type centered on the Basin and Range and Colorado Plateau physiographic regions of interior western North America (Fig. 1). It covers over 40 million ha from western Oregon in the northwest United Sates, eastward to Wyoming and southward to northern Chihuahua in Mexico, then westward to Baja California (Kyllo, 2016). These are low-statured (<10 m) woodlands dominated by pinyon, or nut, pines in combination with juniper trees (Fig. 2). At the lower elevations

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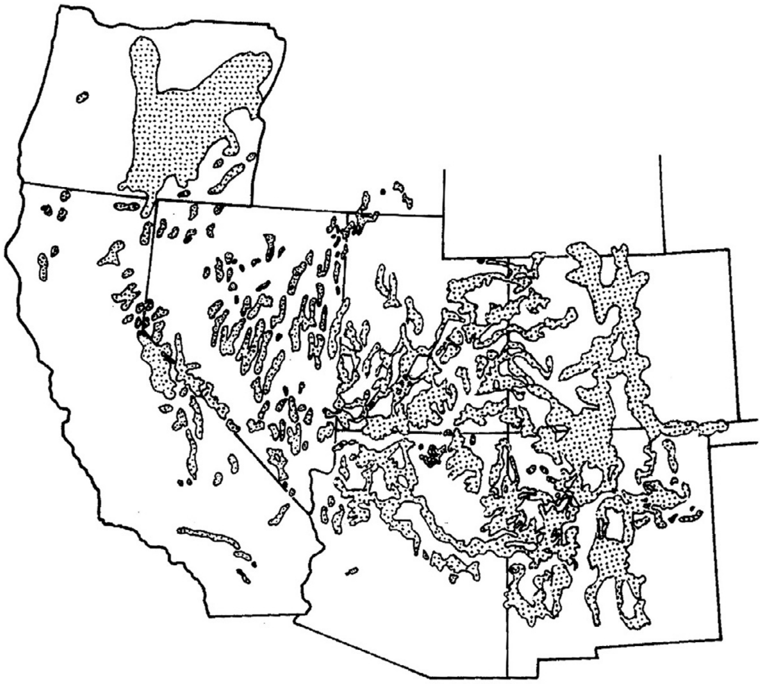

Fig. 1 Distribution of pinyon-Juniper woodlands in the United States. From Evans, R. (1988). *Management of pinyon-juniper woodlands.* General technical Report INT-249. Ogden, UT: Intermountain Research Station.

Fig. 2 Pinyon-juniper woodlands have a broad range of structure and composition across the biome including: (A) open grassy savanna-like woodlands with short trees in a grassy matrix; (B) open shrubby woodlands (or wooded shrublands) with shrubby inter-tree spaces; (C) closed-canopy long-lived, persistent forests with relatively tall trees with a mix of shrubs, grasses, and forbs in the understory; and (D) very open, often sparse woodlands on cliffs, escarpments and other rocklands. Photos: A, C, and D by E. H. Muldavin; B by F. A. Martin.

of valley plains, plateaus, and foothills, junipers tend to prevail and typically form very open-canopied (>10%–25% canopy cover) stands consisting of scattered trees in a shrubland or grassland matrix (colloquially known as "juniper savannas," although the use of "savanna" is a recent adoption of a term originally used to describe tropical and sub-tropical grassland plains with trees, which have different ecological context for their structure than those in N. America). With increasing elevation, pinyons become more prevalent and co-dominate with junipers to form moderate-canopied woodlands between 25% and 70% cover. Farther up mountain slopes, pinyons clearly dominate with junipers in the sub-canopy forming nearly closed-canopied forests that border on montane forests dominated by tall pines and firs.

Climatically, these woodlands lie within the wetter and cooler portion of the semiarid realm where precipitation seldom exceeds 400 mm. While summer precipitation becomes predominant in the eastern portion of the distribution, winter precipitation stored in the soil profile is crucial to sustaining these trees species throughout their ranges, particularly during summer drought years. Increasing temperatures at lower elevations leads to greater evaporative demand and limits the lower-elevation range of the type while extreme cold and competition from more mesic and productive species may limit the woodlands at upper elevation. Within this semiarid framework, fire plays a complex role in ecological dynamics from the tree to landscape level, varying in intensity and frequency with differences in composition and structure across the woodland domain. For example, following fires where shrubs were prevalent in the understory, successional communities dominated by shrubs such as mountain mahogany or oaks may prevail as long-standing elements of pinyon–juniper woodland landscape. Similarly, under natural conditions repeated fires in open-woodlands with a grassy matrix may prevent successful pine and juniper reproduction that would otherwise lead to expansion of the biome.

Overall, this biome occupies a unique environmental envelope within North America, and with it comes a diverse complement of plant and animal species with the center of their ranges within its confines. For example, 90% of the range of Pinyon Jays, a bird species dependent on nut-producing conifers, lies within the distribution of the four pinyon pine species. In turn, the birds are important dispersers of pinyon pine nuts leading to tree regeneration (Boone et al., 2018). Similarly, gray vireos are tied to the range of juniper species within the biome. The flora is diverse, with its share of endemics (43 species; Sivinski and Knight (1996) and Goodrich et al. (1997)) as well as a wide range of vegetation communities across the biome (150 plant associations; see Pinyon–Juniper Types section below).

Across their domain, pinyon–juniper woodlands have been economically important in the lives of the people of western North America. Pinyon nuts were not only nutritionally valuable, they have played a central cultural role among indigenous peoples and later in colonial Euro-American communities. Similarly, while the woodlands provide limited timber resources, they have provided fuel wood to all communities over the centuries into the present day. Beyond this, livestock grazing has been a nearly constant element of the landscape since European settlement and has a significant influence on land management practices. But now, given a growing human population in the region, increased landscape fragmentation, and potential climate change impacts, particularly on water availability, this biome is on the cusp of a transformation not yet seen in its history.

Types of Pinyon–Juniper Woodlands

Given its wide distribution and environmental complexity, the pinyon–juniper (P-J) woodland biome offers a wide diversity of vegetation types (some 150 plant associations have been identified across the P-J domain). Using the International Vegetation Classification (IVC) framework (Faber-Langendoen et al., 2014, 2017), P-J woodlands occur in both warm-temperate and cool-temperate forest and woodland formations that reflect climates with relatively warm winters versus cold winters, respectively (Table 1). Within the warm-temperate formation, the woodlands are further subdivided geographically into California and Madrean-Balconian divisions corresponding to west coast versus southwestern United States and Mexican distributions, respectively. The California P-J woodlands are dominated by California juniper (*Juniperus californica*) and four-needled or Parry's pinyon (*Pinus quadrifolia*) whose distribution is strongly influenced by the Mediterranean-like winter precipitation-dominated climate of southern California, southwestern Arizona, and adjacent Baja California in Mexico. In contrast, in Madrean-Balconian woodlands, monsoonal summer precipitation is predominant and P-J woodlands fall within Madrean Lowland Evergreen Woodlands dominated by a different set of pinyons—border pinyon (*P. cembroides* and *P. discolor*) and to a limited degree two-needled pinyon (*P. edulis*)–along with junipers such as redberry juniper (*Juniperus coahuilensis*), alligator juniper (*J. deppeana*), dropping juniper (*J. flaccida*), and Pinchot's juniper (*J. pinchotii*).

