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Gaps and hotspots in the state of knowledge of pinyon-juniper communities

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ABSTRACT

Pinyon-juniper (PJ) plant communities cover a large area across North America and provide critical habitat for wildlife, biodiversity and ecosystem functions, and rich cultural resources. These communities occur across a variety of environmental gradients, disturbance regimes, structural conditions and species compositions, including three species of juniper and two species of pinyon. PJ communities have experienced substantial changes in recent decades and identifying appropriate management strategies for these diverse communities is a growing challenge. Here, we surveyed the literature and compiled 441 studies to characterize patterns in research on PJ communities through time, across geographic space and climatic conditions, and among focal species. We evaluate the state of knowledge for three focal topics: 1) historical stand dynamics and responses to disturbance, 2) land management actions and their effects, and 3) potential future responses to changing climate. We identified large and potentially important gaps in our understanding of pinyon-juniper communities both geographically and topically. The effect of drought on *Pinus edulis,* the pinyon pine species in eastern PJ communities was frequently addressed, while few studies focused on drought effects on *Pinus monophylla*, which occurs in western PJ communities. The largest proportion of studies that examined land management actions only measured their effects for one year. Grazing was a common land-use across the geographic range of PJ communities yet was rarely studied. We found only 39 studies that had information on the impacts of anthropogenic climate change and most were concentrated on *Pinus edulis*. These results provide a synthetic perspective on PJ communities that can help natural resource managers identify relevant knowledge needed for decision-making and researchers design new studies to fill important knowledge gaps.

1. Introduction

Pinyon-juniper communities, which include woodlands, savannas, and closed canopy forests, have been a focus for a wide array of research topics such as paleoecology, dendroecology, ecophysiology, restoration, and the effects of drought. However, it is unclear if past studies on pinyon-juniper communities encompass the large variation in the structure, composition, and physical properties that exist across their geographic range. This variation is compounded by the interacting effects of disturbance, management actions, and responses to climate change. Biophysical variation and the growing effects of climate and land-use change underscore the importance of evaluating the state of knowledge of pinyon-juniper communities to predict potential changes in extent and characteristics and to guide land management decisions. Identifying geographic areas and associated climate space with a lack of research will highlight gaps in our understanding of pinyon-juniper communities that could be addressed by research and may be associated with unanticipated outcomes associated with management actions or disturbance. Synthesizing both the state of knowledge on the drivers of increasing tree density and expansion into shrublands and the effects of management actions across the wide distribution of pinyon-juniper communities could help clarify best practices. In addition, identifying the potential trajectories for the structure and function of pinyon-juniper communities in the 21st century can both direct research efforts and inform management strategies.

Pinyon-juniper communities are a “diverse and variable vegetation type” (Romme et al., 2009) because they occupy a broad geographic area with substantial variation in environmental conditions and disturbance regimes that support a range of vegetation structures and species compositions. The most common dominant tree species within pinyon-juniper communities are the pine species *Pinus edulis* Engelm. and *Pinus monophylla* Torr. and Frem., and the juniper species *Juniperus monosperma* (Engelm.) Sarg., *Juniperus osteosperma* (Torr.) Little, and *Juniperus scopulorum* Sarg. Other species include *Pinus cembroides* Zucc., *Pinus discolor* D.K. Bailey & Hawksw., *Juniperus deppeana* Steud., *Juniperus virginiana* L., and *Juniperus occidentalis* Hook., but are not the focus of this review owing to a lack of co-occurring pinyon species (*J. occidentalis*, *J. virginiana*) or because the majority of their ranges are compositionally and climatically distinct within Madrean pinyon-juniper communities (*J. deppeana*, *P. cembroides*, *P. discolor*). These five focal species occur in varying proportions and locations across western North America. *P. edulis* often grows with *J. monosperma* in the states of New

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Mexico, eastern Colorado and portions of eastern Arizona, or with *J. osteosperma* in northern Arizona, Utah and western Colorado (Little Jr, 1971). *P. monophylla* is commonly found in the higher elevations of the Great Basin with *J. osteosperma* in Nevada and extreme southeastern California. *J. scopulorum* occurs throughout the Rocky Mountain region and can be found with *P. edulis* (Little Jr, 1971). Three broadly-defined stand structural categories were described by Romme et al. (2009) based on tree density, understory composition and disturbance regime: 1) persistent pinyon-juniper woodlands, characterized by a canopy composition ranging from small trees to large dense stands with a sparse understory, 2) pinyon-juniper savannas, which support a continuous herbaceous understory and a moderate tree density, and 3) wooded shrublands, which are co-dominated by trees and shrubs, particularly of the genus *Artemisia*. Because of this variability, recognizing gradients in stand structure and dynamics is essential to identify appropriate management actions and predict future climate responses.

Pinyon-juniper communities have many intrinsic values. They provide a wide range of resources for humans, including firewood (Samuels and Betancourt, 1982), pine nuts (Fogg, 1966), ceremonial plant materials for indigenous people (Koyiyumptewa, 1993), and have a long history of utilization for livestock grazing. Pinyon-juniper communities provide habitat for a wide range of plants and animals (Francis et al., 2011), including numerous endemic and imperiled species (e.g. Todsen's pennyroyal (*Hedeoma todsenii)*, pinyon jay (*Gymnorhinus cyanocephalus)*, BirdLife International, 2017, Ligon, 1978). Pinyon-juniper communities are increasingly used for recreation such as hiking, mountain biking, camping or off-road vehicle use; these uses can be a source of anthropogenic wildfire ignitions and can require subsequent restoration (Weise, 1990). Synthesizing the state of knowledge on pinyon-juniper communities can aid resource practitioners in effectively ensuring these values and services are maintained.

Studies are often limited in their geographic and climatic scope, and this synthesis seeks to understand the stand structure, dynamics and the disturbance responses of pinyon-juniper communities across broad environmental gradients. While previous reviews on pinyon-juniper communities have been comprehensive on the topics of restoration (Baker and Shinneman, 2004; Floyd and Romme, 2012), mortality (Hicke and Zeppel, 2013; Meddens et al., 2015), and stand dynamics (Romme et al., 2009), these syntheses do not have the explicit goal of identifying species-specific patterns in the state of knowledge across topics throughout the geographic and climatic ranges of pinyon-juniper communities.

To fill this need, we first cataloged the entirety of published information on pinyon-juniper communities by topic, species, location, and climate space to provide insight on potential gaps in knowledge and research patterns for this variable and widespread vegetation type. We then conducted more in-depth synthesis focused on three specific topics relevant to management for pinyon-juniper communities: 1) historical stand structure, dynamics, and responses to natural disturbance, 2) management practices and their effects, and 3) expected future long-term trajectories under an increasingly arid climate. We evaluated the state of knowledge on pinyon-juniper communities by topic across time and space and provide a review of the current knowledge within the three topic areas.

2. Methods

2.1. Literature search

We searched within the Web of Science Core Collection on 2 August 2018 to capture all peer-reviewed articles for our five-focal species: *P. edulis*, *P. monophylla*, *J. osteosperma*, *J. monosperma*, and *J. scopulorum*. We also searched with the terms “pinyon”, “piñon” and “piñon-juniper” to capture research associated with these species that did not use the species scientific name. We focused our search on communities that included at least one species of pinyon with at least one co-occurring species of juniper. This criteria excluded *J. occidentalis* and *J. virginiana* woodlands because these species generally do not co-occur with pine species. We also excluded publications with a focus on Madrean pinyon and juniper species such as *P. cembroides, P. discolor,* and *J. deppeana*. Madrean pinyon-juniper is often co-dominant with oak species and is described as occurring in a sub-tropical or tropical climate as opposed to the temperate climate of the core pinyon-juniper communities (NatureServe 2018). We only retained studies which were primarily focused on the five focal pinyon-juniper species rather than associated plant or animal species such as sagebrush, mule deer or sage grouse. We excluded studies which focused on social science, biofuel, or horticulture topics as well as methods papers, opinion pieces, book reviews and books (Appendix A). All data generated during this study are available from the USGS ScienceBase-Catalog (Hartsell et al., 2019).

2.2. Topical analysis

For each included study, we recorded publication date, beginning and end year of management or experimental treatment, and beginning and end year of measurements. We categorized studies into one of five types (observational, experimental, modeling, review, paleoecology) and identified which of the five focal species were included in the study.

We tallied the number of studies that addressed our three focal topics: natural disturbance, management actions, and responses to climate change. For the natural disturbance category, we noted whether a study included information on the major categories addressed in the reviewed literature: drought, wildfire, or beetle infestation. Within the management action category, we recorded studies which included tree removal, prescribed fire, seeding, grazing, or multiple overlapping treatment types. Finally, we counted the number of studies that documented the effects of anthropogenic climate change.

For all focal topics we identified the presence of major categories of measured variables within each study, including tree age, density, size, establishment, succession, mortality, dendroecology or understory cover. We also tracked if the study reported and/or modeled the paleo, current or future distribution of our focal species. We also tracked any experimental manipulation such as a drought or water addition treatment. Counts were not mutually exclusive with respect to species or focal topic, resulting in sums of studies across species or topic greater than the total number of studies. For example, studies containing *P. edulis* could also contain *J. osteosperma*, or a study counted as having a wildfire component could also have a seeding component.

2.3. Geographic analysis

We extracted locations for all studies with location information available from coordinates, figures, or written descriptions. We identified which species were associated with each location where possible. For larger study sites characterized with a polygon (as opposed to a point), we selected the centroid of the polygon as the study location. Due to wide variation in descriptive information, as well as the variety of study extents and types included in our review, we classified the accuracy of the location as < 1 km, 1 km, 10 km, or ≥ 100 km. We excluded studies for this part of the analysis with extremely broad location descriptions (i.e. the western US).

For each species, we plotted the locations by category and their general geographic ranges (Little Jr, 1971). We adjusted the ranges for recent taxonomic distinctions for *J. monosperma* (occurrences in Mexico misidentified, Adams, 2014) and *J. scopulorum* (coastal Washington locations identified as a new species, Adams, 2007). Approximately 12% of the locations (164) had unclear designations for at least one of the five focal species (e.g. “juniper” or “*Pinus*” mentioned without species name) yet occurred within the ranges of the focal species and are highly likely to be among the focal species. We also calculated the density of study locations per 50 km pixel. For most plotting and spatial analysis, we removed the studies (36 of 361) where large polygons were mapped (> 100 km). These studies tended to be species distribution modeling studies or remote sensing studies across large extents. For three papers we were unable to determine the locations used in the study due to lack of detail or multiple locations matching the site description.

We compared the climate space of study locations (after removing paleoecology studies and points mapped as the centroids of large polygons) to the climate space of the studied species' entire geographic range. Climate space was characterized by three pairs of variables using bivariate contour plots: mean annual temperature and mean annual precipitation, maximum temperature of the warmest month and minimum temperature of the coldest month, and precipitation of the warmest quarter and precipitation of the coldest quarter from 1970 to 2000 (30 arc-second, ~1 km resolution, WorldClim vs. 2, Fick and Hijmans, 2017). The comparison of climate space for mean annual precipitation and temperature represent broad climate gradients, whereas the space related to minimum and maximum temperatures represent climatic extremes across the distribution. The climate space associated with warm season (warmest quarter) and cool season (coldest quarter) precipitation describe the dominance of the North American Monsoon, which produces precipitation over a portion of our study region from July – September.

