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Managing for ecological resilience of pinyon–juniper ecosystems during an era of woodland contraction

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Abstract

Dryland woodland ecosystems worldwide have experienced widespread drought- and heat-related tree mortality events coupled with extreme wildfire behavior. In contrast to other forest types where the emphasis has been on the silvicultural enhancement of ecosystem resilience and restoration of structural heterogeneity, limited frameworks are available for management to improve drought resilience in semiarid woodlands. This challenge is especially acute in pinyon–juniper woodlands, a dominant vegetation type across western North America that has experienced extensive tree die-off over the past several decades while simultaneously undergoing expansion in portions of its range. In this paper, we describe the critical and urgent need to manage for future drought resilience in these highly vulnerable ecosystems and synthesize the current state of knowledge on how to enhance woodland resilience to drought coupled with high temperatures and associated disturbances. We present a landscape prioritization framework for guiding management goals and practices that requires prioritization of efforts based on the need for action and the probability of a positive outcome. Four guiding factors include historical woodland structure and drivers of long-term landscape change, current vegetation structure and composition, future climate suitability, and habitat and resource value. In summarizing the strength of evidence supporting our recommendations, we identify critical knowledge gaps and highlight the importance of adaptive management strategies that reflect current uncertainties. This will ultimately allow for improved management of diverse semiarid woodland ecosystems that are undergoing substantial changes due to past and present land use, biological invasions, and climate change.

KEYWORDS

forest dieback, global change, hotter drought, juniper, landscape prioritization pinyon pine, pinyon–juniper, restoration, semiarid woodland, tree die-off, woodland resilience

INTRODUCTION

Global climate change has led to widespread tree mortality in many forested ecosystems across the globe due to recent droughts coupled with high temperatures (hereafter "hot droughts"), resulting in extensive tree die-off and extreme wildfire events (Allen et al., 2010, 2015; Jolly et al., 2015). Recent drought- and heat-related tree mortality has been documented on every forested continent (Allen et al., 2010, 2015). Hot and dry conditions have also led to extreme wildfire behavior, especially in the western United States where wildfires have become larger and more severe (Westerling et al., 2006). It is increasingly accepted that silvicultural practices for forest restoration can enhance ecological resilience and resistance to drought and wildfire, particularly where they maintain structural heterogeneity (Churchill et al., 2013). Yet semiarid woodlands, which occupy approximately 6% of the terrestrial surface (Malagnoux et al., 2007) and occur on every continent except Antarctica, are not consistently managed in the context of maintaining or enhancing woodland health. To the contrary, in many parts of the world, concerns about expansion of semiarid woodlands have led to extensive tree and shrub removal treatments (Ding & Eldridge, 2019) that over time may contribute to drought-related woodland losses. Despite the fact that these ecosystem types are dominated by some of the world's most drought-adapted tree species, the need to manage for drought resilience in semiarid woodlands needs to be recognized (but see Klein, 2020).

Pinyon (*Pinus edulis* and *P. monophylla*)–juniper (*Juniperus monosperma*, *J. osteosperma*, and *J. scopulorum*) ecosystems, which comprise the dominant semiarid woodland vegetation type of western North America, have experienced unprecedented levels of drought-related tree die-off in recent decades, exceeding 90% mortality in some stands in the Colorado Plateau (Breshears et al., 2005). Simultaneously, drought coupled with the invasion of non-native annual grasses has contributed to a trend of larger and more frequent fires in pinyon–juniper woodlands over the past 30 years (Board et al., 2018; Floyd et al., 2004, 2017). Future loss of tree dominance is likely over large areas given climate change scenarios (Williams et al., 2013), which will strongly impact ecosystem water budgets and energy balance (Morillas et al., 2017; Royer et al., 2012; Stark et al., 2016), many tree-obligate wildlife species (Bombaci & Pejchar, 2016; Boone et al., 2021), ecosystem carbon stocks (Huang et al., 2010), pine nut production (Redmond et al., 2012), and other ecosystem services (Breshears et al., 2011). As a result, there is a critical and urgent need to develop approaches for maintaining and restoring ecologically resilient woodlands.

Novel management approaches are required that enhance drought resilience and reduce fire risk while maintaining tree populations with sustainable levels of surviving tree canopy and seedling regeneration in the understory. These semiarid woodlands differ from closed-canopy forests in that they can be viewed as two-phase mosaics of tree-dominated and understory vegetation, where competition by plants for belowground resources (e.g., water, nutrients) is of comparable magnitude as competition for aboveground resources (e.g., light; Martens et al., 1997). The tree component recovers slowly from episodic disturbance and with high spatial variance (Romme et al., 2009). Therefore, management approaches known to enhance ecosystem resilience in more mesic, closed-canopy forests will likely need to be refined in open woodlands. In this paper, we (1) provide an overview of pinyon–juniper ecosystems and their vulnerability to projected hotter droughts; (2) synthesize the current state of knowledge of how to manage these ecosystems effectively for woodland resilience to global change and the major areas of uncertainty; and (3) provide a landscape prioritization framework for guiding management goals and practices in these diverse and heterogeneous ecosystems.