The cool-temperate P-J woodlands are represented by the Western North American Pinyon–Juniper Woodland and Scrub Division and are further divided into Intermountain Pinyon–Juniper versus Southern Rocky Mountain Two-needle Pinyon–Juniper Woodland macrogroups. The former includes woodlands of Great Basin, Colorado Plateau, and Colorado Plateau regions where winter precipitation is dominant and the winters can be very cold; summer precipitation is dependent on the extension of the "Arizona" monsoon from the south, which can be erratic. These woodlands are dominated by either singleleaf pinyon (*P. monophylla*) to the west or two-needle pinyon to the east in combination with Utah juniper (*Juniperus osteosperma*). Western juniper (*J. occidentalis*) occurs in the far northwest of the domain usually without pinyons. Included here are also curl-leaf mountain-mahogany (*Cercocarpus ledifolius*) shrubby woodlands which can be prevalent across the Great Basin. At lower elevations, these P-J woodlands can border on cold-desert shrublands and grassland communities while at upper elevations they grade to pine and mixed-conifer forests.

Table 1 A classification of pinyon-juniper woodlands following the International Vegetation Classification hierarchy (see Faber-Langendoen et al., 2014, 2017 for definitions of the hierarchy elements). For each level there is a database code per the US National Vegetation followed by the type name (complete descriptions of each element are available at the US National Vegetation Classification website: http://usnvc.org/).

1 Forest & Woodland Class			
1.B Temperate & Boreal Forest & Woodland Subclass			
1.B.1 Warm Temperate Forest & Woodland Formation			
D007	1.B.1.Nc Californian Forest & Woodland Division		
M009	Californian Forest & Woodland Macrogroup		
	G198	Californian Conifer Forest & Woodland Group	
		A3353	Transmontane Desert Pinyon–Juniper Woodland Alliance
D060	1.B.1.Nd Madrean-Balconian Forest & Woodland		
M010	Madrean Lowland Evergreen Woodland Macrogroup		
	G487	Madrean Juniper Open Woodland Group	
		A3134	Madrean Juniper/Grass Open Woodland Alliance
		A3133	Madrean Juniper/Shrub Open Woodland Alliance
	G200	Madrean Pinyon–Juniper Woodland Group	
		A3131	Madrean Pinyon–Juniper/Shrub Woodland Alliance
		A3132	Madrean Pinyon–Juniper/Grass Woodland Alliance
1.B.2 Cool Temperate Forest & Woodland			
D010	1.B.2.Nc Western North American Pinyon–Juniper Woodland & Scrub		
M896	Intermountain Pinyon–Juniper Woodland Macrogroup		
	G900	Colorado Plateau Pinyon–Juniper Woodland Group	
		A3571	Foothill & Lower Montane Pinyon–Juniper/Shrub Dry-Mesic Woodland Alliance
		A4371	Colorado Plateau Utah Juniper Shrubby Woodland Alliance
		A3573	Colorado Plateau Two-needle Pinyon–Utah Juniper Open Woodland Alliance
		A3572	Two-needle Pinyon–Utah Juniper Grassy Open Woodland Alliance
		A3497	Utah Juniper Grassy Open Woodland Alliance
	G248	Columbia Plateau Western Juniper Open Woodland Group	
		A3500	Western Juniper Grassy Open Woodland Alliance
		A3499	Western Juniper Shrubby Woodland Alliance
	G899	Great Basin Pinyon–Juniper Woodland Group	
		A4370	Great Basin Utah Juniper Shrubby Woodland
		A2108	Great Basin Singleleaf Pinyon–Utah Juniper Shrubby Woodland Alliance
		A2109	Great Basin Singleleaf Pinyon–Utah Juniper Grassy Open Woodland Alliance
	G249	Intermountain Basins Curl-leaf Mountain-mahogany Woodland & Scrub	
		A0828	Curl-leaf Mountain-mahogany Scrub Alliance
		A3570	Curl-leaf Mountain-mahogany Grassy Woodland Alliance
		A0586	Curl-leaf Mountain-mahogany Shrubby Woodland Alliance
M897	Southern Rocky Mountain Two-needle Pinyon–Juniper Woodland Macrogroup		
	G252	Southern Rocky Mountain Juniper Open Woodland Group	
		A3575	One-seed Juniper Wooded Grassland Alliance
		A3574	One-seed Juniper Shrubby Woodland Alliance
	G253	Southern Rocky Mountain Pinyon–Juniper Woodland Group	
		A3577	Southern Rockies Pinyon–Juniper Grassy Woodland Alliance
		A3576	Two-needle Pinyon–One-seed Juniper Shrubby Woodland Alliance

To the southeast, the Southern Rocky Mountain Two-needle Pinyon–Juniper Woodland macrogroup prevails along the flanks of the southern Rocky Mountains and among the mountains, plains, and mesa tablelands of Arizona and New Mexico. In this summer-precipitation-dominated climate, singleleaf pinyon and Utah juniper drop out and two-leaf pinyon and one-seed juniper (*J. monosperma*) dominate the woodlands (singleleaf pinyon at higher elevations and one-seed juniper at lower). At lower elevations to the east these woodlands border on grasslands of the southern Great Plains, and to the south they can intermix with Chihuahuan Desert grasslands and scrub.

Detailed Pinyon–Juniper Woodland Descriptions

The following are summary descriptions of pinyon–juniper woodlands at the group level of the IVC (detailed descriptions of each group and its constituent alliances can be found at the US National Classification webpage (USNVC.org). Descriptions are ordered by the hierarchically in Table 1.

G198 Californian Conifer Forest & Woodland Group

Californian Conifer Forest & Woodland Group includes a variety of cypress and pine forests and woodlands along with pinyon–juniper woodlands of the Transmontane Desert Pinyon–Juniper Woodland Alliance.

Environment: These woodlands are found in the montane regions of southern California extending to the western edge of the Mojave Desert and southward into northern Baja California, Mexico. Stands occur on ridges, slopes, valleys, alluvial fans, valley bottoms at elevations ranging from 600 to 2450 m. Soils are porous, rocky, coarse, sandy or silty, and often very shallow.

Vegetation structure and composition: This alliance consists of scrub woodlands, generally <5 m in height, where *Juniperus californica* is codominant with Parry pinyon or singleleaf pinyon. In some stands, the junipers are open-grown trees over grassy understories. In others, the junipers form mixed stands with pinyon. The understory often has Mojave Desert shrubs such as blackbrush (*Coleogyne ramosissima*), Mormon tea (*Ephedra* spp.), and scrub oaks such as Muller oak (*Quercus cornelius-mulleri*).