3. Results and discussion

3.1. Overall study effort and distribution

Our initial search resulted in 1258 total studies, which was reduced to 441 studies (35% of total) based on the inclusion criteria. Of the included studies, the general categories found were observational studies (201 studies, 46%), experiments (118, 27%), reviews including a single meta-analysis (53, 12%), paleoecological studies (33, 7%), and modeling studies (normally broadscale analyses relying on remote sensing or widely available occurrence datasets, 21, 5%). Fifteen of the studies included multiple methodologies and were not able to be clearly grouped in the preceding categories. Of the included studies, 181 included a land management action, such as thinning, and 182 included a natural disturbance. Most studies focused on *P. edulis* (282 studies, 64%), followed by *J. osteosperma* (226, 51%), *J. monosperma* (146, 33%), *P. monophylla* (114, 26%), and *J. scopulorum* (49, 11%). Thirty-nine studies (9%) did not specify what species of pine they focused on and forty-eight studies (11%) did not specify the species of juniper; these studies often only mentioned being in a pinyon-juniper community broadly yet likely included some of the focal species based on their geographic location.

There has been an increase in the number of studies on pinyon-juniper communities across the review period of 1909 to 2018. The earliest study we found was a descriptive paper on *P. edulis* (Phillips, 1909). Observational studies had the highest proportion of broad study type; experimental studies also made up a large proportion of studies across the review period. Reviews were common in the 1990s, and modeling studies have increased from the 1980s through the 2010s (Appendix B. Counts of studies through time).

Location information was acquired for 369 papers (84% of reviewed literature), specifying 1376 unique locations. Some areas were hotspots of research, with as many as 25 studies per 50 km pixel. However, density of research effort was generally much lower; the majority (58%) of areas with any studies only had 1 study per 50 km pixel (Appendix C. Geographic Density of All Included Studies).

The spatial distribution of studies was not uniform, with a high density of studies in north-central New Mexico and Arizona. There were gaps in research effort in southern California for *P. monophylla*, northeastern New Mexico for *P. edulis* and *J. monosperma,* Wyoming and southeastern Idaho for *J. osteosperma*, and numerous areas for *J. scopulorum* outside of hotspots in the southwestern United States (Fig. 1). Through time the most obvious geographic patterns were a high density of research effort in Nevada in the 1980s and a relative lack of studies in the Navajo Nation (“Four-Corners” region between New Mexico, Arizona, Colorado, and Utah) until the 2010s (Appendix D).

Study locations generally occupied a small subset of the climate space occupied by the entire species geographic distribution, but studies were representative of the highest density climate space for some species. Study locations for *J. monosperma* did not encompass much of the relatively cool and wet or warm and dry areas, and areas with cooler temperatures in the warmest month of the year, and study locations were highly represented in areas of higher cool season precipitation than much of the species range (Fig. 2, all species and climate space combinations, Appendix E). Study locations for *J. scopulorum* also did not overlap at high density with cooler areas of the range. Study locations for *P. edulis* also had greater density of studies in areas with greater cold season precipitation than the density of the range, and a greater research effort in the warm and dry portion of its range. Few differences were observed for climate space between study locations and geographic ranges for *J. osteosperma* and *P. monophylla*. Some study locations appeared to fall outside of the geographic range due to a combination of relatively low accuracy location descriptions and approximate geographic range boundaries (Little Jr, 1971). The lack of studies in the warmest and driest portion of the ranges for most of the species, notably *J. osteosperma* and *P. monophylla*, presents an opportunity for research, especially in the context of reduced water availability expected with climate change.

3.2. Historical stand dynamics, structure and responses to disturbance

Understanding the structure and stand dynamics of pinyon-juniper communities and their responses to disturbance and climate is foundational to anticipating responses to climate change and taking appropriate management actions. Weather and climate variation influence the structure and composition of pinyon-juniper communities by altering the timing of episodic high seed production years, establishment, and mortality rates (Betancourt et al., 1993). The North American Monsoon has a gradient of influence across the pinyon-juniper community; the southeastern edge of the range (New Mexico) receives a much higher proportion of total precipitation in summer precipitation compared to the northwestern part of the range (Nevada) (Romme et al., 2009). The distribution of dominant species exemplifies species-specific responses to this seasonal distribution of precipitation. The distribution of *P. edulis* is suggestive of a dependency on summer monsoon precipitation, in contrast to *J. osteosperma*, which occurs in areas with and without monsoon precipitation (West et al., 2007). The variable climate and disturbance regimes across pinyon-juniper communities creates similarly variable patterns of stand dynamics and structure.

We found hotspots and gaps in the coverage of studies on historical stand dynamics, structure, and responses to disturbance. Drought, fire, and insect related mortality are the dominant disturbances in pinyon-juniper communities (Romme et al., 2009). We found that research effort on these disturbance topics was split between drought and fire (101 and 96 studies, respectively), with a lower number of *Ips* beetle

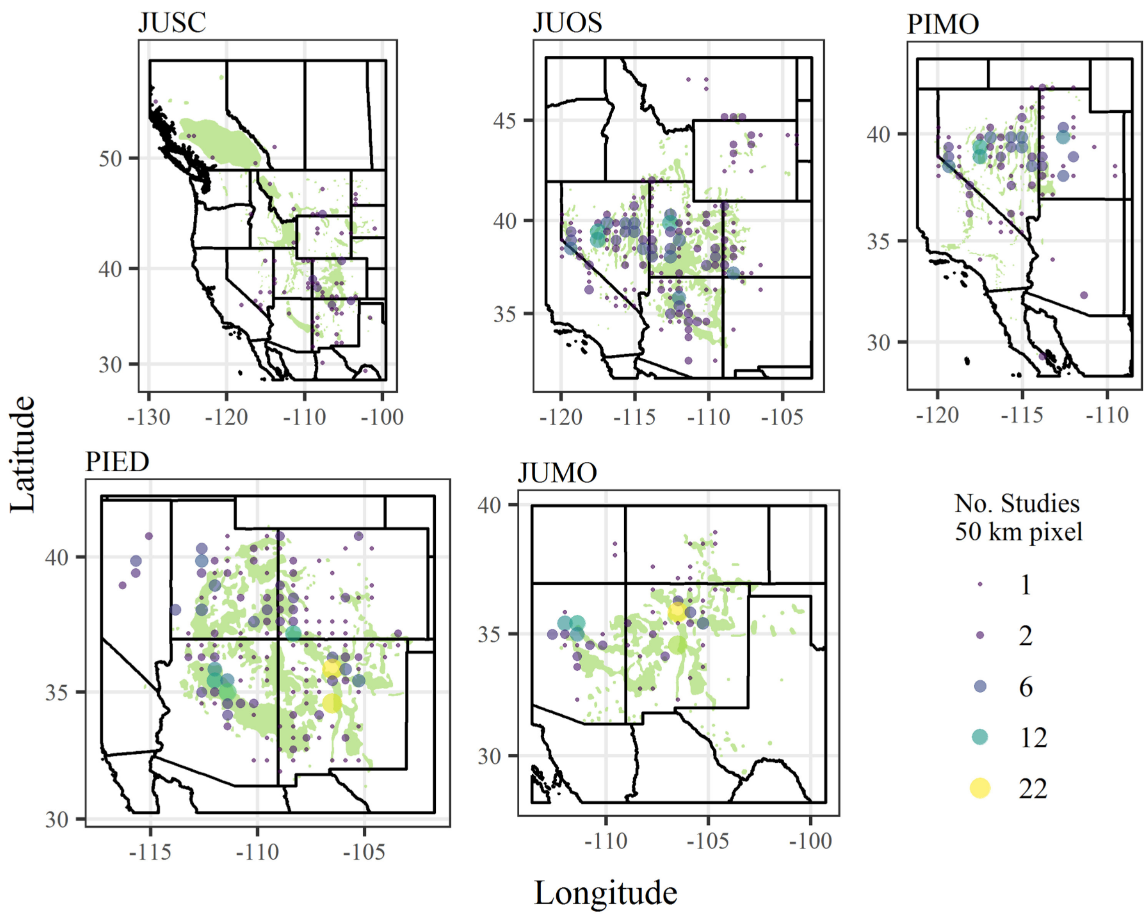

Fig. 1. The density of study locations reveals gaps and hotspots of research effort for each species. The range for each species as described by Little 1971 is displayed in green. Each point is a 50 km pixel where at least one study has occurred. The size of the point corresponds to the number of studies in that 50 km pixel. Species: JUMO = *Juniperus monosperma*, JUOS = *Juniperus osteosperma*, JUSC = *Juniperus scopulorum*, PIED = *Pinus edulis*, PIMO = *Pinus monophylla*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

related studies (30). All studies we found that examined the effects of beetle attacks also included information on drought mortality, supporting the tight association between drought and beetle infestation (Gaylord et al., 2013). In contrast to the abundance of research on disturbance, few studies examined how historical climate affects stand dynamics or structure (Fig. 3). This represents a large knowledge gap for land managers to evaluate if stands have altered density due to climatic causes, rather than anthropogenic causes such as overgrazing, fire suppression, or tree harvesting. Overall, we found that the literature reflected the importance of understanding the effects of drought, fire, and insect infestations on the five focal species, but an increased amount of research on the role of historical climate on stand dynamics or structure of pinyon-juniper communities is needed.

Fire was the dominant disturbance studied until the 2000s when a profound drought from 2002 to 2003, and subsequent mortality of *P. edulis*, spurred an increase in research effort for that species (Fig. 4B, Adams et al., 2009, Breshears et al. 2005, Floyd et al., 2009, Mueller et al., 2005, Shaw et al., 2005). Drought represented a third of studies with *P. edulis* and *J. monosperma* as the focal species, with most effort given to dynamic responses such as tree establishment, mortality or succession. Drought was a topic with a low proportion of studies for *P. monophylla*, *J. scopulorum* and *J. osteosperma* (Fig. 4A, Fig. 3), possibly because large scale drought related mortality events have not occurred. The relative lack of drought research for the other focal pinyon species, *P. monophylla,* leads to uncertainty regarding the effects of drought on the extensive pinyon-juniper communities where it is the dominant species. Although the overall effort toward understanding the effects of drought is large, the spatial distribution of these studies for each species does not span the species range. Drought studies for *J. scopulorum* are limited to Utah and southeastern Idaho. *P. monophylla* drought studies are lacking in California and the Sierra Nevada foothills of eastern Nevada. *J. monosperma* drought studies are lacking in the northeastern and central part of its range. The distribution of drought studies for *P. edulis* and *J. osteosperma* are similar but are fewer for *J. osteosperma* (Fig. 5). The spatial pattern in drought studies suggests that previous research may not accurately predict drought effects on pinyon-juniper communities in understudied areas such as in the northern parts of some species ranges and for the extensive pinyon-juniper communities dominated by *P. monophylla.*

Fire regimes and fire return intervals across pinyon-juniper communities are not uniform. Romme et al. (2009) delineated three categories of pinyon-juniper vegetation with different fire histories: pinyon-juniper savanna, wooded shrubland, and persistent woodland. The savanna vegetation type reflects systems in which frequent, low intensity fires occurred before modern suppression (Margolis, 2014). Fire frequency was historically more frequent in shrublands than persistent woodlands, resulting in a successional sequence from herbaceous to mixed herbaceous-shrub to tree dominance (Koniak, 1985). Persistent pinyon-juniper woodlands experience the lowest frequency of fire; when fire does occur, it is of medium to high intensity with some