PINYON–JUNIPER ECOSYSTEM VULNERABILITY TO GLOBAL CHANGE

Pinyon–juniper ecosystems

Pinyon–juniper ecosystems are one of the most widespread vegetation types in North America, representing 22,863,781 ha across the western United States (Board et al., 2018). These ecosystems span broad regional environmental gradients, encompassing extreme differences in precipitation amount and seasonality, temperature, and soils. Although most pinyon–juniper ecosystems predominantly occur in the rain shadow of the Pacific Crest where total precipitation is relatively low, there is a strong gradient of increasing total annual precipitation in the more northern portions of its range. Additionally, the distribution of this ecosystem type encompasses substantial variation in the timing of precipitation, described by a shift from winter-dominated precipitation in the northwest to monsoonal patterns of bimodal precipitation in the southeast. At local scales, temperature and precipitation are strongly related to elevational gradients, a climate pattern that is reflected by dramatic transitions in vegetation types over short distances. Soils are also highly variable, ranging from shallow exposed bedrock that supports very little herbaceous cover to deep fine-textured soils that support a diversity of grasses and shrubs, affecting fire behavior and drought vulnerability (Peterman et al., 2012; Romme et al., 2009) and vegetation responses following disturbance (Fick et al., 2022).

The current state of pinyon–juniper ecosystems is also the result of regional differences in historical fire regimes and land use legacies. Historical fire regimes were highly variable across the region. Fire in many pinyon–juniper ecosystems was historically infrequent due to surface fuel limitations (Baker & Shinneman, 2004; Bauer & Weisberg, 2009; Huffman et al., 2009), yet in areas with a heavy grass component, such as in portions of eastern New Mexico, fire generally burned frequently (Margolis, 2014). Further, past land use intensity varied greatly in association with human settlement, proximity to the railroad and mining operations, and soil productivity. Harvesting for railroad and mining operations was extensive in the Great Basin in particular, where hundreds of thousands of acres of pinyon–juniper woodlands are estimated to have been cut down to provide fuelwood, charcoal, and timbers for mining operations (Ko et al., 2011; Young & Budy, 1979; Young & Svejcar, 1999). Homestead-related woodcutting in the late 1800s was likely more widespread across pinyon–juniper ecosystems, and was associated with substantial contractions in tree cover in the limited areas examined (Amme et al., 2020; Bahre & Hutchinson, 1985). Grazing by domestic livestock has significantly impacted western landscapes over the last two centuries, shifting the composition of plant communities and altering the distribution of fuels (Miller & Rose, 1999). These ecosystems have also been used for centuries by indigenous peoples across this broad region. Pinyon pine cones are traditionally harvested annually for their coveted pine nuts by many of the tribes, and traditional stewardship and lifestyle practices likely influenced the structure of inhabited woodlands (Anderson, 2013).

Thus, pinyon–juniper ecosystems are incredibly diverse in their origins, legacies, structure, composition, disturbance history, and expected response to management and climate change stressors (Miller et al., 2019; Romme et al., 2009). Management of these ecosystems can involve intensive landscape-level manipulations, typically involving large-scale removals of trees through treatments such as mastication, cutting, herbicides, chaining, or prescribed fire (e.g., Redmond, Golden, et al., 2014). These management efforts have occurred in response to the observation that in some areas, woodlands have become denser and expanded into adjacent vegetation types (such as sagebrush communities) over the past century or more, hypothesized to result from anthropogenic influences such as overgrazing and fire exclusion (Miller & Rose, 1999). Whereas the expansion and infilling of pinyon and juniper trees over the past half century has been well documented in portions of its range, particularly in the Great Basin (Filippelli et al., 2020; Weisberg et al., 2007), there is debate concerning the causes of observed landscape changes, which likely vary geographically and include past deforestation and other stand-replacing disturbances, cool and wet climate conditions that promote tree recruitment, and disturbance regime shifts (Romme et al., 2009). Despite the fact that woodland expansion is ongoing in some areas, there is increasing evidence that many woodland areas are showing signs of contraction and decline (Breshears et al., 2005; Clifford et al., 2011; Flake & Weisberg, 2019; Floyd et al., 2009; Greenwood & Weisberg, 2008; Shriver et al., 2022), highlighting the need for a more nuanced understanding of woodland responses to global change processes.

Vulnerability to global change

Widespread tree mortality due to warmer temperatures, drought, and insect infestations has occurred in many areas across the western United States over the past two decades and resulted in dramatic losses in overstory pinyon pine in the Colorado Plateau (Breshears et al., 2005; Clifford et al., 2011; Floyd et al., 2009; Shaw et al., 2005) and to a lesser extent in the Great Basin (Flake & Weisberg, 2019; Greenwood & Weisberg, 2008). Great Basin pinyon–juniper is dominated by single-leaf pinyon pine (*P. monophylla*), a species that grows under more arid conditions and is considered more drought-adapted than twoneedle pinyon pine (*P. edulis*), the dominant pinyon species in the Colorado Plateau (Burns & Honkala, 1990). These differences in drought adaptation may partially explain the observed regional differences in the severity of recent tree mortality events. Thus far, recovery following recent widespread tree mortality events has been limited in many areas due to high juvenile mortality (Redmond et al., 2015) and limited new seedling establishment (Flake, 2016; Redmond et al., 2015; Redmond & Barger, 2013), and range-wide population models suggest that recent losses of woodland cover will persist into the future (Shriver et al., 2022).

Multiple demographic stages of pinyon pine are highly sensitive to increasing aridity, in addition to recent mortality of mature trees. Pinyon pine radial growth is tightly linked to cool and wet climate conditions (Adams & Kolb, 2004; Barger & Woodhouse, 2015; Biondi & Rossi, 2015), and growth declines have already occurred in some areas (Redmond et al., 2017). Seed cone production for *P. edulis* is also highly sensitive to increasing aridity: cool and wet climate conditions during cone initiation and fertilization are associated with higher seed cone production years (Parmenter et al., 2018; Wion et al., 2020), areas with greater aridity tend to have lower cone production overall (Wion et al., 2020), and recent declines in *P. edulis* cone production have occurred in association with recent warming (Redmond et al., 2012). Further, pinyon pine seedling establishment is often limited to cool and wet climate periods (Barger et al., 2009; Shinneman & Baker, 2009) and to microsites beneath nurse trees and shrubs that provide cooler microenvironments (Chambers et al., 1999; Redmond et al., 2018).