G487 Madrean Juniper Open Woodland Group

Environment: This Madrean juniper woodland and savanna occurs at lower-elevations within the range of the macrogroup from northern Mexico into the southwestern United States. Savanna-like stands occur primarily on loamy rolling plains, alluvial fan piedmonts, plateaus, and lower foothill slopes while the more closed-canopied woodlands are found on cooler aspects of steeper slopes with generally shallow rocky soils.

Vegetation structure and composition: These savannas and woodlands have open to moderately closed tree canopies (10%–60% cover). The lack of pinyon trees and the dominance of the Madrean junipers redberry juniper or alligator juniper are diagnostic. At the northern end of the range, one-seed juniper may replace redberry. Madrean oak trees may be present but do not dominate the tree canopy.

The woodland understories are usually dominated by species with Sierra Madrean affinities. Some communities are distinctly shrubby and make up the Madrean Juniper /Shrub Open Woodland Alliance of associations that may include chaparral species (e.g., manzanita, ceanothus, mountain mahogany, yuccas, and scrub oaks) or warm desert scrub elements (e.g., creosote bush, lechuguilla and mesquite). In contrast, the associations of Madrean Juniper/Grass Open Woodland Alliance have often luxuriant grassy understories and a high mix of forbs and few shrubs. Common Madrean grasses include bull muhly, curlyleaf muhly (*M. setifolia*), and Texas bluestem (*Schizachyrium cirratum*), but elements from more northern woodlands and plains may be prevalent such as blue grama (*B. gracilis*), hairy grama (*B. hirsuta*), or sideoats grama (*B. curtipendula*).

G200 Madrean Pinyon–Juniper Woodland Group

Environment: This P-J woodland group is common in higher foothills, mountains and plateaus within the range of the southwestern United States and northern Mexico. Sites range from gentle to steep slopes. Ground cover often has high cover of rock or bare ground. Elevations range from 1700 to 2200 m. Substrates are variable, but soils are generally shallow, dry and rocky often with rock outcrops.

Vegetation structure and composition: These vegetation communities are characterized by open to moderately closed tree canopies (10%–60% cover and occasionally greater) dominated by Mexican pinyon (*Pinus cembroides* and its variations) and juniper trees that can range from 2 to 10 m in height. Alligator juniper (*Juniperus deppeana*), drooping juniper (*J. flaccida*), or redberry juniper (*J. coahuilensis*) may be common or co-dominant. Two-leaf pinyon and one-seed juniper may become the dominants in the northern distribution of the group. Madrean oak trees may be present but do not dominate the tree canopy.

The understories are usually dominated by species with Sierra Madrean affinities. Some communities are distinctly shrubby and may include chaparral species such as manzanita (*Arctostaphylos* spp.), desert ceanothus (*Ceanothus greggii*), mountain mahogany (*Cercocarpus montanus*), yuccas, and scrub oaks and belong to the Madrean Pinyon–Juniper /Shrub Woodland Alliance. In contrast, the Madrean Pinyon–Juniper/Grass Woodland Alliance has associations that often have luxuriant grassy understories and a high diversity of forbs and few shrubs. Common Madrean grasses include bull muhly (*Muhlenbergia emersleyi*), New Mexico muhly (*M. pauciflora*), and pinyon ricegrass (*Piptochaetium fimbriatum*).

G900 Colorado Plateau Pinyon–Juniper Woodland Group

Environment: This P-J woodland group occurs in dry mountains and foothills of the Colorado Plateau region including the western slope of Colorado and the Wasatch Range, south to the Mogollon Rim, and east into the northwestern corner of New Mexico. Winter precipitation in the form of snow predominates while summers can be warm to hot. Elevations range from 1500 to 2440 m. Sites often have high cover of rock or bare ground and soils are generally shallow, dry and rocky often with rock outcrops.

Vegetation structure and composition: These communities are characterized by stands with moderate to closed tree canopies (30%–60% cover and occasionally greater) which are dominated by twinleaf pinyon and Utah juniper trees that can range from 2 to 10 m in height.

A suite of communities are distinctly shrubby and make up the Foothill & Lower Montane Pinyon–Juniper/Shrub Dry-Mesic Woodland, Colorado Plateau Utah Juniper Shrubby Woodland, and Colorado Plateau Two-needle Pinyon–Utah Juniper Open Woodland alliances representing over 40 plant associations. These associations may include montane chaparral species such as manzanita (*Arctostaphylos* spp.), desert ceanothus (*Ceanothus greggii*), mountain mahogany (*Cercocarpus montanus*), yuccas, and scrub oaks, or cold desert shrubs such as sagebrush (e.g., *Artemisia tridentata*, *A. nova*) and antelope bitterbrush (*Purshia tridentata*).

In contrast, Two-needle Pinyon–Utah Juniper Grassy Open Woodland and Utah Juniper Grassy Open Woodland alliances are made up of associations with grassy understories that are commonly dominated by cool-season (C3) grasses. These thrive on winter moisture and the cooler temperatures of early summer, e.g., needle and thread grasses (*Hesperostipa comata; H. neomexicana*), bluebunch wheatgrass (*Pseudoroegneria spicata*) and Indian ricegrass (*Achnatherum hymenoides*). Cheat grass (*Bromus tectorum*) is also a cool-season grass that is nonnative and invasive that has become important in these communities, altering fire regimes and competitive relationships among the native grasses.

G248 Columbia Plateau Western Juniper Open Woodland Group

Environment: This P-J woodland group is found on the Columbia Plateau and extends to the northern and western margins of the Great Basin, from southwestern Idaho along the eastern foothills of the Cascades south to the Modoc Plateau of northeastern California. Elevations range from 200 to 1500 m. Soils are generally medium-textured, with abundant coarse fragments, and derived from volcanic parent materials.

Vegetation structure and composition: Western juniper is typically the only tree species and pinyons are absent. The tree form of curl-leaf mountain mahogany (*Cercocarpus ledifolius*) may also occasionally co-dominate. In Western Juniper Shrubby Woodland Alliance associations, the spaces between trees are dominated by tall shrubs such as big sagebrush or curl-leaf mountain mahogany along with rabbitbrush (*Chrysothamnus viscidiflorus, Ericameria nauseosa)* and antelope bitterbrush with a scattering of cool-season grasses. In contrast, the Western Juniper Grassy Open Woodland Alliance communities are dominated by cool-season grasses such as Idaho fescue (*Festuca idahoensis*), bluebunch wheatgrasses, and Sandberg bluegrass (*Poa secunda*) in the inter tree spaces and occasionally co-dominate with shrubs.

G899 Great Basin Pinyon–Juniper Woodland Group

Environment: This P-J woodland group occurs on dry mountain ranges of the Great Basin region and eastern foothills of the Sierra Nevada, and south in scattered locations throughout southern California. They are typically found at elevations from 1500 to 2600 m. Stands occur on warm, dry sites on mountain slopes, mesas, plateaus and ridges.