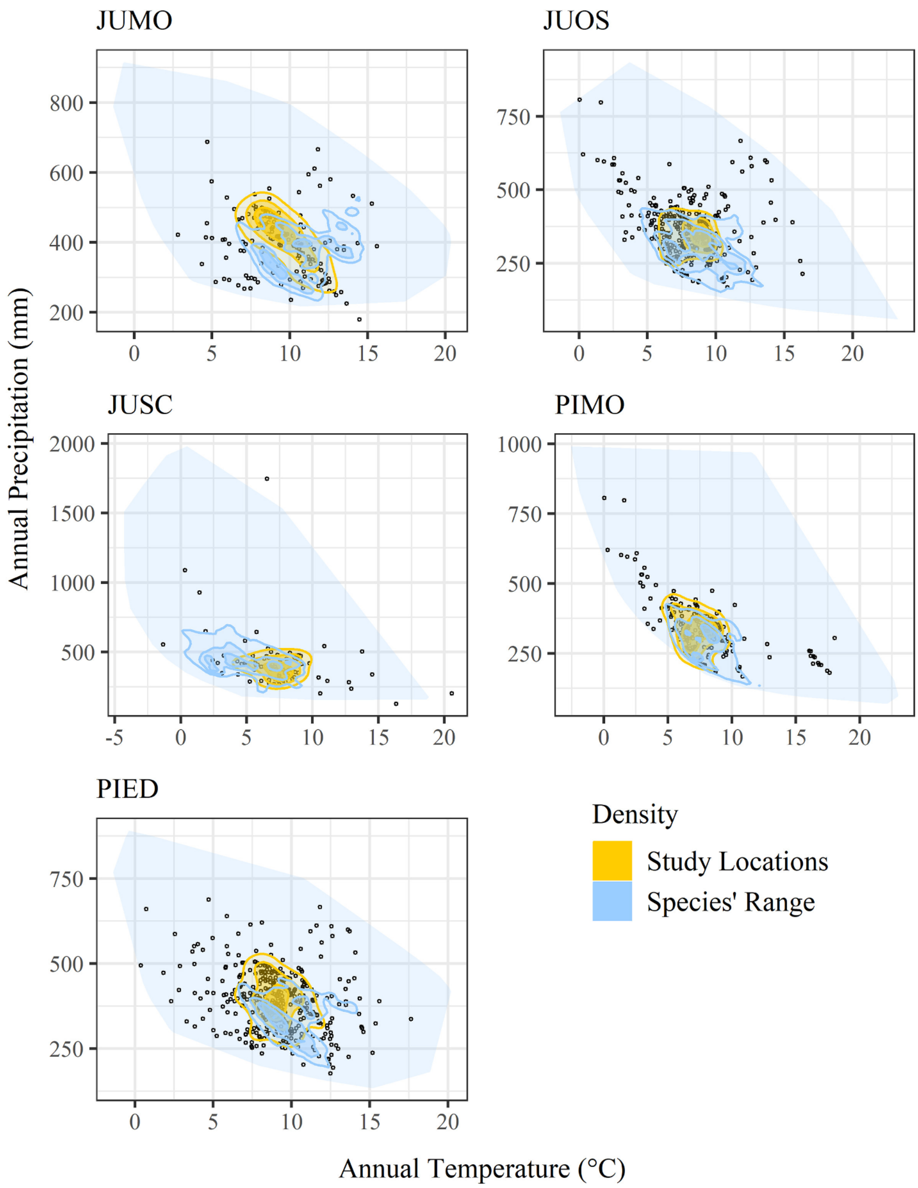

Fig. 2. Climate conditions for published studies by species, illustrating that the climate conditions in studied locations are typically not representative of climate across the entire range for each species. The density of the location climate is as described by Little 1971. Individual points represent the climate for individual studies. Blue contour lines represent increasing density of range location climate space. Yellow contours represent increasing density of study location climate space. The light blue shading represents the breadth of climate space for that species. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

torching depending on the environmental conditions present (Romme et al., 2009). In some stands, high intensity stand replacing fires repeating every 340 to 400 years or longer is common, with the frequency contingent upon site productivity and natural fire breaks (Baker and Shinneman, 2004; Floyd et al., 2004; Huffman et al., 2008). Recovery from wildfire can be slow, taking > 60 years for trees to become dominant again (Koniak, 1985); and this recovery can result in divergent successional trajectories. In a fire chronosequence study in northern Arizona, approximately half of the oldest stands exhibited no regeneration of pinyon even hundreds of years post fire, instead becoming nearly pure juniper stands (Huffman et al., 2012). Although *J. monosperma* had the lowest proportion of fire studies relative to the other five focal species, past research has found that juniper is generally more resistant (lower mortality) and resilient (faster post-fire recruitment) to fire than pinyon (Tausch and West, 1988). Unfortunately, the studies including wildfire are not necessarily evenly distributed across species ranges. For instance, *P. monophylla* studies with wildfire are lacking for California and there are few wildfire studies for *J. osteosperma* and *P. edulis* in the central Colorado Plateau (Fig. 5). Inferences on fire effects, and the interaction of fire and succession are currently limited to the areas where studies have been conducted but could be expanded to encompass more variability in the ranges of these species as fire becomes more pervasive across the western United States due to warming temperatures and earlier spring snowmelt (Westerling et al., 2006).

Successional patterns after disturbance generally result in an initial dominance of juniper followed by an increase in pinyon, and in *P. monophylla* stands this often results in eventual dominance by pinyon (Blackburn and Tueller, 1970a). These successional patterns may be associated with facilitative effects of “nurse plants” on the survival of pinyon seedlings and saplings, which are often observed to be spatially associated with woody canopies, leading to many anecdotal references to facilitation. One quantitative assessment across sites in northern Arizona found significantly greater pinyon seedling and sapling survival beneath established woody canopies, with the effect increasing in soils with greater available water holding capacity (Redmond et al., 2015). In a broader-scale analysis across the Colorado Plateau, Redmond et al. (2018) found no consistent effects of shrub cover on pinyon or juniper

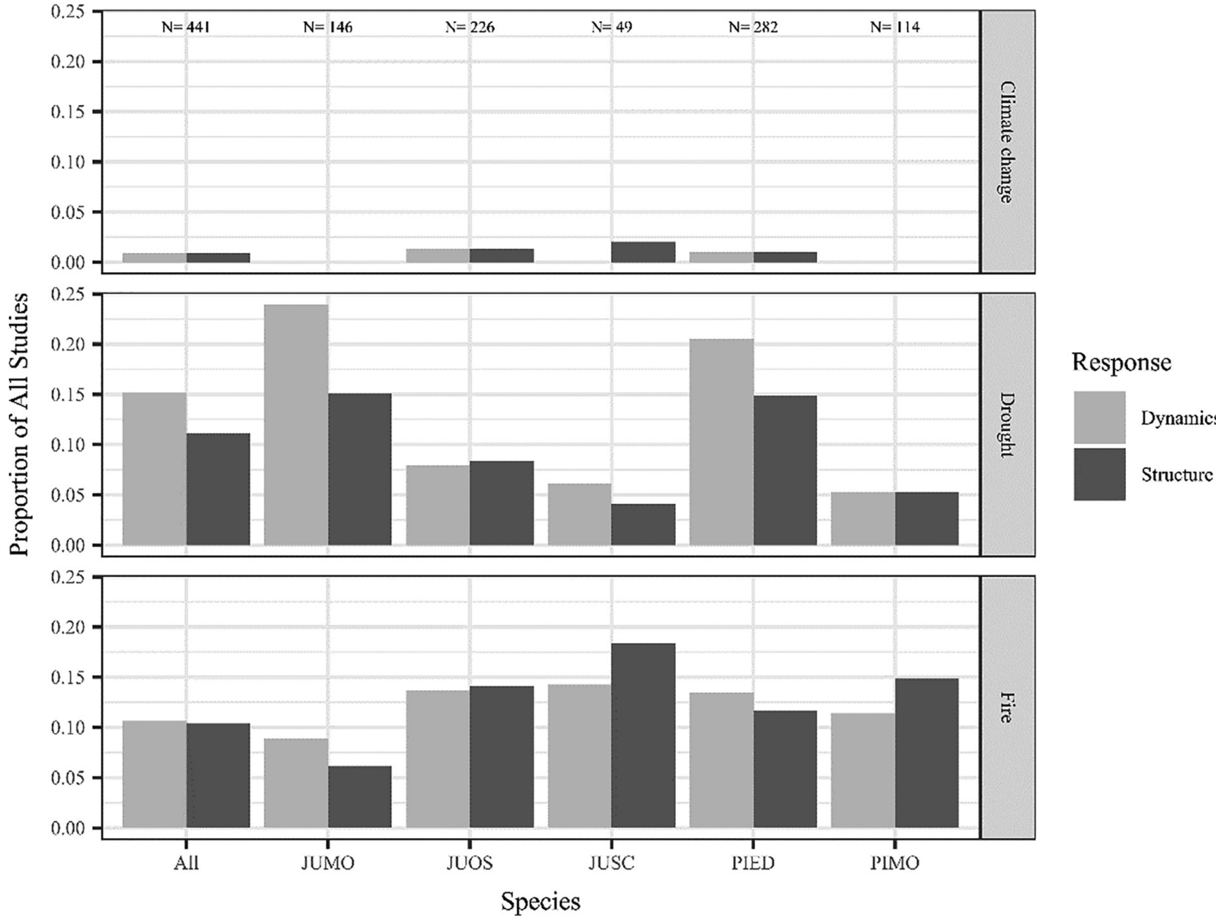

Fig. 3. The proportion of studies which focused on aspects of stand structure (tree age, tree density or tree size) or stand dynamics (tree establishment, mortality or succession) in response to either historical climate change, drought or fire illustrates that few studies examined stand dynamics or stand structure in combination with historical climate variation, and a higher proportion of studies evaluated stand dynamics with drought.

regeneration, however grass cover consistently suppressed tree regeneration. In general, a greater understanding of the endogenous (e.g. biotic interactions) and exogenous (e.g. climate, soils) drivers of pinyon-juniper recruitment are needed.

Stand structure of pinyon-juniper communities varies as a function of environmental characteristics and time since disturbance. Within the 42% of studies that focused on disturbance, 100 (54%) examined stand dynamics (tree establishment, mortality or succession), and 87 (47%) examined stand structure (tree density, age or size). The spatial distribution of stand dynamics or structure studies are relatively well distributed across the distributional range for each species, except for most of the range for *J. scopulorum* and northwestern New Mexico for *J. monosperma* (Appendix F, Geographic Distribution of Studies with Stand Dynamics or Structure). In general, the composition of juniper and pinyon species is related to elevation: the relative abundance of juniper tends to decrease with increasing elevation, and that of pinyon to increase (Tausch et al., 1981). Age structure can be somewhat variable and inconsistently distributed among juniper stands, whereas pinyon tends to show more consistent, unimodal age distributions, suggesting sporadic juniper recruitment alongside more consistent pinyon recruitment (Huffman et al., 2012; Tausch and West, 1988).