The various juniper species that occur in association with pinyon pine do not appear to be as sensitive to recent and projected increases in aridity, although there has been substantially less research focused on juniper climatic sensitivity. Juniper has water use characteristics that allow leaf water potential to drop along with declining soil water potential, allowing it to continue photosynthesizing at considerably lower soil water potentials than pinyon (West et al., 2008). Unlike recent widespread mortality of pinyon pine over the past two decades, there has been substantially less juniper mortality (Flake & Weisberg, 2019; Floyd et al., 2009). Yet recent drought-induced juniper mortality has been observed for *J. monosperma* in northcentral New Mexico and eastern Colorado (authors' personal observations) and *J. osteosperma* in southeastern Utah (Kannenberg et al., 2021), western Utah, northern Arizona, and eastern Nevada (authors' personal observations). Further, Flake and Weisberg (2019) documented substantial canopy dieback of *J. osteosperma* during a recent drought, suggesting that continued increases in drought will lead not only to increased rates of pinyon mortality but also juniper. Notably, juniper is less dependent upon the cooler microsites created by overstory trees and shrubs for seedling establishment and survival as compared with pinyon (Redmond et al., 2018) and has greater seed longevity (Chambers et al., 1999), and as a result, it is faster to recover following disturbances (Bristow et al., 2014; Redmond et al., 2013). Research on climate effects on juniper seedling establishment and growth is limited, but one study on *J. monosperma* seed production found that large seed crops occur following cool and wet years (Parmenter et al., 2018), suggesting that projected increases in aridity will reduce juniper fecundity. In summary, juniper appears to be less drought susceptible than pinyon pine, but the limited data available suggest the possibility of juniper decline in certain areas with projected increases in aridity.

In addition to the direct drought-related impacts on tree demography, wildland fire has also resulted in a reduction in woodland area. Because historical fire return intervals in pinyon–juniper woodlands were generally long (>300 years) and highly variable (Baker & Shinneman, 2004; Bauer & Weisberg, 2009; Huffman et al., 2009), it is difficult to interpret changes in fire regimes based on the short record of reliable wildland fire occurrence and size. Nonetheless, there has been a trend of larger and more frequent fires in pinyon–juniper woodlands over the past 30 years (Board et al., 2018; Floyd et al., 2017), and individual large fires have been far outside the local historical range of variability (Floyd et al., 2004). Following fire, there is a risk of invasion by disturbance-adapted non-native species, particularly on warmer and drier sites. Non-native species such as cheatgrass (*Bromus tectorum*), prickly Russian thistle (*Salsola tragus*), and Russian knapweed (*Acroptilon repens*) can form extensive monocultures in burned areas (Condon et al., 2011; Coop et al., 2017; Fenner, 2008; Gelbard & Belnap, 2003). The establishment of these invasive species strongly affects ecosystem function and can lead to extensive losses in livestock forage and other critical ecosystem services (Fenner, 2008). The establishment of invasive species can also prevent the establishment of native understory vegetation and result in landscape conversion to an alternate vegetation type from which the recovery of native plant communities is particularly challenging.

MANAGING FOR ECOSYSTEM RESILIENCE IN AN ERA OF WOODLAND CONTRACTION

Recent and projected woodland losses may have cascading ecosystem consequences, including potential reductions in water availability (Morillas et al., 2017), altered energy balance (Royer et al., 2012; Stark et al., 2016), declines in tree-obligate wildlife species (Bombaci & Pejchar, 2016; Boone et al., 2021), and increases in invasive plant establishment (Flake & Weisberg, 2021). Further, pinyon–juniper ecosystems are central to the worldviews, social identities, and cultural practices of many indigenous peoples. Pinyon pine seeds ("pine nuts") have been a dietary staple and are considered to be among the most important cultural food resources in the United States (Anderson, 2013; Bye, 1985). In some areas of the western United States, the commercial harvest and sale of pine nuts also provide an important source of income to local communities.

It is critical to manage for woodland resilience given the sensitivity of these species to future climate change and the critical function and ecosystem services these woodlands provide. Yet managing for woodland resilience is challenging due to the wide array of knowledge gaps (see below). Further, regional differences in species, soil, and climate mean that management recommendations may not be generalizable across ecoregions and in different woodland types. As a result, it is essential that scientists and managers use adaptive management approaches (e.g., Baker et al., 2017; Holling, 1978) to iteratively improve the management of these critical ecosystems. Below we summarize the current state of knowledge on management approaches for increasing woodland resilience and highlight critical areas of uncertainty.

How should these ecosystems be managed to reduce the likelihood of drought- and beetle-induced tree die-off events? *This is an area of high uncertainty. Light thinning of overstory trees may increase survival of remaining overstory trees, yet experimental studies are lacking. If thinning is done, it is critical to leave some juvenile trees in the understory in case a tree die-off event occurs. Priority should be given to maintaining sufficient tree cover, seed trees, and suitable microsites to allow for tree regeneration.*

In many dryland ecosystems, tree thinning has been a recommended silvicultural practice to reduce forest water stress during drought and ultimately increase tree survival (Dore et al., 2012; Grant et al., 2013). Yet the evidence is mixed for whether high tree density leads to greater rates of mortality due to drought and insect infestations in pinyon–juniper ecosystems (see Meddens et al., 2015, for a review). In *P. monophylla* dominated or co-dominated ecosystems, greater stand density is associated with higher rates of mortality and canopy dieback caused by drought and insect infestations (Flake & Weisberg, 2019; Greenwood & Weisberg, 2008). This suggests that thinning would be effective at reducing mortality of overstory trees, although notably climate and soil type were much stronger predictors of tree mortality than tree density (Flake & Weisberg, 2019). Most research has found no association between tree density and likelihood of mortality in *P. edulis*-dominated or co-dominated ecosystems (Meddens et al., 2015), suggesting that thinning may have limited potential to reduce tree mortality rates during drought. However, to our knowledge, all prior research has been observational by assessing the relationship between stand density and tree mortality. There are numerous other influences that co-vary with stand density, such as climatic and edaphic conditions, that limit our ability to draw conclusions from observational studies. Refinement of thinning practices to achieve drought resilience will require experimental research that manipulates stand density and structure (e.g., Giuggiola et al., 2013; Stephens & Moghaddas, 2005) and monitors resulting impacts on tree water stress and mortality in the context of site water balance.