Vegetation structure and composition: The vegetation is characterized by stands with open to moderately dense tree canopy typically composed of a mix of singleleaf pinyon and Utah juniper. In some regions of southern California, Utah juniper is replaced by California juniper. There are two alliances where shrubs dominate the inter-tree spaces with or without a grass layer: Great Basin Singleleaf Pinyon–Utah Juniper Shrubby Woodland and Great Basin Utah Juniper Shrubby Woodland that lacks the singleleaf pinyon. The most common shrub dominants are big sagebrush, black sagebrush, little sagebrush (*Artemisia arbuscula*), curl-leaf mountain mahogany, littleleaf mountain mahogany (*Cercocarpus intricatus*), blackbrush (*Coleogyne ramosissima*), and antelope bitterbrush among others that are also elements of cold-desert communities found at lower elevations. Those associations that lack a strong shrub component belong to the Great Basin Singleleaf Pinyon–Utah Juniper Grassy Open Woodland where cool-season grasses such as basin wild rye (*Leymus cinereus*), needle and thread grass, and bluebunch wheatgrass tend to dominate between the trees.

G249 Intermountain Basins Curl-leaf Mountain-mahogany Woodland & Scrub

Environment: Stands of this woodland and shrubland group occur in hills and mountain ranges of the Intermountain West basins from the eastern foothills of the Sierra Nevada northeast to the foothills of the Bighorn Mountains of Wyoming. It typically occurs from 600 m to over 2650 m in elevation on rocky outcrops or escarpments and forms small- to large-patch stands in forested areas. Most stands occur as shrublands on ridges and steep rimrock slopes, but they may be composed of small trees in steppe areas.

Vegetation structure and composition: This woodland and shrubland group includes stands dominated by either the tree or shrub form of curl-leaf mountain mahogany. Scattered junipers or pines may also occur. Curl-leaf Mountain-mahogany Shrubby Woodland and Curl-leaf Mountain-mahogany Scrub alliances are typically co-dominant with other Great Basin cold-desert shrubs such as big sagebrush, antelope bitterbrush or more montane elements such as Gambel oak (*Quercus gambelii*), snowberry (e.g., *Symphoricarpos oreophilus*), or rockspirea (*Holodiscus dumosus*). The Curl-leaf Mountain-mahogany Grassy Woodland associations tend to have a high cover of cool-season grasses such as basin wild rye, Idaho fescue, and bluebunch wheatgrasses under the curl-leaf mountain mahogany.

G252 Southern Rocky Mountain Juniper Open Woodland Group

Environment: This P-J woodland and woodland-savanna group occurs along the eastern and southern foothill slopes of the southern Rocky Mountains and mesa tablelands, and plains of the southeastern Great Plains. They occur on a range of sites from steep, colluvial slopes of escarpments with rocky soils to lower toeslopes and valley bottoms and plains with loamy soils.

Vegetation structure and composition: Stands of this group typically have open tree canopies (10%–60% cover) that are dominated by short-statured (2–5 m) one-seed juniper (*Juniperus monosperma*). Two-needle pinyon may be present but usually growing within the canopy of the juniper. On plains, tablelands, and gentle foothill slopes, savanna-like stands develop with widely spaced juniper trees with lush perennial grass cover between trees (One-seed Juniper Grassy Woodland Alliance). Grasses tend be warm-season species that are prevalent in the adjacent plains and desert regions such as blue grama, sideoats grama, or galleta (*Pleuraphis jamesii*), but occasionally cool-season grasses such as needle and thread grass can dominate the sites. On the rockier, steeper sites, stands tend to have a strong shrub component, particularly scrub oak (e.g., *Quercus x pauciloba)* or mountain mahogany and belong to the One-seed Juniper Shrubby Woodland Alliance. In addition, yuccas and prickly pear or cholla cacti (e.g., *Opuntia phaeacantha* and *Opuntia imbricata*) can be common.

G253 Southern Rocky Mountain Pinyon–Juniper Woodland Group

Environment: This P-J woodland group occurs on dry mountains and foothills in southern Rocky Mountain in Colorado east of the Continental Divide down through the mountains and plateaus of northern New Mexico extending east into the southeastern Great Plains (on limestone and shale breaks, escarpments and hills). Stands are found on warm, dry sites on mountain slopes, mesas, plateaus, and ridges. Elevations range from near 1500 to 2900 m with high-elevation stands restricted to relatively warm, dry ridges and south and west aspects. Lower-elevation stands are often restricted to cooler north- and east-facing slopes. Soils vary in texture ranging from stony, cobbly, gravelly or sandy loams to clay loam or clay.

Vegetation structure and composition: The vegetation is characterized by two-needle pinyon that dominates or codominates the tree canopy with one-seed juniper. Rocky Mountain juniper (*Juniperus scopulorum*) may codominate or replace *Juniperus monosperma* at higher elevations. At higher elevations on mountain slopes stands can have the stature (>10 m tall) and canopy closure (>60% canopy cover) of forests. In contrast, at lower elevations tree size diminishes to as low as three meters and canopies become very open, forming woodland savannas. The forest-like woodlands have a mixture of grasses and shrubs in the understory and overall cover can be sparse. Most these communities belong to the Two-needle Pinyon–One-seed Juniper Shrubby Woodland Alliance where Gambel oak, mountain mahogany, and cool-season grasses such as Scribner needle and thread grass (*Achnatherum scribneri*) are prevalent. In contrast, the P-J woodland savannas of this group have a predominantly grassy inter-tree space and belong to the Southern Rockies Pinyon–Juniper Grassy Woodland Alliance. Grasses tend be warm-season species that are prevalent in the adjacent plains and desert regions such as blue grama, sideoats grama, or galleta, but occasionally cool-season grasses such as New Mexico needle and thread grass can dominate the sites.

Ecological Dynamics in Pinyon–Juniper Woodlands

Fire Regimes

Fire is integral and a natural element in most pinyon–juniper woodlands, but the regimes vary depending on the environmental context and vegetation composition and structure. Among the types described above, three basic structural types emerge primarily at the alliance level: those woodlands with open canopies and grassy interspaces, those with moderate canopies and well-developed shrub strata, and those with near-closed, forest-like canopies with understories that are a mix of shrubs and grasses at low to moderate cover. These correspond roughly to three P-J fire regimes types described by Romme et al. (2009) as grass-dominated savanna, shrubby woodland (or wooded shrubland), and persistent woodland (the last also includes the woodlands of rocklands with little or no understory). These structural types are primarily driven by the amount of precipitation and its seasonality whereby winter precipitation that results in deep soil moisture storage will tend to favor trees and other deep rooted woody species while transient shallow summer moisture tends to favor more shallow-rooted grasses and forbs (Fig. 3). Accordingly, they have different proportions of tree, shrub, and grass fuels that generate different types of fire of frequencies and intensities. In general, under normal conditions savanna woodlands are likely to have low intensity fires that kill only small seedlings and sapling trees, keeping the stands open, but the fires can be spatially extensive since the stands commonly occur in gentle terrains of rolling hills and plains (fire regime type I). They also tend happen more frequently than other P-J types because of the rapid recovery of grasses to a fire-ready state—every 10–30 years depending on the plant association (Wright et al., 1979; West and Young, 2000).