3.3. Management actions and responses

Increasing densities of pinyon-juniper communities have prompted widespread management actions. Increasing tree density in existing pinyon-juniper communities and invasion into shrub and grass dominated areas have led to extensive thinning and removal of pinyon-juniper stands (Redmond et al., 2013). We found a correspondingly large amount of research on tree removal across all species, as this topic had the highest proportion of studies for any land management activity (Fig. 4C). Dense, persistent pinyon-juniper woodlands have sparse understories which lack adequate forage for livestock and game animals and has motivated treatments designed to remove overstory woody vegetation to increase grass and forb cover (for example, Stephens et al., 2016). Tree removal is also utilized for fuel reduction to reduce the risk of stand replacing fires and threats to property (Huffman et al., 2009, Redmond et al., 2014). While the objectives of management actions are clear, the factors driving increasing density and encroachment are less certain and are often assumed to be caused by fire suppression and overgrazing leading to unnaturally dense woodlands (e.g. Blackburn and Tueller, 1970b; Baker and Shinneman, 2004; Margolis, 2014). Yet other factors have also led to increasing tree density, including cool and wet climate conditions in the early 20th century (Shinneman et al., 2008; Barger et al., 2009), recovery following disturbances, including extensive woodcutting that occurred in the 19th century by homesteaders (Evans, 1988), and to provide charcoal for mining operations (Bahre and Hutchinson, 1985; Ko et al., 2011; Morris and Rowe, 2014). Resolving the drivers of infilling and encroachment is an important step to addressing appropriate management responses,

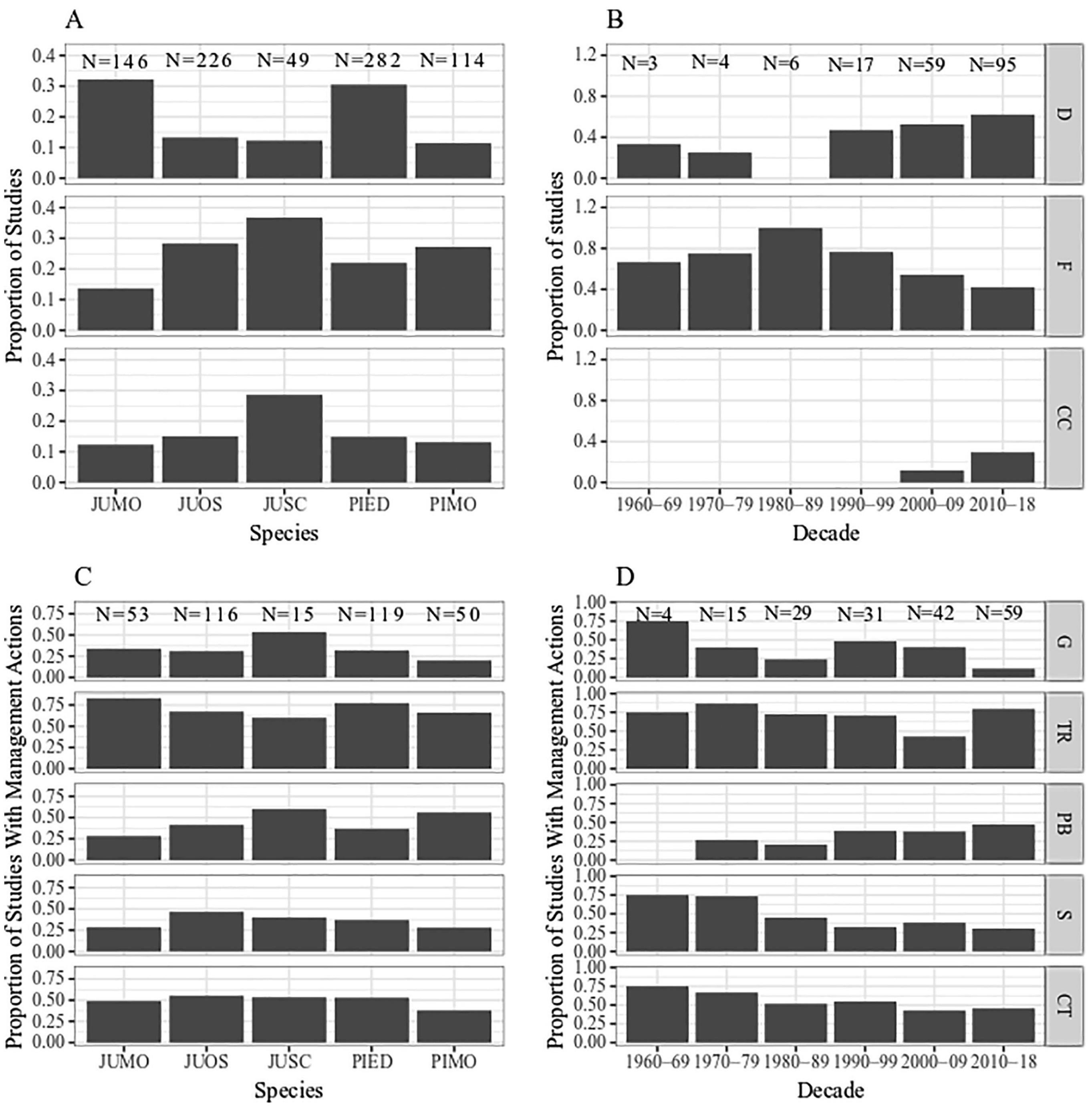

Fig. 4. Proportions of study focus by species and by decade. Abbreviations: D = drought, F = wildfire, CC = anthropogenic climate change, G = grazing, TR = tree removal, PB = prescribed burn, S = seeding, CT = combined treatments. Proportions of studies across species are not exclusive, leading to a sum of proportions > 100%. A) The proportion of studies focused on drought, wildfire, or anthropogenic climate change varied for each species. B) The proportion of studies on drought and anthropogenic climate change are increasing while the proportion of studies focused on wildfire are decreasing. C) The proportion of studies with a treatment illustrates tree removal is the highest for all species. D) The proportion of studies with actions illustrates that grazing or seeding treatments have decreased while prescribed burning treatments have increased.

such as changes in grazing practices or the use of prescribed fire.

The geographic distribution of studies with a focus on understanding management actions differ for each species, and significant gaps remain. Relatively little information is available regarding land management treatments that occurred across the range of *J. scopulorum*. The available information is limited to the southeastern portion of its range and only addresses prescribed burning in the extreme south and seeding of preferred species with combined treatments in western Colorado (Fig. 6). Treatment information for *J. osteosperma* is relatively even except for a lack of studies the northeastern portion of its range. Tree removal studies dominate the central New Mexico and Arizona range of *J. monosperma*, but information on treatments is lacking for

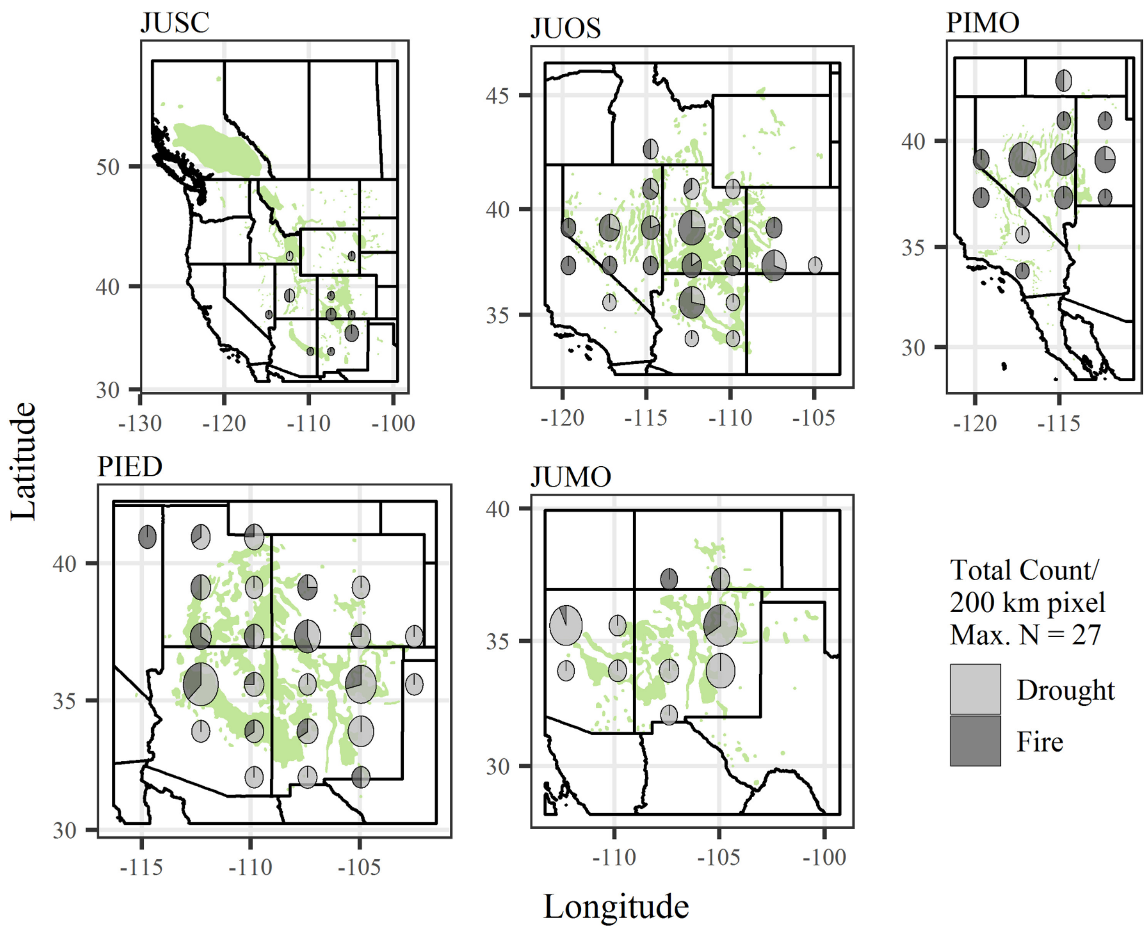

Fig. 5. Geographic density of published studies by species, illustrating that studies are lacking over much of the range for *J. scopulorum*, while other species have more coverage but have a bias toward either drought or fire across their range. The green shading denotes the range map for each species as described by Little 1971. Larger pie sizes indicate a greater number of studies per 200 km pixel. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

most of its Texas distribution. Treatment types are well distributed for *P. edulis*, though are lacking in the southeastern Colorado Plateau. As with other study categories for *P. monophylla*, research is lacking in the southwestern portion of its range and a large proportion of studies in central Nevada have focused on prescribed burning treatments. (Fig. 6).

Studies focused on understanding land management actions in pinyon-juniper communities have largely focused on tree removal. Over half of the studies addressing land management actions included a tree removal treatment (125 studies, 69%). Tree removal was often coupled with seeding of preferred species, which were used in 39% of studies (71 studies) and prescribed burning was included in 36% of the studies (66 studies). Tree removal was first implemented in the 1950s based on perceptions that pinyon and juniper were expanding due to overgrazing and fire suppression (Aldon et al., 1994). However, the goals of these treatments have diversified from historically creating forage for livestock and big game, to more recently increasing species richness (Fornwalt et al., 2017), improving wildlife habitat (Bates et al., 2017), improving hydrologic function (Wilcox et al., 2003), and reducing fire risk (Hunter et al., 2011). Our results demonstrate that the pattern of research effort across time has mirrored these changing goals. Studies examining grazing have declined in proportion over time, studies on prescribed burning have increased in recent decades, and the proportion of studies that included tree removal treatments have remained a consistently high proportion of total studies, except for a dip in the 2000s (Fig. 4D). Only about a third of studies that described treatments (31%, 56 studies) incorporated grazing as a treatment. This amount of research effort does not seem representative of the amount of grazing across pinyon-juniper communities as grazing remains a common practice in pinyon-juniper communities (Morris and Rowe, 2014), and treatments to reduce tree cover are focused in part on increasing the amount of forage for grazing. Studies seeking to evaluate the long history of grazing in pinyon-juniper communities has confined studies of grazing control treatments to remote mesas that pre-date periods of intensive livestock utilization (Barger et al., 2009). Despite this limitation, we found that some studies inferred pre-grazing pinyon-juniper communities from packrat midden samples (Cole et al., 1997), and few restricted grazing from the site to evaluate short term grazing exclusion (Orourke and Ogden, 1969).