In persistent upland pinyon–juniper woodlands, advanced regeneration is critical for woodland recovery following severe pinyon die-off (Redmond et al., 2015, 2018). Pinyon pine establishment is limited by short duration of seed viability and the need for suitable microsites (Chambers et al., 1999), and thus establishment of new seedlings following drought-induced die-off (Redmond et al., 2015, 2018) can be slow and protracted. Furthermore, overstory trees and shrubs as well as logs and rocks facilitate pinyon pine and to a lesser extent juniper seedling establishment and survival (Redmond et al., 2015; Sthultz et al., 2007; Urza, Weisberg, Chambers, & Sullivan, 2019), illustrating the importance of maintaining microsite variability in managed stands. Low thinning (the removal of small-diameter tree classes) and mechanical surface fuel reduction (Huffman et al., 2019) may thus inhibit stand recovery after a die-off event by removing advanced regeneration and homogenizing surface structures. As a result, uneven-aged silviculture that manages tree densities across multiple age cohorts and creates a diversity of stand structures (e.g., Gottfried, 2004; Gottfried & Severson, 1994; Page, 2008; Figure 1) may be a more appropriate approach to reducing tree competition while maintaining adequate regeneration, microsite heterogeneity, and providing a diversity of woodland structure that supports important wildlife species, such as the Pinyon Jay (Boone et al., 2021).

How should these ecosystems be managed following drought- and beetle-induced tree mortality events? *Keep sufficient snags and logs in place as these facilitate tree establishment and are important for a diverse array of taxa. In areas with limited established pinyon pine juveniles, plant pinyon pine seeds and seedlings in microsites with a greater probability of success. Consider managing to promote ecosystem conversion to a desired state in areas where resistance to non-native plant invasion is low and where tree recovery is unlikely.*

Following overstory tree mortality events, we recommend keeping sufficient dead snags, logs, rocks, and shrubs in place as these microsites facilitate tree establishment (Flake, 2016; Redmond & Barger, 2013). In addition, pinyon pine has greater survival during drought beneath the canopy of trees and shrubs (Redmond et al., 2015; Sthultz et al., 2007; Urza, Weisberg, Chambers, & Sullivan, 2019), suggesting that these shaded microsites will become increasingly important with projected increases in aridity. This is likely because microsites beneath the canopy of trees (Royer et al., 2012) and shrubs (Urza, Weisberg, Chambers, & Sullivan, 2019) have reduced mean maximum daily soil temperature, leading to lower soil potential evapotranspiration (Royer et al., 2012) and ultimately enhancing juvenile survival (Urza, Weisberg, Chambers, & Sullivan, 2019). Further, logs and snags provide important microsites for certain ground-dwelling arthropod and avian species (Delph et al., 2014; Pavlacky & Anderson, 2001). However, during active bark beetle outbreaks, sanitation felling (i.e., the complete removal or debarking of trees with beetle infestations) can be an effective way to