Woodlands with significant shrub cover typically have mixed to high-severity regimes with some tree torching and top-killing of shrubs (Fig. 4). This is followed by a longer recovery period leading to somewhat lower frequencies, (perhaps 25–80 years; Gori and Bate, 2007). Spatially, under extreme conditions they can reach landscape scale, but more commonly they are small to large patch fires. Persistent woodlands with near-closed canopies tend to have moderate surface to high-intensity canopy fires that occur at frequencies from 60 to >100 years or more, usually as small to medium patches, but extreme events can reach landscape scale (Fig. 5). There are also persistent woodlands of escarpment rocklands where fire is very rare or absent because of the spacing of trees and the lack of surface fuels.

Fire in P-J woodlands has been impacted by human activities, and particularly following European settlement beginning in the early 17th century (Jacobs, 2008). Historical fire regimes were disrupted following the introduction of livestock. Grazing passively suppresses fire by removing fine fuels needed to carry surface and low to mixed-severity fires that likely maintained the structure and composition of pinyon–juniper savannas and pinyon–juniper shrub woodlands historically. Active fire suppression was also practiced by the Federal government during the last 100 years (Swetnam and Baisan, 1996). As fire became less frequent, pinyon and juniper trees became denser and subsequent fires became more severe. Over the last century, a reduction in fire frequency has caused a conversion of some juniper savanna to juniper woodland, as well as invasion of juniper trees from areas of naturally low fire frequency, (e.g., rocky ridges) into adjacent communities, especially sagebrush steppe (Wright et al., 1979; West and Young, 2000; Romme et al., 2009). In contrast, nonnative grasses such as annual cheatgrass can quickly invade and promote increased fire frequencies, particularly in the western regions dominated by winter precipitation.

Given a site's land use history and woodland type, post-fire responses can vary. Woodland savannas are likely to recover quickly if grass cover was not reduced by increased density of trees from fire suppression. That is, with increased density and more extreme fire events, burned sites will require a longer period for grasses to colonize bare zones left by dead trees and return the site to an optimal grassy fire-ready state. In shrubby woodlands where large patch or landscape-scale canopy fires have occurred, shrubs, particularly those that resprout after fire, can come to dominate the landscape and slow the tree recolonization process because of seed source loss and competitive exclusion of those tree seedlings that do germinate. Response to extreme fire events in persistent woods may be similar, but localized seed sources may be more common and therefore likely provide more sites for successful seedling establishment to speed recovery to mature woodland.

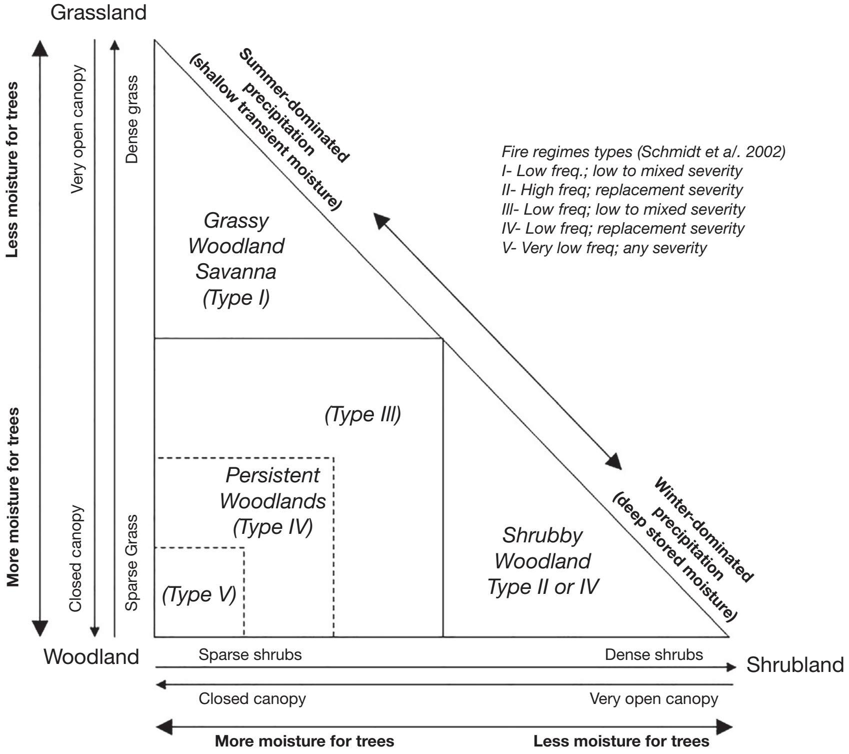

Fig. 3 A general framework for the distribution of three broad types of western pinyon-juniper woodlands with respect to soil moisture gradients and associated fire regimes. Fire regime classes adpated from Schmidt, K. M., Menakis J. P, Hardy C. C., Hann W. J. and Bunnell D. L. (2002). Development of coarse scale spatial data for wildland fire and fuelmanagement. *General Technical Report RMRS-87*. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station.

Fig. 4 A firefighter crew hiking out from a wildland fire burning in a pinyon-juniper woodland along the Utah-Nevada border. Photo: Dan Jimenez, U.S. Forest Service.

Insect Pathogens

Although pinyon pines and junipers are drought tolerant, prolonged droughts can weaken trees and promote mortality by secondary agents. For example, trees play host to a set of endemic insect pathogens such pinyon bark beetle (*Ips confusus*) or cypress bark beetle (*Phloeosinus cristatus*), and associated fungal agents such as blackstain root-rot (*Leptographium wageneri*) that can cause