Both prescribed fire and mechanical treatments are common management methods for removing trees from pinyon-juniper communities. Redmond et al. (2014) estimate that \$26.7 million has been spent on pinyon-juniper treatments across 2470 km^2 of Bureau of Land Management lands from 1950 to 2003 on the Colorado Plateau alone. Mechanical treatments include chaining, bulldozing, cabling, herbicide, hydro-axe thinning, and rollerchopping, and have shifted through time to reduce soil disturbance and maximize recovery of desirable vegetation (Redmond et al., 2014). Romme et al. (2002) and others (Floyd et al., 2008, 2015, 2017) argue that persistent pinyon-juniper forests historically experienced very infrequent, stand-replacing fires and the fire regime of a stand should be evaluated before applying prescribed fire treatments. Limited studies on fire in some regions and for some species, as stated above, may be constraining the appropriate use of prescribed fire. Some studies have documented differences in treatment effects, including higher abundances of non-native species and lower

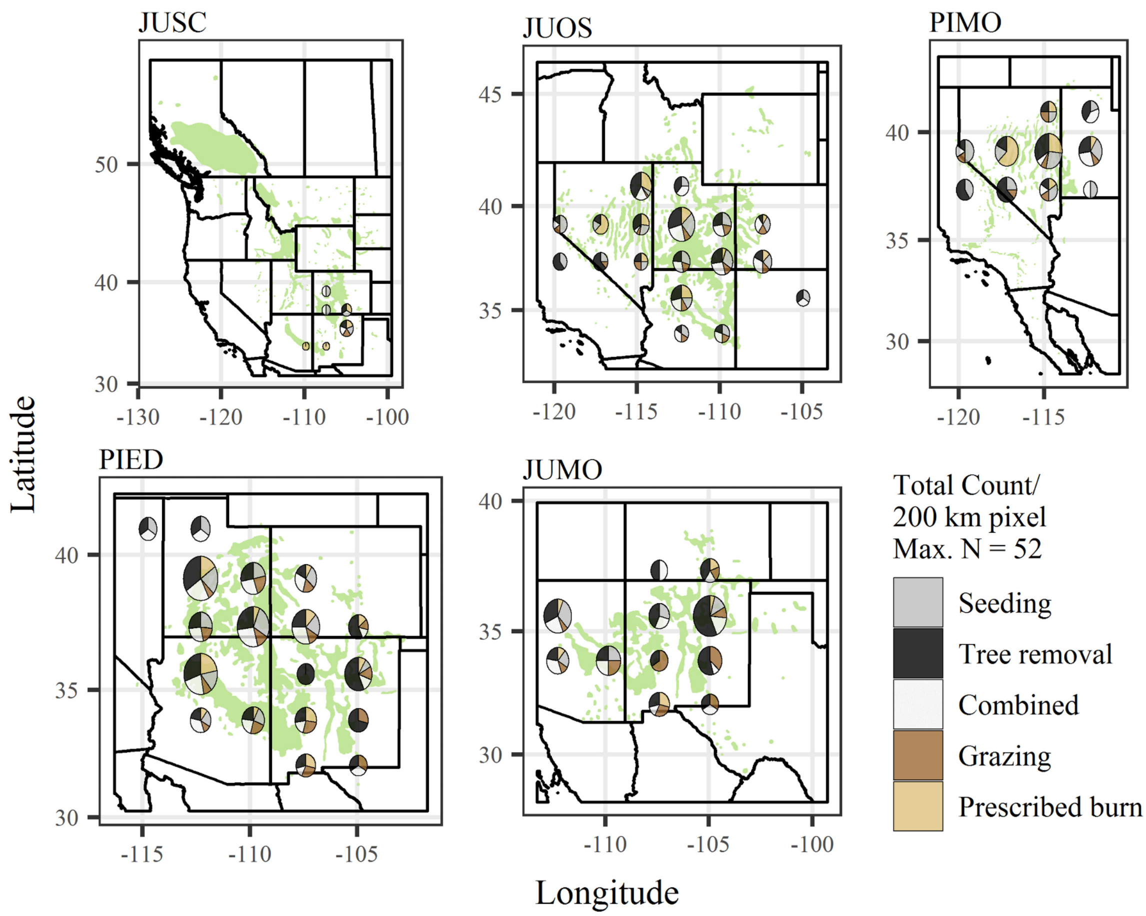

Fig. 6. The proportion of management actions (combined, prescribed burn, seeding, tree removal or grazing) within each 200 km pixel, illustrating areas with few or no studies across the management actions evaluated. Larger pie charts denote regions of greater research effort. Green shading denotes the range for each species as described by Little 1971. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

abundances of native grasses in burn compared to mechanical thinning treatments (Floyd et al., 2006; Williams et al., 2017). Juniper tends to have higher survival rate and increase more rapidly than pinyon following both fire and mechanical treatments (Bristow et al., 2014; Vanpelt et al., 1990; Wood et al., 2012), though in certain cases neither species recovered (Hessing et al., 1982). Studies have increasingly focused on the effects of removing woody biomass on carbon and nutrient cycling (Rau et al., 2009).

We found that studies with management actions had consistently short timescales for evaluating post-treatment effects and were not representative of the possible spatial or temporal extent of responses to management actions. The timespan in years for treatment length and measurement length (before and after treatment) was calculated from 131 studies that provided time of treatment and measurement information. Most studies with management actions measured treatments applied within a one-year period and measured the post-treatment effects for one year (Fig. 7, Appendix G). Only 10 studies measured treatment effects for > 20 years; these studies often compared relict sites (e.g. mesa tops with grazing exclusion) to historically grazed lands (Barger et al., 2009), modeled long-term fuelwood harvesting (Samuels and Betancourt, 1982), observed succession after wildfire and subsequent seeding (Koniak, 1985), and reviewed land treatments across the Colorado Plateau (Redmond et al., 2014b). Although short term studies capture the immediate and near-term impacts of management actions, they are not able to capture long-term community dynamics in response to management actions such as long-term regeneration responses to drought (Redmond et al., 2015). More long-term studies are needed to fully address community and population dynamics of the long-lived tree species which dominate pinyon-juniper communities.

In almost all studies, tree removal resulted in increased understory plant abundance, production, and diversity due to reduced competition for resources (Clary, 1989; Everett and Sharrow, 1985; Huffman et al., 2017). This compensatory effect can be boosted by seeding herbaceous species following tree removal. Seeding trials have revealed differential success of understory species, and various effectiveness of complementary treatments to increase seedling germination (mulching, chipping, spreading woody biomass, furrowing, Lavin et al., 1981, Johnsen and Gomm, 1981). Grass species can suppress tree regeneration and reduce the spread of invasive species (Vanpelt et al., 1990), though many non-native grass species used in seed mixes may persist over the long-term (Redmond et al., 2013).

The effects of tree removal on overstory structure, and seeding on understory composition, are largely dependent on the ecohydrological conditions where the treatment occurred, and whether these conditions support the growth of deep- or shallow-rooted species (Chambers et al., 2014; Urza et al., 2017). Across all species and management action studies, very few studies (15, 8%) measured tree ages either before or after tree removal. Understory cover (shrub, grass, herbaceous, rock, etc.) was the most measured, followed by soil characteristics and tree density (Fig. 7A). These measurements reflect the widely stated motivation by managers to increase understory cover, reduce tree cover, and improve soil characteristics such as infiltration. Although most of these studies did not consider how the hydrological conditions of the treated site supported a balance between woody plants and grasses, this context is increasingly relevant to determine whether treatments will be effective over the long-term. Adopting an ecohydrological perspective

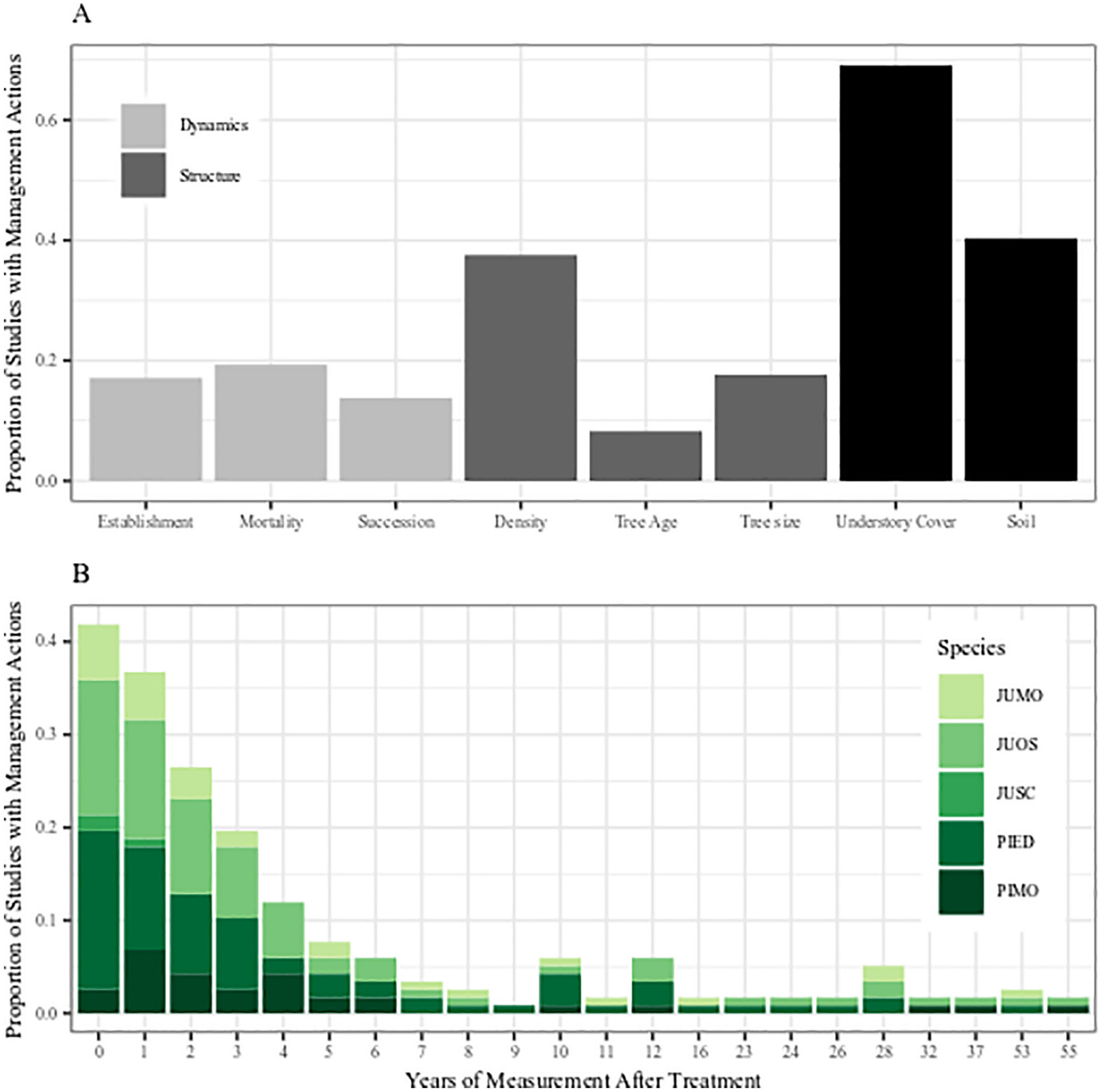

Fig. 7. A) The proportion of focal measurement topics of studies with treatments illustrate that most studies measured understory cover, with little focus on tree age. Light grey bars denote measurement topics pertaining to dynamics, and dark grey bars denote measurement topics pertaining to stand structure. The black bars denote neither a structure or dynamic measurement topic but were commonly measured in the studies reviewed. B) The length of measurement for studies with treatments for each species in years, illustrating that most studies with treatments had one year of measurement after treatment.

can also help resolve the long-running debate on whether pinyon-juniper is encroaching on grasslands and shrublands, or is a potential climax community, across its distribution (Aldon et al., 1994).