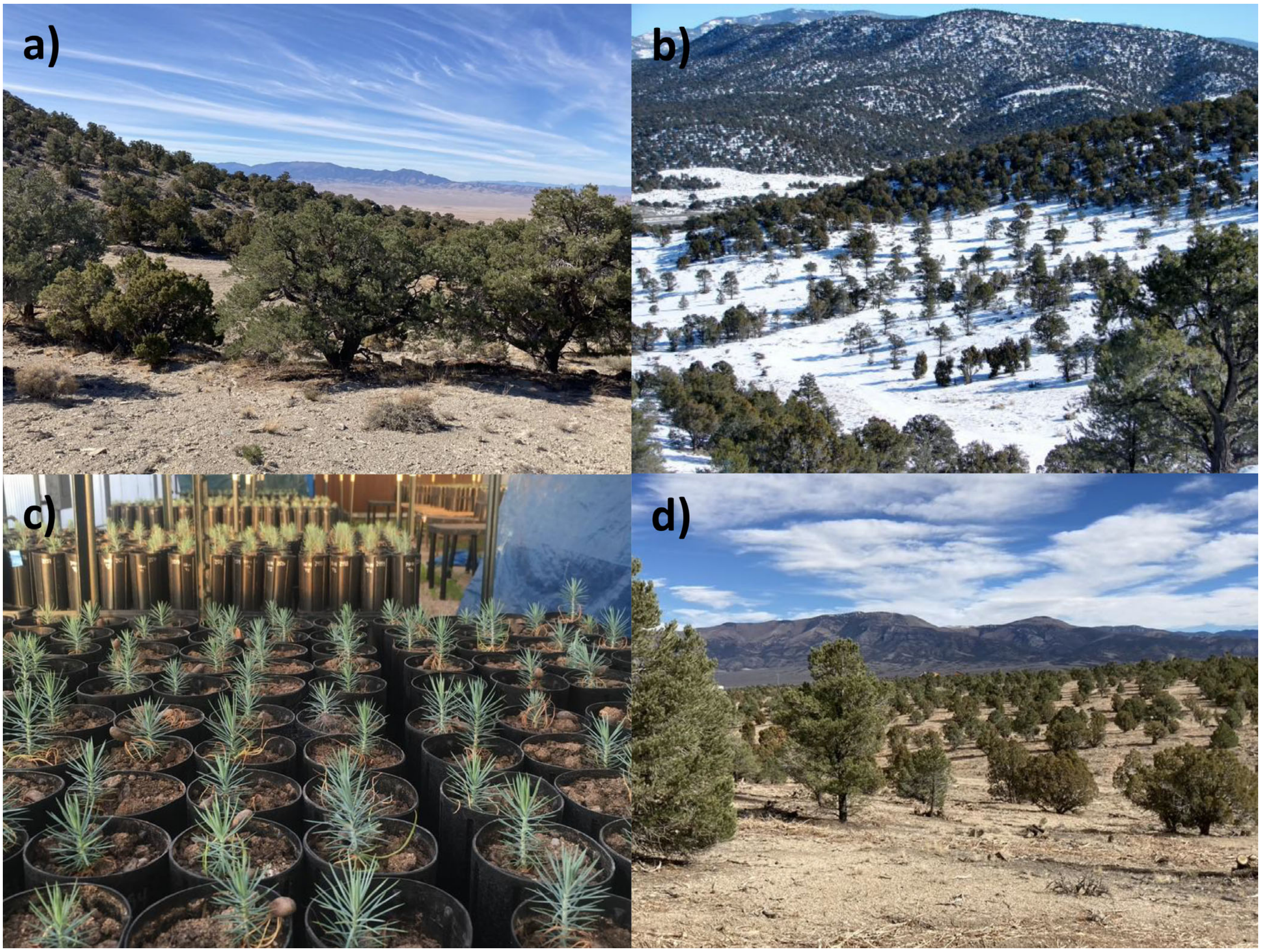

FIGURE 1 Treatment options for different management objectives in pinyon–juniper ecosystems. (a) No treatment in woodlands with high-value habitat and trees with old-growth characteristics (photo credit: Alexandra Urza). (b) Uneven-aged silviculture to reduce tree competition and increase heterogeneity while maintaining multiple age classes (photo credit: Doug Page). (c) Propagation of pinyon pine seedlings for restoration plantings to promote woodland recovery (photo credit: Alexandra Urza). (d) Mechanical thinning and mastication to reduce fuel loading and continuity near the wildland–urban interface (photo credit: Alexandra Urza).

reduce the severity of the outbreak in other forested ecosystems (Stadelmann et al., 2013), although the evidence for its efficacy is equivocal and context-dependent (Leverkus et al., 2021) and it is unclear how effective this is in pinyon–juniper woodlands and warrants further research.

Due to low seed viability after one year and limited amounts of wind or animal dispersal into disturbed areas (Chambers et al., 1999), recovery following large-scale pinyon pine mortality events is largely dependent upon advanced regeneration (Redmond et al., 2018). In areas where few pinyon juveniles have already established, planting seedlings may help to speed the recovery of a pinyon structural component. In planting pinyon pine, there are three factors of primary importance for fostering successful establishment, survival, and growth: (1) the climatic conditions of the site in the context of future climatic suitability; (2) the microenvironment in which the seeds or seedlings are being planted; and (3) the seed source used. Given the resources required to conduct planting operations (Fargione et al., 2021), we recommend prioritizing efforts in areas that will be most climatically suitable for pinyon pine under recent and future projected hotter droughts (see *Landscape prioritization strategies* below). Within a site, it is also critical to plant in microenvironments that have the greatest probability of success, such as adjacent to logs (Flake, 2016), under shrubs (Redmond et al., 2015; Urza, Weisberg, Chambers, & Sullivan, 2019), and within the canopy of overstory trees (Redmond et al., 2015). Pinyon pine and juniper populations are likely to be locally adapted to the climatic conditions historically experienced, similar to other tree species (Aitken et al., 2008). For example, pinyon pine growing in drier areas exhibit drought-resilient functional traits such as narrower stomata to reduce water loss (Mitton et al., 1998; Mitton & Duran, 2004), larger and heavier seeds (Vasey et al., 2022), and more rapid seedling growth rates (Vasey, 2021). Using seeds sourced from more arid climates may result in trees more resilient to future droughts, but exactly which seed sources and any unintended effects, such as greater susceptibility to pathogens or insects (e.g., Grady et al., 2015), need to be extensively researched. In addition, research is needed on how to most effectively propagate pinyon pine and juniper in nurseries and outplant in diverse field-settings (such as in areas with shallow, rocky soils or high grass cover) to promote restoration success.

In landscapes where tree recovery is unlikely due to reduced climatic suitability or a high probability of repeated disturbance, we recommend managers consider promoting ecosystem conversion to a desirable native plant community. Overstory tree mortality events can facilitate the invasion of non-native annual grasses and forbs (Flake & Weisberg, 2021), which can form extensive monocultures in disturbed areas (Coop et al., 2017; Fenner, 2008; Gelbard & Belnap, 2003) and prevent the recovery of native perennial species. Establishment of native perennial herbaceous species with strong potential to outcompete invasive annual grasses can be critical for establishing resistance to annual grass invasion (Chambers et al., 2007), particularly in those areas where canopy loss is particularly widespread, with invasive species already established and with limited tree regeneration potential.