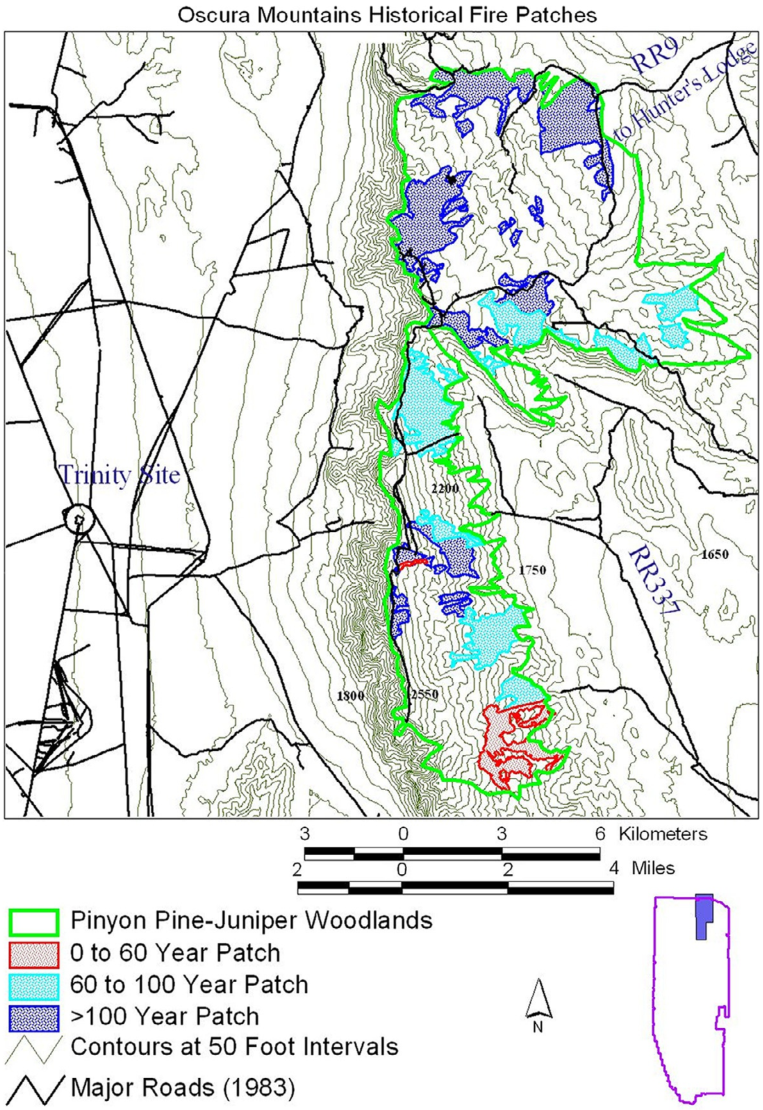

Fig. 5 Fire-patches in the Oscura Mountains of southern New Mexico based on comparative aerial photo analysis. Adapted from Muldavin, E., Baisan, C., Swetnam, T. DeLay, L. and Morino, K. (2003). *Woodland fire history studies in the Oscura and Northern San Andres Mountains, White Sands Missile Range, New Mexico*. Natural Heritage New Mexico Publ. No. 03-GTR-256. Albuquerque, NM: Natural Heritage New Mexico, University of New Mexico.

whole stand die-offs that are often are correlated with droughts (Clifford et al., 2008) (Fig. 6). These mortality events may be localized or widespread but can result in 50%–90% mortality of pinyon in affected areas (Harrington and Cobb 1988). Yet die-offs can be patchy even in local landscapes and there is more to be learned about the underlying mechanism of spread and specific triggers of outbreaks (Meddens et al., 2015).

Ecosystem Services and the Changing Land Use of Pinyon–Juniper Woodlands

The diversity of land use and ecosystem services in pinyon–juniper is as varied as the ecology, composition, and structure of these woodlands (Comer et al., 2003; Moir and Carlton, 1986; Romme et al., 2009). While we acknowledge the wide range of services that have supported subsistence and livelihood, including watershed function, plant production, and drinking water, we focus on some of the most important socioeconomics of woodlands and their land use legacies involving pine nut gathering, livestock use, and fuelwood. This narrow set of uses are broadly applicable to North American woodlands and are in large part the same uses that have affected their environmental conditions and trends, sometimes in positive feedbacks. Carbon storage is another key ecosystem service of pinyon–juniper that we consider in a later section on climate.

Fig. 6 Pinyon pines in New Mexico in 2002, stressed from drought and an associated bark beetle outbreak. Photo by Craig D. Allen, US Geological Survey.

History and Land Use Impacts (e.g., Involving Herbivory, Changes in Fire Regime)

Pinyon nuts

In North America humans have a long history of exploiting pinyon–juniper woodlands for raw materials for building, medicine, and food that continues to this day (Cartledge and Propper, 1993, Mayes et al., 1989, Scurlock, 1998). Pinyon nuts are usually collected in early autumn directly from the tree by dislodging cones or seeds or by picking seeds from mature cones that have fallen to the ground (Gillihan, 2006). The brown nut shells within cones must be opened to expose the small nut inside. Immature cones can be opened by heating and the seeds roasted. The nuts are also eaten raw or boiled and were historically ground into paste or cooked in soups (Janetski, 1999). Roasted nuts lend themselves to long- term storage and were a key source of protein and fats to native people going back at least a couple of millennia (Bettinger, 1976; Lanner, 1981).

There is some evidence that the amount of pinyon nuts as a staple, and pinyon–juniper resources in general, fluctuated considerably in the southwestern United States. For instance by the 13th century AD, after hundreds of years of occupation, Puebloans had abandoned the Four Corners region perhaps as a result of deforestation of pinyon–juniper woodlands (Lekson and Cameron, 1995; Flint-Lacey, 2003). Archeological evidence indicates a time of widespread clearing of woodlands near the end of this period of Four Corners occupation (Litzinger, 2003). To the southeast, at present-day Bandelier National Monument in New Mexico, available evidence reveals significant changes to pinyon–juniper leading up to peak occupation of the area at about 1500 AD (Gottfried et al., 1995). Still, pinyon nuts remained important to native peoples of the Four Corners region for nutrition, medicine, and for ceremonial purposes (Mayes et al., 1989).

Today, nut gathering represents a pastime for some and an important cash crop for others, adding to the need for the sustainable management of woodland resources (Gottfried and Severson, 1994). Pound-for-pound pinyon nuts are by far the most value product of pinyon–juniper woodlands. By one estimate, the crop production in the species of two-needle pinyon alone is over 900,000 kg, though in some years commercial crops are nearly nonexistent (Ronco Jr, 1990). Commercial-scale crops occur on cycles of three to five years. Resource management that integrates permitting ensures that users can harvest what they need while preventing nuts from being over-collected and impacting the pinyon's ability to furnish other services such as tree regeneration and food for wildlife forage (Vander Wall and Balda, 1977; Stone, 1993).

Livestock use

The most widespread use of pinyon–juniper woodlands has been livestock grazing, especially for cattle and sheep (Aro, 1971; Gottfried et al., 1995). In many areas these woodlands offer essential spring and fall range resources for grazing animals. Though consensus is lacking, there may also be some noneconomic advantages to light to moderate grazing of woodland understories including nutrient cycling, simulated gap disturbance, and stimulation of plant production (Milchunas, 2006). Economic and subsistence benefits to rural communities are clearly linked to the availability and quality of forage available to livestock in woodlands and other vegetation types, an ecosystem service dependency going back centuries (Allred, 1996; Scurlock, 1998).

Livestock grazing and fire suppression are the two most regarded agents of 20th-century change in pinyon–juniper, including increased tree densities through ingrowth along with the expansion of woodland into neighboring grasslands (Ronco Jr, 1990). Fire suppression coupled with land use patterns that are ubiquitous to fire-adapted woodlands of Mexico and the western United States have substantially reduced the frequency of fire. Past decades of overgrazing by livestock, and now management for uncharacteristically high levels of wild ungulates, has reduced grass competition to favor woody ingrowth of trees and shrubs. As a result, overutilization by both native and nonnative herbivores is often a component within a feedback system involving fewer fine fuels to facilitate fire spread that, in turn, promotes higher tree densities and decreased grass growth and forage availability (Allen, 2007; Gori and Bate, 2007). A notable effect of these agents in combination has been a major increase in juniper savannah cover types as grasslands submit to tree growth and woodland succession, expanding the pattern of reduced livestock forage. Increasing tree density in juniper savannah, and in fire-adapted pinyon–juniper generally, promote a positive feedback with elevated tree seed sources. While changes to woodland structure and composition have been linked to climate, there is some evidence to suggest that climate forcing is secondary to grazing and that the effects of grazing can be exacerbated by climate (Fuhlendorf and Smeins, 1997).