3.4. Pinyon-juniper responses to climate change

Much of the range of pinyon-juniper communities may be impacted by increasing aridity associated with climate change. Pinyon-juniper communities exist at the intersection of dry forests, grasslands, and shrublands, representing some of the most abundant communities between broad vegetation types in North America. Ecotones in pinyon-juniper communities have been noted to shift before the core of a species range and can provide insight on responses to climate change; a 2 km replacement of ponderosa pine with pinyon-juniper over the course of < 5 years has been documented (Allen and Breshears, 1998). Increasing aridity has also been recognized as a factor for widespread *P. edulis* mortality. With increasing temperatures and aridity, there have been largescale die-offs of *P. edulis* in the Southwestern United States in the 1990s and 2000s (Meddens et al., 2015). The effects of drought on the physiology and mortality of *P. edulis* is the most studied of any tree species (Breshears et al., 2018). The abundance of paleoecology studies in pinyon-juniper communities illustrates how species responded to historical climate variability and may inform predictions of species' range shifts under anthropogenic climate change (Weppner et al., 2013).

Anticipating potential shifts in the geographic distribution of species is a critical contemporary knowledge gap for informing resource management and targeting future research (Bradford et al., 2018). However, compared to other topics, relatively few studies have included information on paleo, current, or future distribution of pinyon-juniper species; within the total number of studies for each species, the topic with the lowest proportion of studies was anthropogenic climate change (Fig. 4A). Among distribution studies, future distribution was the least studied type across all species (Fig. 8). Only 4% (18) of the 441

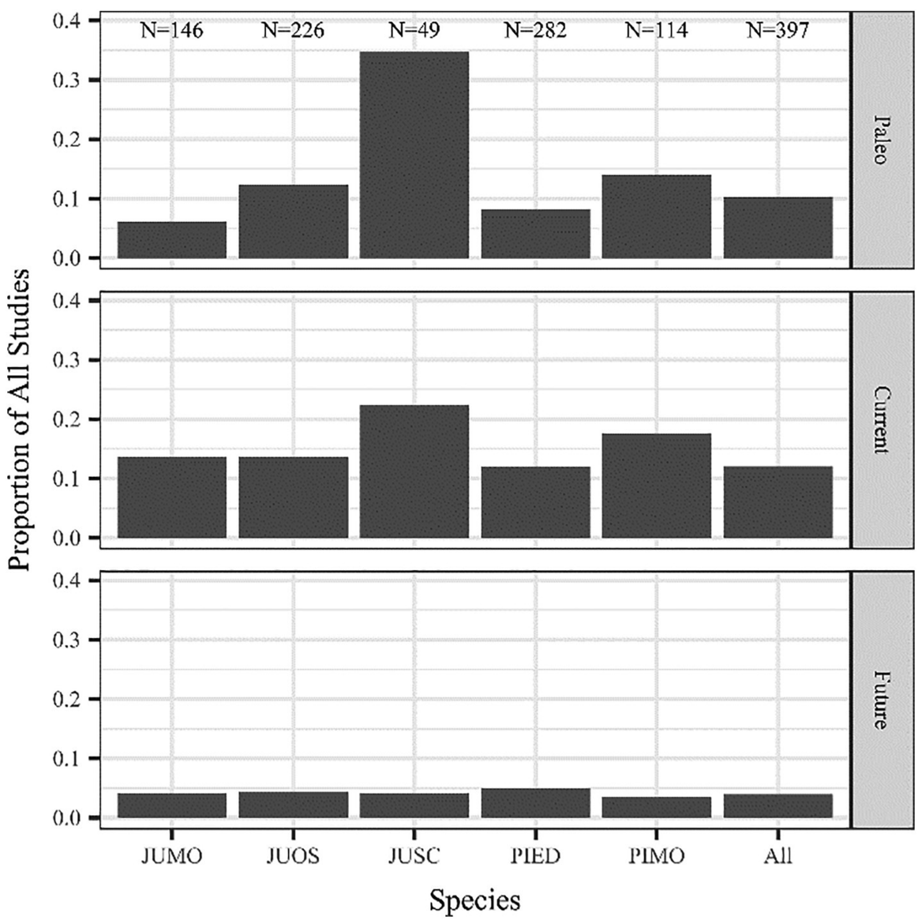

Fig. 8. Proportion of studies that examine geographic distribution of pinyon-juniper in response to climate, illustrating that only a small proportion of all studies have examined future distribution. JUMO = *Juniperus monosperma*, JUOS = *Juniperus osteosperma*, JUSC = *Juniperus scopulorum*, PIED = *Pinus edulis*, PIMO = *Pinus monophylla*, All = all pinyon-juniper species in this study.

included papers had future distribution information. Of those 18 papers, half (9 studies) included information with anthropogenic climate change (five modeling, 2 reviews and 2 experiments.)

Evaluating how the distribution of species responded to past climate shifts over millennial time scales can provide useful insights into future climate impacts. For all species except *J. scopulorum*, many paleoecology studies are concentrated at the periphery of the species' ranges and often outside of the current distribution (Appendix H). Few paleoecology studies (relative to the total number of studies) provide information on *P. edulis*, and none occur in the western edge of the species range. While paleoecology studies for *P. monophylla* are relatively abundant in the southeastern part of the range, including outside of the modern range, fewer address the core of the modern range and none occur in the southwestern edge of the range. Paleoecology studies are better represented compared to other topics for *J. scopulorum* but are lacking in parts of central Utah and eastern Colorado (Appendix H). While paleoecological reconstructions have suggested that long-term fluctuations in precipitation can alter the relative abundance of pinyon and juniper (Breshears et al., 2005a; Cole et al., 2013; Gray et al., 2006), relatively few studies have attempted to assess how climatic changes in the 21st century may impact pinyon-juniper distributions with a general focus on *P. edulis* (Adams et al., 2009; Adams, 2007; Roberts and Hamann, 2016; Rocca et al., 2014). Despite the relatively limited number of studies examining climate impacts, the available results suggest that the future distributions of our focal pinyon-juniper species are likely to shift in response to climate change. Pinyon-juniper communities respond to cycles of cool-wet years resulting in regeneration and range expansion, and dry years with resulting mortality (Barger et al., 2009). Expansion and shrinking events are increasingly recognized as a response to changing climate in which the leading edge of pinyon-juniper communities' geographic distribution may move northward and recede on the trailing southern edge (Powell et al., 2013). The underlying processes may be more influenced by extreme weather events such as drought, and management has the potential to influence the rates and locations of these shifts.

Much of the research on pinyon-juniper response to climate change is associated with observations of the impacts of drought on the component species, such as mortality patterns and physiological responses. Both pinyon pine species are considered isohydric, such that they maintain leaf water potential by reducing stomatal conductance in response to drying soils (Williams and Ehleringer, 2000). This strategy avoids severe embolisms and associated hydraulic failure, but also decreases rates of leaf gas exchange and photosynthesis, potentially leading to long-term carbon deficits. In contrast, co-occurring juniper species are considered anisohydric, such that they maintain stomatal conductance and thus sustain gas exchange and photosynthesis but allow leaf water potential to decline and potentially risk embolisms and hydraulic failure under extreme vapor pressure deficits (Voelker et al., 2018). High mortality of *P. edulis* in response to drought and subsequent *Ips* beetle outbreaks is well documented (Breshears et al., 2005b5, Gaylord et al., 2013, Meddens et al., 2015). Related experiments have indicated that higher temperatures exacerbate the risk of mortality in *P. edulis* (Adams et al., 2009), specifically by shortening the length of drought necessary to cause mortality and implying that the frequency of mortality-inducing drought events will increase along with rising temperatures expected in coming decades (Adams et al., 2017). Across soil types in sites where *J. monosperma* and *J. osteosperma* co-occurred with *P. edulis*, drought conditions led to widespread mortality of the pinyon species and $<$ 1% mortality for the juniper species. Lower mortality for co-occurring *J. monosperma* with *P. edulis* with drought has also been observed in other studies (Mueller et al., 2005; Plaut et al., 2012). While drought-induced mortality of *J. monosperma* may be less common, it can also occur (Bowker et al., 2012). Juniper mortality could indirectly affect *P. edulis* recruitment by limiting the availability of favorable microsites under juniper trees, which tend to promote *P. edulis* establishment (Redmond et al., 2018). In contrast to the focus on drought impacts on *P. edulis*, there is little information available on drought mortality for *P. monophylla*. The available evidence suggests that *P. monophylla* may be more vulnerable to drought in sites with higher density and lower elevation, drier sites (Flake and Weisberg, 2019, Greenwood and Weisberg, 2008), though relatively low mortality rates in response to drought have also been observed (Biondi and Bradley, 2013).

Among studies directly addressing the impacts of climate change on species distributions, most have focused on drought and *P. edulis*. Higher frequency droughts that may occur with climate change are expected to interact with bark beetle outbreaks to lead to increasing mortality for *P. edulis* (Adams et al., 2009, Adams et al., 2017, Williams et al., 2010). Modeling studies also suggest that *P. edulis* may be vulnerable to drought die-offs in core areas of suitable habitat for the species, not just on the edges of the species range (Lloret and Kitzberger, 2018). Simulation scenarios for smaller areas (national forest units) suggest that management and/or fire will interact with climate change to affect the abundance of *P. edulis* and *J. monosperma* and/or *J. osteosperma* (Flatley and Fulé 2016, Loehman et al., 2018, Shive et al., 2014).

Paleoecology records for pinyon-juniper communities suggest that the vegetation type has shifted dramatically in response to past climate fluctuations (Coats et al., 2008, Jackson et al., 2002, Lyford et al., 2003). The paleoecological record for both *P. edulis* and *P. monophylla* suggests that precipitation seasonality has a strong effect on their respective distributions and migration rates are not likely to keep up with the expected rates of future climate warming if precipitation patterns change significantly in the near future (Cole et al., 2013), though long-distance dispersal range extensions by both pinyon and juniper species have occurred (Betancourt et al., 1991; Jackson et al., 2002; Lyford et al., 2003). Generally, the abundance of paleoecological information for pinyon-juniper communities suggests that these data are a potentially valuable resource for understanding responses of the component species to anthropogenic climate change.

Studies including information on anthropogenic climate change represented only 8% of included studies yet are increasing over time. These studies began in the 2000s and have increased in the present decade (Fig. 4B). The response of species to past climate can be a good predictor for responses to future climate (Swetnam et al., 1999). Overall, the paleorecord for pinyon-juniper communities is relatively robust, but it isn't necessarily integrated with future climate response studies. Leveraging the known variability of past climates for predicting future possible range shifts under the uncertainty of future climate would be one way to integrate the two types of studies.

4. Conclusion

This synthesis identifies gaps and hotspots in knowledge on pinyon-juniper communities. We compiled the available literature on five focal species dominant in the core of these communities. We did not include information on *J. occidentalis*, *J. virginiana* or Madrean pinyon-juniper communities. While our research review was restricted to pinyon-juniper communities as defined by the five focal species, research on other species may provide some insight to address the research gaps we identified. For example, there has been research conducted on thinning of *J. occidentalis* (Bates et al., 2005, Bates et al., 2011, Davies and Bates, 2019), but it is unclear how applicable these studies are to communities with a pinyon component due to differences in composition between these ranges even if there are physiological and management similarities.

We identified gaps in the state of knowledge for pinyon-juniper communities. Noteworthy gaps include a more restricted spatial and climatic range of studies relative to the inhabited range for each species, a lack of long-term studies to evaluate responses to management actions, and a missed opportunity to leverage paleoecology research to understand future range shifts. We found a need for more studies in the hottest and driest portions of the range for most species, especially in the context of increasing aridity due to climate change. Under an increasingly arid climate, responses at the warmest and driest portion of a species range can provide insight for responses to aridity in other portions of the range. We found that most studies evaluated responses to management actions for 1 year, and a small subset of studies evaluated responses for > 20 years, which limits the ability to predict long-term community responses and provide recommendations for management actions. The relatively robust amount of paleoecology research has potential to provide insight about future distribution for these species because past responses to a changing climate can be indicative of possible future responses. This application could help address the low proportion of studies focused on anthropogenic climate change, although these studies are increasingly common. Addressing these gaps can improve the ability to manage pinyon-juniper communities under an increasingly arid climate future.