How should these ecosystems be managed to prevent wildfire-facilitated landscape conversion to invasive species? *To reduce the risk of post-fire dominance by non-native invasive species, maintain or increase native perennial understory cover in unburned stands and promote recovery of perennial understory species after fire. This can be accomplished through grazing management, including resting burned areas from grazing, and through seeding or planting desired species. Following the postfire establishment of understory vegetation (including "nurse shrubs"), planting pinyon pine seeds and seedlings in appropriate microsites may increase the speed of woodland recovery. There is limited evidence that woody fuel reduction reduces fire risk; additional studies are needed.*

Postfire recovery of pinyon–juniper woodlands is a slow process, taking decades to centuries (Miller & Tausch, 2001). Because pinyon and juniper seedlings typically require nurse objects for successful establishment, tree recruitment into burned areas usually follows a period of dominance by understory shrubs and herbaceous species. During the recovery process, many pinyon–juniper woodlands are susceptible to invasion by non-native species such as cheatgrass (Condon et al., 2011; Floyd & Romme, 2012), although the risk of fire-induced ecosystem transformation varies based on initial site conditions and climatic suitability for invading species (Chambers et al., 2007; Floyd et al., 2006). Environmental settings that are colder and wetter, particularly during winter and early spring, tend to be relatively resistant to cheatgrass invasion due to less suitable conditions for cheatgrass establishment (Chambers et al., 2007; McMahon et al., 2021) and a more rapid recovery of native perennial herbaceous species (Roundy et al., 2018; Urza, Weisberg, Chambers, Board, & Flake, 2019). Within the range of environmental conditions susceptible to postfire invasion, much research has found a negative relationship between native perennial herbaceous species abundance and non-native plant invaders (e.g., Condon et al., 2011; Goodrich & Rocks, 1999). Postfire plant species composition tends to be driven by species that were present before the fire, which are then able to regrow or establish on burned sites through root resprouting, soil seed banking, or seed dispersal from nearby unburned patches. Dense woodland stands with sparse cover of understory perennial species have limited capacity for natural regeneration following fire, leaving an ecological void that increases susceptibility to cheatgrass invasion (Floyd et al., 2006; Urza et al., 2017), particularly in soils with low biological soil crust cover (Floyd et al., 2006; Shinneman et al., 2009).

We recommend management actions that maintain or increase native perennial herbaceous species in the understory of unburned woodland ecosystems to increase postfire recovery potential. Managing grazing at appropriate levels and resting burned areas from grazing for a period of years can maintain native perennial grasses and forbs, while overgrazing can reduce perennial herbaceous cover and limit potential for postfire recovery (Floyd & Romme, 2012). Uneven-aged stand thinning that creates mosaics of canopy openings and tree clumps in pinyon–juniper woodlands may promote perennial herbaceous understory establishment where competition with trees is reduced (Ellenwood, 1994; Ernst-Brock et al., 2019), although there is limited empirical research that has tested this. Leaving some of the wood on-site following thinning can be effective at providing cool and wet microsites conducive to tree seedling establishment (Flake, 2016), and may also reduce soil erosion (Karban et al., 2021).

Following a fire event, managers should first assess the recovery potential of native vegetation and the risk of invasion by non-native species. Miller et al. (2015) have developed a useful guide to assist with this assessment. If a site is at high risk of conversion to invasive species, we recommend management actions that promote the recovery of native perennial understory species. Grazing deferment can allow native species enough time to fully establish prior to herbivory, and the length of deferment should be determined based on site productivity, burn severity, and invasive plant abundance (Miller et al., 2015). In sites where prefire perennial herbaceous cover is low, such as in dense woodlands stands, native perennial species can be seeded or planted (Urza, Weisberg, Chambers, Board, & Flake, 2019), although postfire seeding has had mixed success in burned woodlands (Floyd et al., 2006; Shinneman et al., 2009). If the recovery of the pinyon–juniper woodland community is a priority, tree seedlings can be planted following the recommendations in the previous section. Tree planting will be most successful if it occurs after shrub establishment, whose cover facilitates tree seedling establishment (Redmond et al., 2015; Urza, Weisberg, Chambers, & Sullivan, 2019).

Some managers are implementing treatments aimed at reducing fire risk by reducing woody fuels via tree thinning or removal, but very few fire behavior modeling studies have evaluated the effects of these treatments. Under moderate burning conditions, active crown fire is often limited in woodlands by sparse or discontinuous surface fuel loads (Linn et al., 2013; Strand et al., 2013), yet extreme conditions capable of supporting crown spread are becoming increasingly frequent. Mechanical "lop and scatter" and mastication treatments, common fuel treatment types in pinyon–juniper, are considered effective at reducing the risk of crown fire (Wozniak et al., 2020) but can increase surface fuel loads (Bernau et al., 2018; Coop et al., 2017; Young et al., 2015). The limited fire behavior modeling studies done in western juniper ecosystems suggest that old-growth woodlands may indeed burn at a lower intensity than sagebrush-dominated sites (Yanish, 2002), highlighting the uncertainty of the efficacy of common fuel reduction treatments and the need for fire behavior modeling.

Tree removal by mechanical treatment, prescribed fire, or mastication can increase the cover of herbaceous species, including fire-adapted invasive grasses like cheatgrass (Havrilla et al., 2017; Redmond, Zelikova, et al., 2014; Urza et al., 2017), and the subsequent increases in fine fuel loads (Coop et al., 2017; Young et al., 2015) may actually increase fire ignition probability and rate of spread (Davies & Nafus, 2012). Mechanical treatment and pile burning has a reduced risk of invasive species establishment compared with broadcast prescribed fire (Redmond, Zelikova, et al., 2014). Broadcast burning is most appropriate in woodlands in cool/wet climates that are less susceptible to invasion (Urza et al., 2017), and patchy burning may be used in persistent pinyon–juniper woodlands to maintain natural woodland structure (Huffman et al., 2019). Where managers aim to reduce fire risk while maintaining tree cover, low thinning and pruning lower tree limbs may reduce woody fuel loads and ladder fuels, but evidence that these approaches reduce overall fire risk is limited.