Resource managers and land owners have sought ways to reduce tree cover in pinyon–juniper, including woodland types where fire was infrequent and tree densities were characteristically elevated. In recent decades the drive for additional big game habitat has furthered efforts for woodland-to-grassland conversion. Among the approaches used to clear trees, the process of "chaining" began in earnest in the 1950s as a means to convert woodlands to enhance forage production. Though approaches vary, chaining often involves two bulldozers pulling a large chain, such as from a ship anchor, between them to knock down and uproot trees (Fig. 7). In recent years chaining has become more targeted and fallen out of use because of issues with soil erosion and habitat loss among other concerns (O'Meara et al., 1981).

While some woodlands have been converted to grassland, on balance the extent and density of pinyon–juniper has increased considerably, with pollen evidence suggesting that these woodlands are more abundant now than at any time in the past 5000 years (Miller and Wigand, 1994). The most remarkable changes in the structure of woodlands are concentrated in fire-adapted types that were historically more open and less connected. The over 40 million hectares occupied by pinyon–juniper in the intermountain United Sates represents an important resource for livestock management to be managed sustainably (Miller and Wigand, 1994).

Fuelwood

In Mexico and the western United States, pinyon–juniper woodlands have long been a major source of fuel for heating, cooking, and other uses. In the southwestern United States and Mexico the wood is still the main fuel in many rural communities. Pinyon–juniper woodlands have been used as a fuelwood source longer than any other of its provisioning services (Barger and Ffolliott, 1972; Ffolliott et al., 1999) and these tree species have exceptional heat content. On a given hectare there are about 58 cubic meters of wood volume (6.5 cords per acre). In the state of Nevada alone there are an estimated 125 million cubic meters of wood volume in pinyon–juniper woodlands (Born et al., 1992).

Beginning in the 19th century, these woodlands became a source of materials for many products including railroad ties, and a source of materials for mining operations, especially as fuel for processing metals but also for building materials for adits, shafts, and operations and processing facilities (Ffolliott et al., 1999). It follows that notable episodes of unsustainable use were concentrated near geologic resources and near human communities, as was likely the case with the decline of woodlands in the Four Corners region near the middle of the last millennium (Lekson and Cameron, 1995; Flint-Lacey, 2003). In the Chaco Canyon area of New Mexico, Samuels and Betancourt (1982) determined that human demography and fuelwood use of the time infers that woodlands would have been driven to depletion in about 200 years.

Fig. 7 Chaining of pinyon-juniper trees in southern Colorado, circa 1958. Note the chain is attached to a bulldozer on the left and one out of sight on the right. Photo by Jack Rottier, USDI Bureau of Land Management.

By the mid-20th century the demand for pinyon–juniper trees as a domestic fuel source gave the woodlands commercial value that peaked in the early 1980s (Born et al., 1992). Harvesting is done by commercial operators and by individuals for personal use, with private use representing the majority of cutting permits sold for federal lands (Wagstaff, 1987). Commercial woodyards exist in many urban centers of the western United States and on many tribal reservations, making the sale of fuelwood important for income and economies. In recent decades public land agencies have been driven to implement sustainable harvest policies with permitting and designated harvest areas. Such policies prevent local depletion of woodland resources despite that, in general, there has been a pronounced increase in the density and extent of pinyon–juniper woodlands (Gedney et al., 1999; Miller and Tausch, 2000). These woodlands collectively represent a vast resource capable of sustaining the production of fuelwood as a byproduct of the restoration and maintenance of ecosystem function.

Pinyon–Juniper Woodlands and Climate

A changing climate is altering the types and amounts of ecosystem services from pinyon–juniper. The vulnerability of these woodlands and the biodiversity and human communities that depend on them is based on their exposure to changing climate at a given location, their sensitivity to change, and their ability to adapt (USGCRP, 2011). Climate vulnerability is uneven across the extent of pinyon–juniper in North America due to the varying magnitude of projected change, the intrinsic sensitivity of human and natural systems in a given place, and their adaptive capacity (Hand et al., 2018). These factors and human interventions will determine how the provision of ecosystem services may be modified.

Pinyon–juniper woodlands, particularly in the southwestern United States, have become hotspots for a changing climate and warmer temperatures (Notaro et al., 2012; Garfin et al., 2013; Thorne et al., 2017). Expected changes include increased summer temperatures and enhanced variability of precipitation and temperature (Seager et al., 2007; Gutzler and Robbins, 2010). Because pinyon–juniper woodlands are inherently moisture-limited they are especially vulnerable to extended drought and higher temperatures (Allen and Breshears, 1998).

Tree Mortality and Plant Composition Changes

Marked change in the distribution and composition of pinyon–juniper systems is anticipated in the coming decades, especially at lower ecotones where conversion to juniper savannahs and grasslands is expected (Allen and Breshears, 1998). Vulnerability forecasts coupled with spatial information on tree density for Arizona and New Mexico (Mellin et al., 2008; Triepke et al., 2019) suggest that shifts are already occurring, with high vulnerability areas seeing a decline in the amount of tree cover and low vulnerability sites remaining on an overall trajectory of increased tree density (Table 2).

Ironically, the woodlands that are forecast to be the most vulnerable to future climate may be the least at risk to mortality from fire (Triepke et al., 2019). There is some evidence indicating that decreased plant productivity from warmer and more arid conditions may be associated with decreased fuel levels and reduced fire risk (Rocca et al., 2014).

Table 2 Chi-square test evaluating the relationship of tree density and projected climate vulnerability, where high-vulnerability areas reflect less tree cover in comparison to background levels and low-vulnerability areas express greater tree cover.