We identified some areas with a rich history of research, including an overwhelming majority of drought research focused on *P. edulis*, and geographic research hotspots around Mesa Verde National Park in southwestern Colorado, the San Francisco Volcanic field in northern Arizona, Los Alamos National Laboratory, and Sevilleta National Wildlife Refuge in central and northern New Mexico. These hotspots are likely associated with proximity to universities (i.e. Northern Arizona University & University of New Mexico) and locations with widespread drought mortality of *P. edulis.* Similar patterns of high study density near research institutions is likely for other forest types and/or research questions.

Despite the large amount of research on pinyon-juniper communities, our review suggests that important geographic and topical gaps in the literature remain. The lack of research in certain geographic areas, topics, and species is particularly challenging given the potential variability in species response to land management and climate change across the multitude of landscapes where these communities occur. There are a limited number of grazing studies, which was surprising considering that grazing is a widespread land use in pinyon-juniper communities. Understanding the impacts of climate change and management, such as thinning and grazing, may require research at the edges of the species geographic and climate distribution because the leading edge may show effects of a changing climate before the core of a species distribution. Similarly, differences in dominant species physiology suggest that species-specific research, as opposed to assuming similar responses among co-occurring species or similar species in the same genus, is warranted due to variation in responses to past climate changes. Overall, the knowledge base on pinyon-juniper communities is a rich source for understanding the historical, current, and future patterns of this community in the western United States. Remaining knowledge gaps identified by our synthesis can help direct future research.

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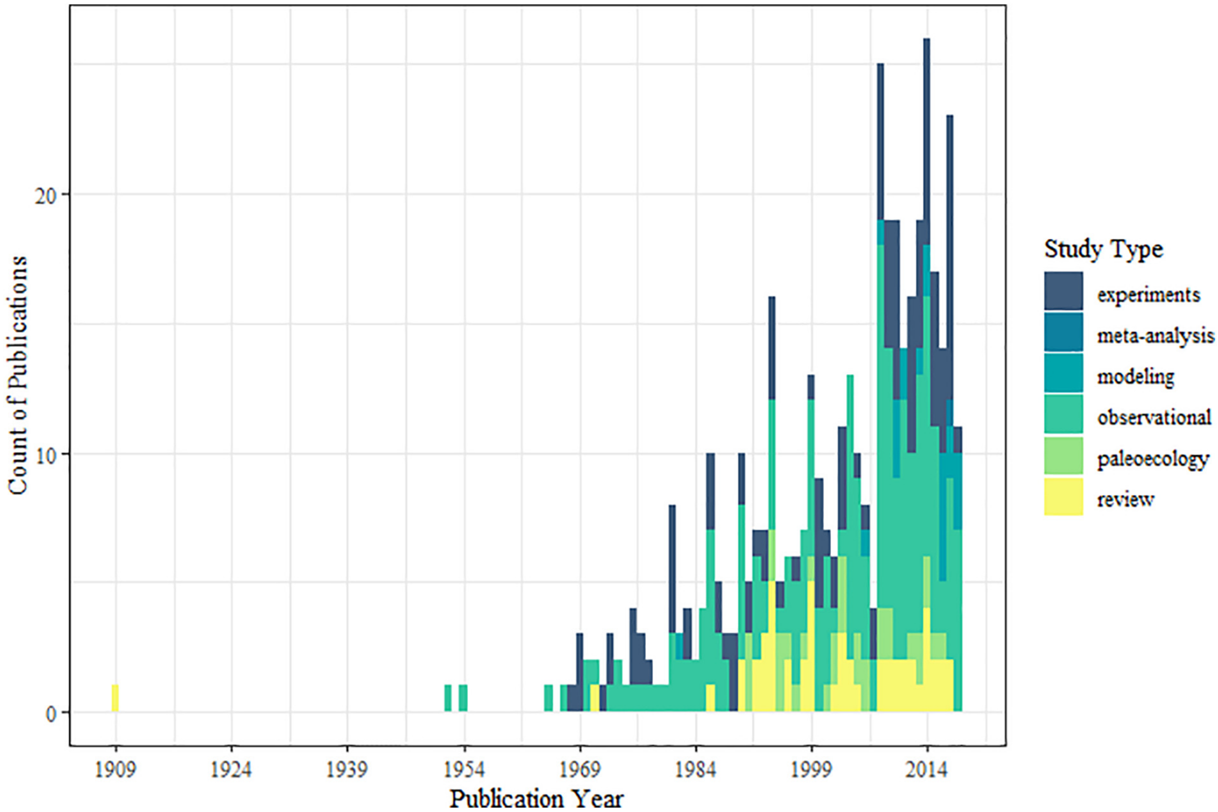
Appendices

Appendix A. Counts of excluded studies

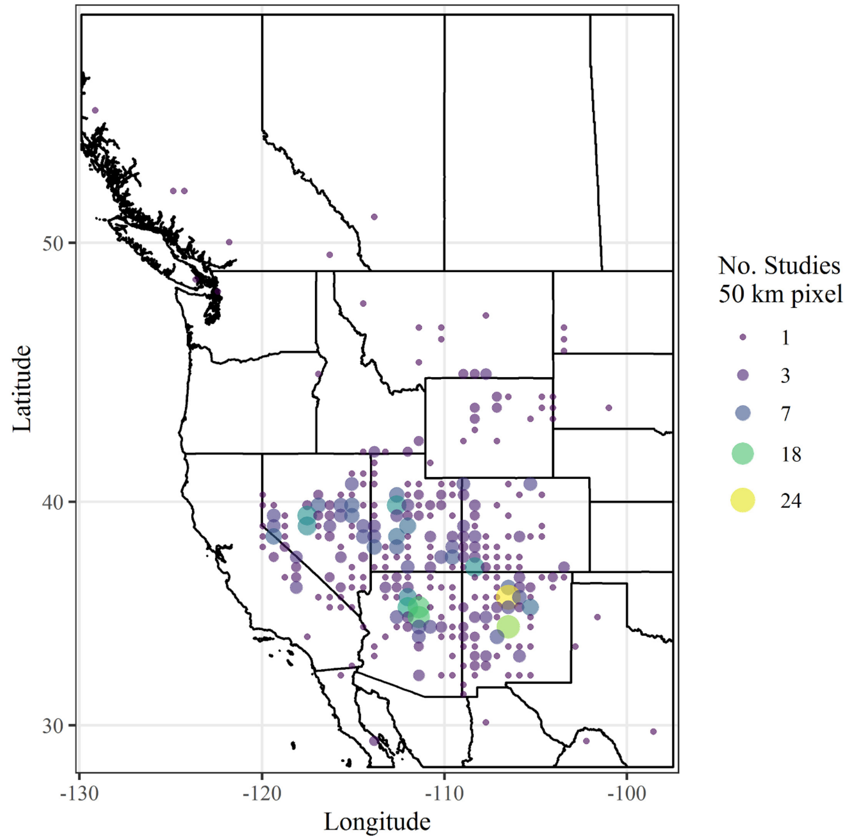
Reason for exclusion	Count
Biofuel	5
Book	20
Book review	1
Genetics	23
Habitat/interacting species	340
Landscape uses/cultivars	6
Meeting abstract	5
Methods	65
Mistletoe	2
Opinion piece	1
Pathogens	9
Pests	45
Physiology/traits	197
Social	40
Treatment effects on habitat/interacting species	58
Total	817

Appendix B. Counts of studies through time



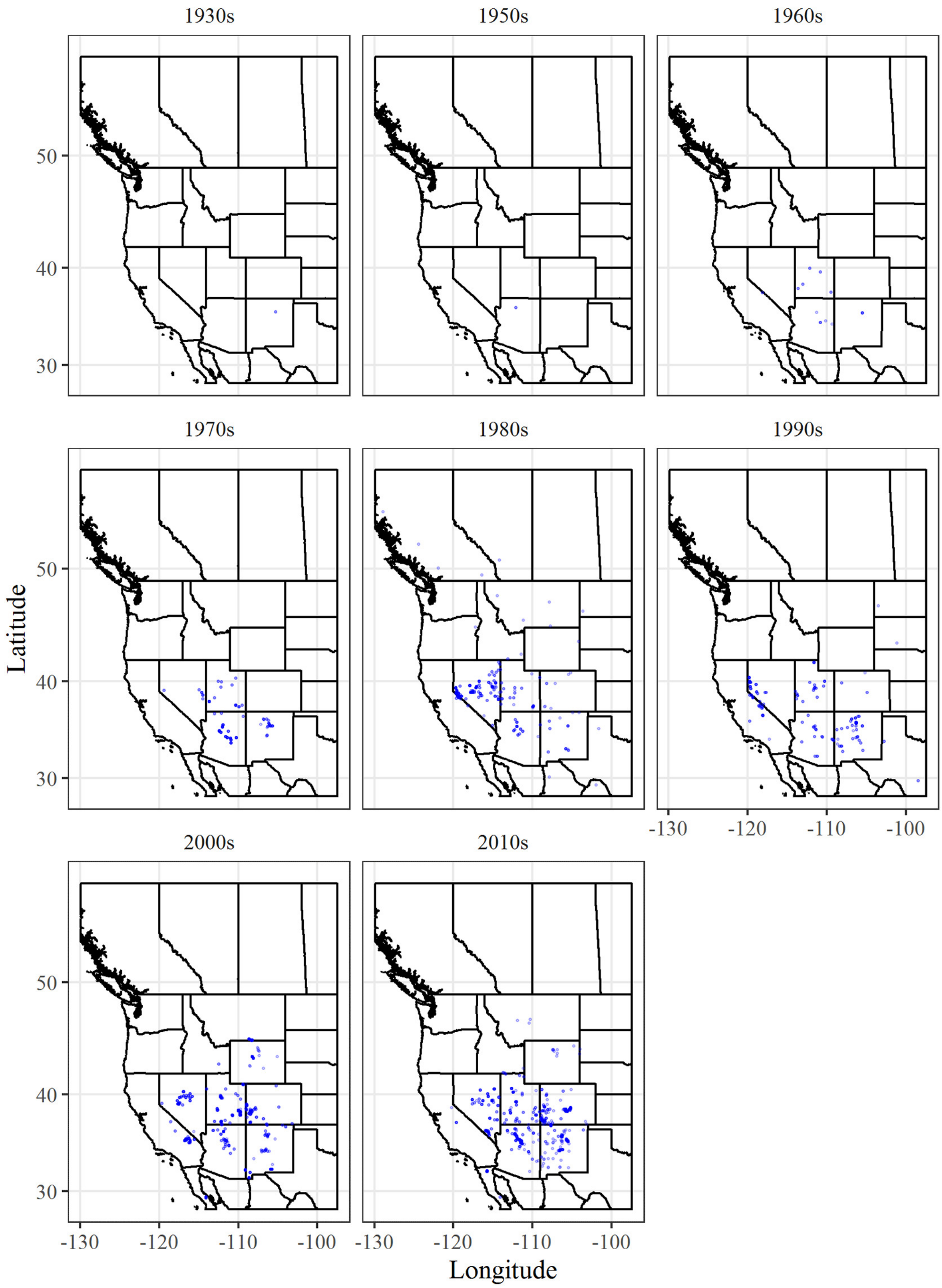
Overall research effort in pinyon-juniper communities has increased during this review period of 1909–2018.