LANDSCAPE PRIORITIZATION STRATEGIES FOR THE MANAGEMENT AND CONSERVATION OF PINYON–JUNIPER ECOSYSTEMS

Management in a changing world requires understanding of past drivers, current conditions, and projected future climatic suitability. The diversity of pinyon–juniper ecosystems negates a one-size-fits-all approach to management and requires managers to prioritize management efforts based on the need for action and the probability of a positive outcome. Further, there is a suite of potential management options to increase woodland resilience to drought and insect infestations, promote tree recovery and range expansion under future climate, prevent the likelihood of stand-replacing wildfire, and reduce the likelihood of invasive species establishment and spread (Table 1). A landscape-level prioritization of potential management actions is needed that considers past and future trajectories and the habitat use and resource value of different vegetation types.

We recommend four factors that land managers consider in the development of a landscape prioritization plan for pinyon–juniper ecosystems:

1. *Historical woodland structure and drivers of landscape change*: It is critical to first determine the current stand structure of a given pinyon–juniper ecosystem to identify whether the trees are old-growth (i.e., established and survived prior to the past 150+ years) or whether most trees had been recently established. This can be done by using dendrochronological dating techniques and tree morphology to estimate age structure (Weisberg & Ko, 2012). If most trees had been recently established, then it is important to assess whether recent tree establishment is due to post-disturbance recovery, past climate conditions, or fire suppression and grazing. Post-disturbance recovery can be assessed by searching for evidence of burned (wildfire) or unburned (drought) stumps or logs, or cut stumps, nearby charcoal kilns or pits, or early settlement evidence of prior tree cutting (Ko et al., 2011; Page et al., 2015; Straka & Wynn, 2008). In the absence of evidence for post-disturbance recovery, dendrochronology studies such as those by Barger et al. (2009) can help determine whether tree

TABLE 1 Priority areas and treatment options for different management objectives common in pinyon–juniper ecosystems.

Management priority	Treatment type(s)	Desired effect(s)	Target areas	Confidence from evidence
Maintain healthy woodlands	- No treatment	- Maintain tree populations - Avoid risk of harming biological soil crusts and understory vegetation - Maintain adequate tree regeneration	- Woodlands with high-value habitat or old trees - Woodlands with intact understories or high biological soils crusts	*Moderate*: Some observational studies find no association between stand density and tree mortality[1]; avoids risks of soil disturbance and loss of tree populations associated with treatments.[2]
Increase woodland resilience to drought, insects, and pathogens	- Uneven-aged silviculture to reduce tree densities to desired level in each age/size class and to manage tree spacing for a diversity of structures (clumps and openings)	- Reduce tree competition - Maintain adequate tree regeneration and stimulate understory vegetation - Enhance mosaic nature of the woodland	- Uneven-aged woodlands - Dense homogenous woodlands with high-value habitat - Dense stands in trailing edge, or declining core woodlands	*Low*: Greater tree densities associated with greater mortality in some studies,[1] but this may be associated with fine-scale proximity.[3] More long-term research needed for uneven-aged silvicultural treatments.[4,5]
Fire risk reduction	- Mechanical treatments to reduce surface fuels, ladder fuels, and canopy bulk density, including low thinning and pruning lower limbs - Prescribed burning in areas with low susceptibility to invasive annuals	- Reduce the probability of a large fire - Reduce fire intensity for fire suppression actions and firefighter/public safety - Reduce likelihood of fire-induced conversion to alternate stable state (annual grassland)	- Areas near the wildland–urban interface - Prescribed burning better suited in woodlands in cool/wet climates due to greater resistance to annual grass invasion. Burning may be difficult to implement where understory cover is sparse.	*Low to moderate*: limited studies on the efficacy of fuel treatments for reducing fire risk in pinyon–juniper. Potential adverse effects of thinning on fire behavior due to increases in abundance and continuity of fine fuels.[6,7]
Invasive species management	- Manage or remove livestock to maintain native herbaceous species - Seed or plant native perennials	- Reduce the risk of invasive plant species establishment and spread	- Recently disturbed woodlands with limited native vegetation cover - Warm/dry woodlands with low resistance to invasion	*High*: Seeding of native perennials can reduce invasive plant establishment following disturbances[8,9] and managing livestock grazing is critical for restoring understory vegetation.[2]
Promote woodland recovery	- Plant tree seedlings under nurse shrubs or other shaded microsites (esp. pinyon pine)	- Increase tree recovery following a stand-replacing disturbance	- Disturbed woodlands that are climatically suitable	*Moderate*: Limited new pinyon pine establishment following disturbances[8,9] and strong evidence for

(Continues)

TABLE 1 (Continued)

Management priority	Treatment type(s)	Desired effect(s)	Target areas	Confidence from evidence
				the importance of nurse plants for pinyon pine.[10,11] Few studies on the efficacy of planting seedlings of pinyon or juniper.
Assisted migration	Plant seedlings from climate-adapted source populations or with climate-adapted traits	- Increase tree recovery under hotter and drier conditions (assisted population migration) - Promote tree expansion to climatically suitable regions (assisted range expansion)	- Recently disturbed woodlands with high-value woodland habitat - Habitat at the leading edge prioritized for woodland (newly climatically suitable)	*Low*: Pinyon and juniper trees have limited ability to keep pace with climate change[12] and assisted migration may become an important management tool. Yet limited research exists on how to implement assisted migration.
Convert to grassland or shrubland	- Tree removal treatments with the goal of deforestation (i.e., clear-cutting without intended reforestation). Treatment options include mechanical cutting, mastication, and prescribed burning. - Seed or plant native perennials following treatment	- Promote ecosystem conversion to a desired grassland or shrubland dominated community - Enhance forage production for grazing	- Low density, trailing edge expansion woodlands without evidence of past disturbance - High-value nonwoodland habitat	*Moderate*: Many studies have documented increases in herbaceous vegetation following tree removal,[13] although the long-term efficacy is less clear.[14] Herbaceous cover is often enhanced when tree removal treatments are followed by seeding,[13] but it less clear how effective seeding is alone.