Tree density	*Deviation from expected*		*Sample number and significance*
	Low vulnerability	*High vulnerability*	
All Pinyon–Juniper			
Stands with low tree cover (10%–29.9%)	−9.6%	12.1%	$n = 255{,}047$
Stands with high tree cover (30%+)	10.7%	−13.5%	P-value $<.00000$
Juniper Grass (savannah)			
Stands with low tree cover (10%–29.9%)	−17.6%	2.0%	$n = 19{,}143$
Stands with high tree cover (30%+)	38.2%	−4.4%	P-value $<.00000$
Pinyon–Juniper–Evergreen Shrub			
Stands with low tree cover (10%–29.9%)	−11.5%	9.5%	$n = 89{,}233$
Stands with high tree cover (30%+)	9.8%	−8.2%	P-value $<.00000$
Pinyon–Juniper with Grass			
Stands with low tree cover (10%–29.9%)	−15.5%	14.3%	$n = 40{,}367$
Stands with high tree cover (30%+)	14.2%	−13.0%	P-value $<.00000$
Pinyon–Juniper Persistent Woodlands			
Stands with low tree cover (10%–29.9%)	−2.0%	6.4%	$n = 98{,}286$
Stands with high tree cover (30%+)	2.8%	−8.8%	P-value $<.00000$
Pinyon–Juniper with Sagebrush			
Stands with low tree cover (10%–29.9%)	−28.6%	34.0%	$n = 8018$
Stands with high tree cover (30%+)	24.1%	−28.7%	P-value $<.00000$

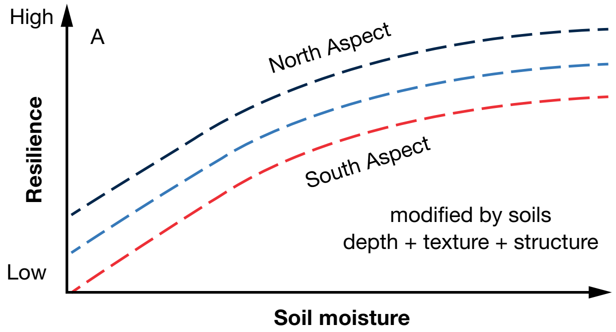

Fig. 8 Conceptual model showing the variation in ecosystem resilience to stress between upper and lower ecotones according to aridity, elevation, and soil properties. The middle line is the resilience as related to elevation and moisture, whereas the upper and lower lines show adjustments for aspect and soil properties. Adapted from Maestas, J., Campbell, S., Chambers, J., Pellant, M. and Miller, R. (2016). Tapping soil survey information for rapid assessment of sagebrush ecosystem resilience and resistance. *Rangelands* ***38***, 1–9.

The lower warm-dry woodland ecotones of pinyon–juniper communities are inherently vulnerable to periods of warmer temperatures and drought (Allen and Breshears, 1998; Maestas et al., 2016) (Fig. 8). The difference between upper and lower ecotones is reflected by ecosystem resilience in the face of long-term temperature increases that drive the upward expansion of woodlands into montane forest zones and the expansion of grassland and shrubland systems into areas previously occupied by woodlands (Clifford et al., 2011).

It stands to reason that warmer temperatures likewise favor changes in woodland understory vegetation, including trends in shifts from C3 to C4 grasses with increasing aridity. In addition to tree mortality, summer heat events have resulted in widespread mortality of many species of grasses, shrubs, and even cacti (Allen, 2007). Climate controlled changes in overstory and understory vegetation composition and plant productivity ultimately impact ecosystem and human communities that rely on the services of pinyon–juniper.

Carbon Storage as an Ecosystem Service

Vegetation biomass is an integral component of woodland carbon cycling. Through the process of photosynthesis atmospheric carbon dioxide is converted to carbohydrates as *carbon fixation* (Archer, 2011). Carbohydrates are used by plants to grow both belowground tissue in the form of roots and tubers and aboveground tissue in the form of stems and leaves. These components together with standing dead vegetation, downed woody debris, and the litter-duff surface make up woodland *biomass*, about half of which is *carbon stock* (USDA Forest Service, 2015). In pinyon–juniper woodlands there are approximately three to 55 metric tons per hectare of biomass carbon depending on the type of pinyon–juniper and the stage of succession (Fernandez et al., 2013; Weisz et al., 2010). Soil organic carbon makes up an additional 40–85 metric tons per hectare depending on soil type (Strenger et al., 2007). The amount and kind of soil organic carbon represents and controls soil development and woodland productivity (Van Cleve and Powers, 1995). Carbon can be conversely released from these woodlands to the atmosphere through decomposition and burning. Pinyon–juniper woodlands provide an important carbon storage service by their considerable extent, biomass, and soil reserves which are constantly changing through natural succession and disturbance.

As implied by the discussion on woodland expansion and ingrowth, the balance of carbon stock has increased significantly in pinyon–juniper (Strand et al., 2008; Neff et al., 2009; Fernandez et al., 2013) despite localized carbon losses linked to tree dieback, woodland clearing, stand replacement fire, and erosion. Carbon increases are the likely result of fire suppression and are especially concentrated in fire-adapted types. Trends in the levels of soil organic carbon are mostly influenced by the growth of vegetation, by activities that remove biomass from the soil surface, and by climatic factors of temperature and moisture that influence weathering and decomposition. Causes of carbon loss from woodland soils include fire and erosion from grazing, land conversion, and development. Losses in woodland vegetation cover coupled with climate-induced increases in the intensity of rain lead to reductions in soil aggregate stability and an increase in erosion rates (Allen and Breshears, 1998). For the moment, land use patterns and carbon accumulation appear to be offsetting the effects of climate forcing on the reduction in woodland extent and density (Table 2). There is some debate on the probable effects of 21st-Century climate on decomposition rates and the stability of soil organic carbon (Davidson and Janssens, 2006). But the net effect of climate forcing and land use on pinyon–juniper may be continued increase in total carbon storage.

Conclusion—Climate and Carbon

Increasing temperatures and drought conditions in the interior western United States. will likely to lead to further tree mortality in woodlands, in turn affecting disturbance processes of soil erosion, insect outbreaks, fire, and additional mortality (Allen, 2007).

Climate vulnerability forecasts for pinyon–juniper woodlands in North America (e.g., Comer et al., 2012; Rehfeldt et al., 2006; Triepke et al., 2019) likewise infer vulnerability to plant and wildlife habitat along with risks to provisioning services including pinyon nut production, livestock grazing, and fuelwood.

Future Trends and Conservation

Because P-J woodlands are so extensive in the western United States and northern Mexico, significant efforts are being made to install effective management prescriptions to meet the challenges of conserving biodiversity and natural resources in a rapidly chaining world (Aldon and Shaw, 1993; Gottfried et al., 2008). Given increasing frequency of droughts, fire, insect outbreaks, and changes in resource use and management, managers are faced with complex scenarios in their attempt to maintain P-J woodlands in optimal conditions. For example, pinyon jays (*Gymnorhinus cyanocephalus*) have a range that is strongly tied to P-J woodland distribution (across all that shown in Fig. 1 with some minor extension into neighboring forest biomes), but despite their wide range their numbers are significantly declining (Boone et al., 2018). Management strategies implemented to uniformly increase fire frequency across all types through tree thinning or the mechanical treatment to create more open, grassy stands for grazing coupled with increased tree die-off caused by droughts and insect outbreaks may be collectively altering the woodland structure that may be driving downward trend in species populations. This type of scenario likely applies to other animals and plants, each with their unique niche, and where there competing needs for biodiversity and society that mangers must address. Looking to the future there is a growing awareness that an integrated ecosystem management approach will increasingly be needed to solve these issues at site to landscape scales across this widely distributed and diverse ecosystem.

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Relevant Website

http://explorer.natureserve.org/servlet/NatureServe or http://usnvc.org/—For detailed descriptions of vegetation types according to the International Vegetation Classification (IVC) system.