Note: References are: 1, Meddens et al. (2015); 2, Floyd and Romme (2012); 3, Flake and Weisberg (2019); 4, Page (2008); 5, Gottfried and Severson (1993); 6, Young et al. (2015); 7, Coop et al. (2017); 8, Redmond, Golden, et al. (2014); 9, Urza, Weisberg, Chambers, Board, and Flake (2019); 10, Redmond et al. (2018); 11, Urza, Weisberg, Chambers, and Sullivan (2019); 12, Minott and Kolb (2020); 13, Hartsell et al. (2020); 14, Bristow et al. (2014).

establishment was due to climate or grazing and dendrochronology tools can be used to assess fire history (Margolis, 2014).

2. *Current composition and structure of understory and overstory plants*: Ecosystem response to future climate, disturbances, and invasive species will strongly vary depending upon the structure and composition of not only the trees but also the understory vegetation. For instance, stands dominated by *P. edulis* have been more vulnerable to recent drought and insect infestations than stands dominated by *P. monophylla* (Flake & Weisberg, 2019; Shaw et al., 2005). Low perennial understory cover is generally associated with increased susceptibility to invasion by annual grasses (Floyd et al., 2006; Urza et al., 2017), except in stands with high bedrock or biological soil crusts, such as in portions of the Colorado Plateau (Shinneman et al., 2009). Importantly, stands with high grass cover or adjacent to grasslands, especially of annual grasses, may be more likely to experience wildfire than woodlands with sparse fine fuels, due to a greater probability of fire spread (Arendt & Baker, 2013; Board et al., 2018). Edaphic conditions exert strong controls on plant species composition, as well as potential responses to

disturbance, management, and climate change, and soil maps can be combined with vegetation data to delineate landscape units for prioritization plans (e.g., Fick et al., 2022).

3. *Future climate suitability*: As climate conditions continue to become more arid throughout the US Southwest (McKinnon et al., 2021), it is important to identify the future climatic suitability of a given pinyon–juniper ecosystem. Populations at the trailing edge (i.e., where the climate is projected to no longer be suitable within the next century) are at greatest risk of ecosystem conversion due to drought- and insect-induced tree mortality and subsequent tree regeneration failure. These areas are where land managers should conduct tree removal treatments if nonwoodland habitat is valued, such as for forage production or shrubland-obligate wildlife species, and also should be of low priority for reforestation efforts following disturbances given the lower probability of success. In contrast, management efforts should prioritize reforestation efforts for populations projected to remain in climatically suitable areas and potential expansion areas at the leading edge (i.e., where the climate is projected to become suitable within the next century) in areas prioritized for woodland occurrence. Notably, there are considerable challenges with determining trailing edge compared with leading edge populations, which can be assessed using bioclimate envelope or niche modeling (e.g., Rehfeldt et al., 2015; Urza et al., 2020), evidence of recent tree mortality and canopy dieback (Flake & Weisberg, 2019), and recent recruitment (Redmond et al., 2015, 2018).
4. *Habitat and resource value*: Landscape prioritization must also consider the importance of pinyon–juniper ecosystems for habitat, biodiversity conservation, and the provision of cultural resources. Habitat conservation concerns can be addressed by overlaying woodland categories (e.g., trailing edge decline vs. leading edge expansion) with existing habitat maps and landscape connectivity models (e.g., Crist et al., 2017) for focal species (e.g., woodland-obligate species such as Pinyon Jay, Black-throated Gray Warbler, and Juniper Titmouse; sagebrush-obligate species such as pygmy rabbit and Greater Sage-Grouse; Zeller et al., 2021). This is especially important given that many grassland- and sagebrush-obligate wildlife species benefit from more open, treeless areas (Crawford et al., 2004). Cultural resource values including firewood and pine nut production need to be considered in a holistic way, taking into account traditional uses, existing land management designations, and the needs of both commercial and noncommercial harvesters.

CONCLUSION

Pinyon–juniper woodlands have undergone dramatic landscape changes in the last two centuries, including declining use by indigenous peoples, widespread harvesting by Euro-Americans that began in the late 1800s and, more recently, extensive tree mortality due to drought and insect infestations that are projected to increase with climate change. Present-day management is often focused on tree removal in "expanding" woodlands, yet it is important to consider prior land use legacies and future responses to global change in developing management plans. The landscape prioritization framework presented here provides key considerations for developing management plans and recommended treatment options for a given management objective. Notably there are considerable gaps in knowledge for many of the recommended strategies (i.e., confidence column in Table 1) and uncertainty in future trajectories of these ecosystems, which presents a major challenge. Given this uncertainty, managers can hedge their bets by using diverse treatment options (including no treatment), allowing for redundancy, and using adaptive management to learn the best approaches. Collaborative efforts between researchers and managers will be critical to understand potential use of silvicultural treatments to increase woodland resilience to drought, promote pinyon pine nut production, reduce fuel loads and fire risk, and to enhance understory perennial herbaceous plants, forage production, and wildlife habitat. This will ultimately allow for improved management of this critical ecosystem that is undergoing substantial changes due to past and present land use, biological invasions, and climate change.

AUTHOR CONTRIBUTIONS

All authors contributed equally to this work.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

No data were collected or analyzed as part of this study.

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