Appendix C. Geographic density of all included studies



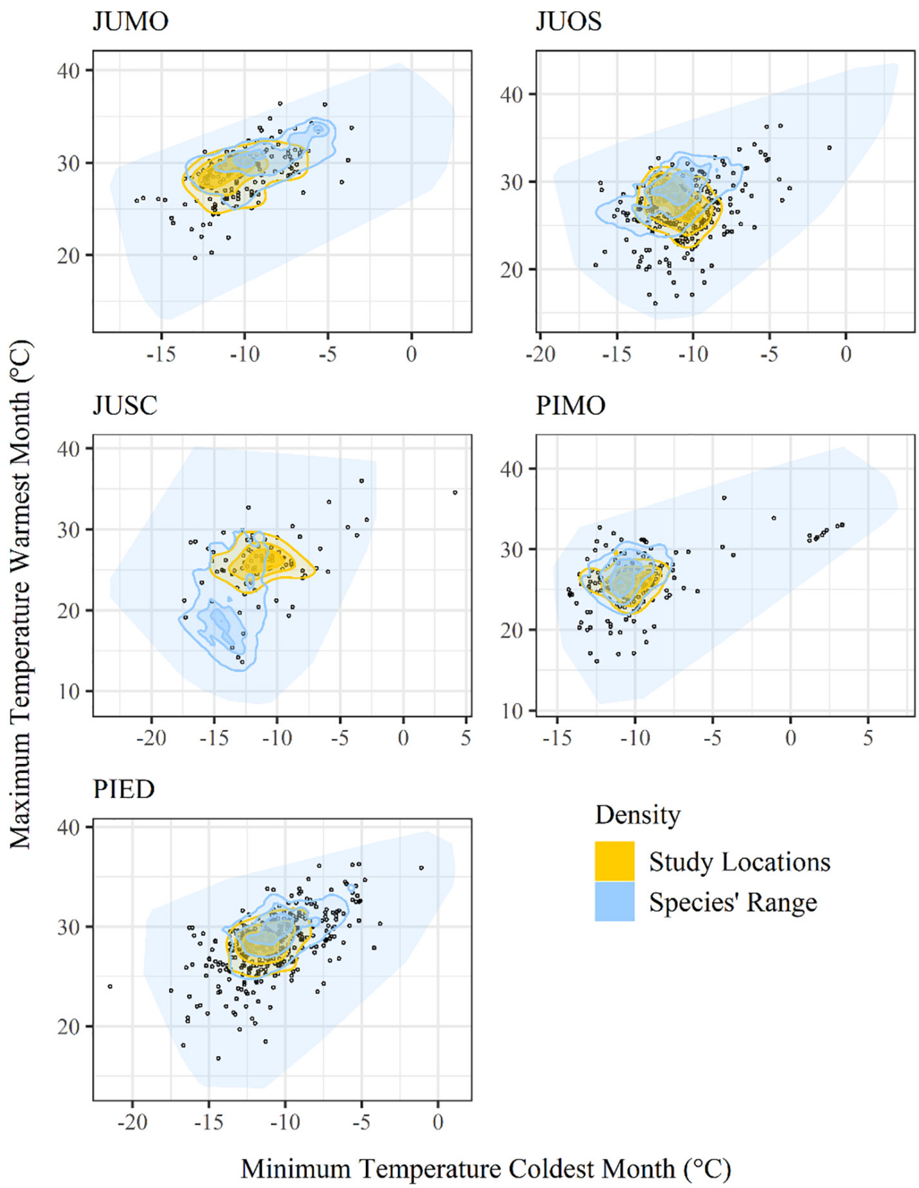
The density of included studies for this review demonstrate a good amount of coverage across the pinyon-juniper cover type. Density of all included studies per 50 km pixel. Larger points denote a higher density of studies per 50 km. Thirty-seven percent of locations were assigned accuracy of < 1 km, 25% were accurate to 1 km, 27% accurate to 10 km, and 12% to 100 km or greater accuracy.

Appendix D. Geographic distribution of all studies by decade

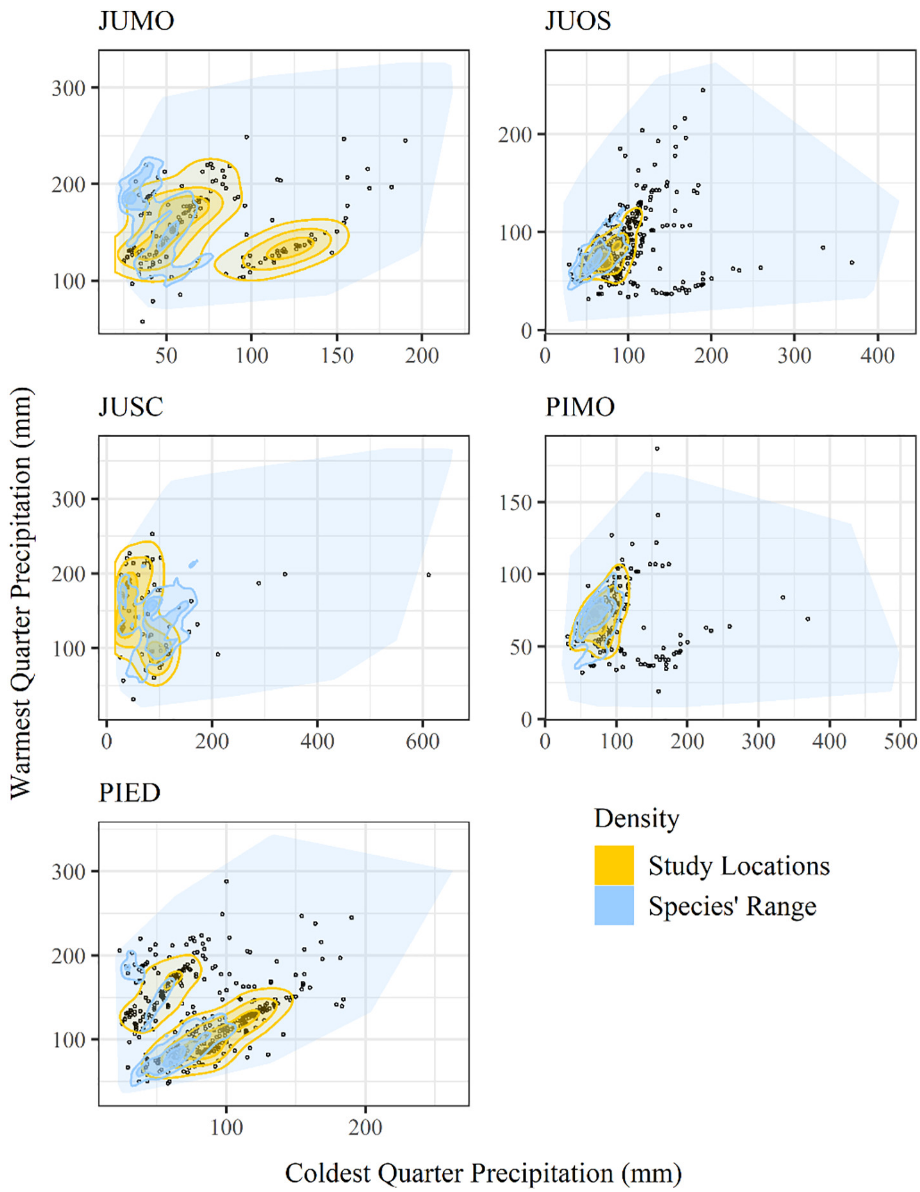


There has been an increase of research effort and spread across the distribution of pinyon-juniper cover through the years of this review. The included studies from 1930 to 2010s. Points are single study locations and include paleoecological studies.

Appendix E. Bivariate climate contour plots for each species

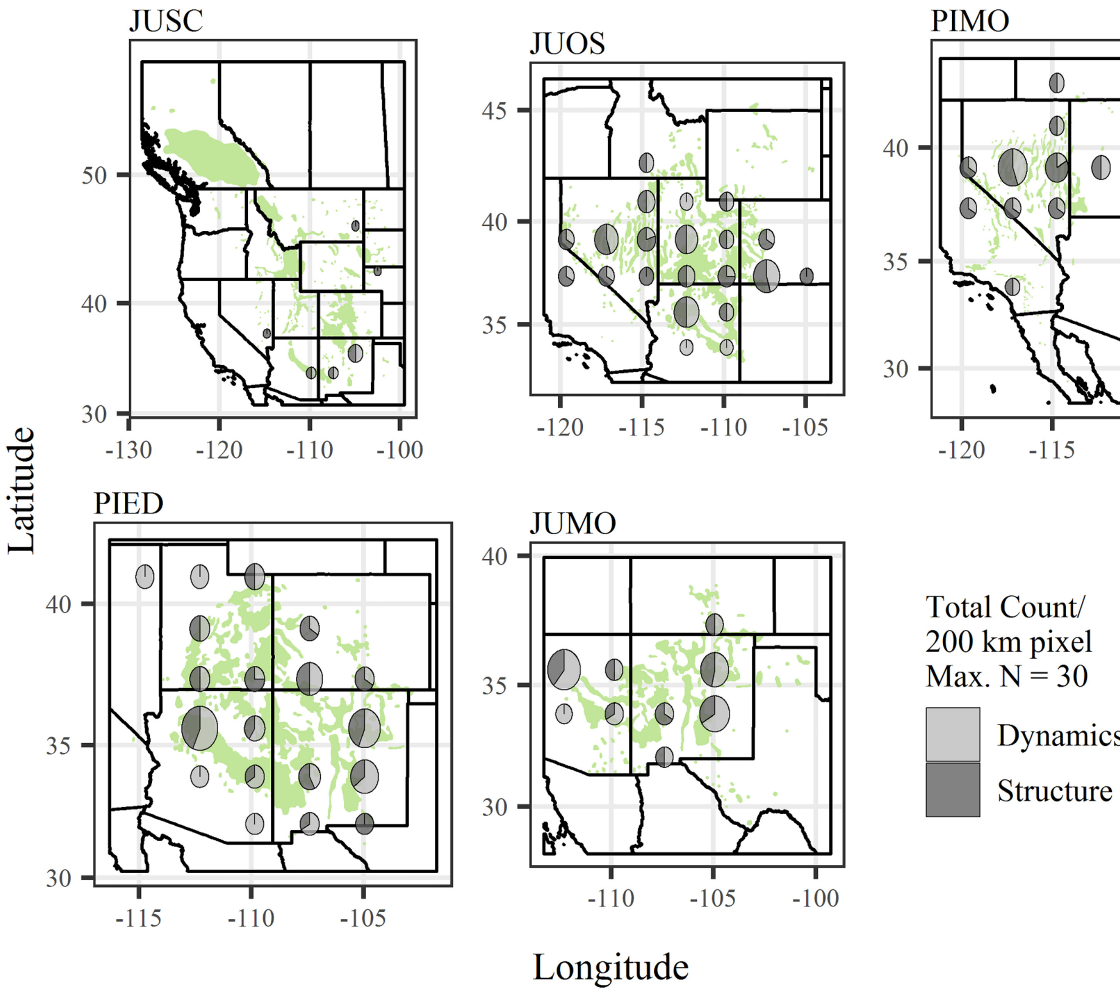


Bivariate climate contour plots (maximum temperature in the warmest month and minimum temperature in the coldest month) for each species show good coverage for most species, but a mismatch for J. scopulorum climate space. Yellow contour lines indicate increasing density of climate space for study locations. Blue contour lines denote increasing climate space across the distribution for each species as described by Little 1971. Blue shading shows the overall climate space across the distribution of each species.



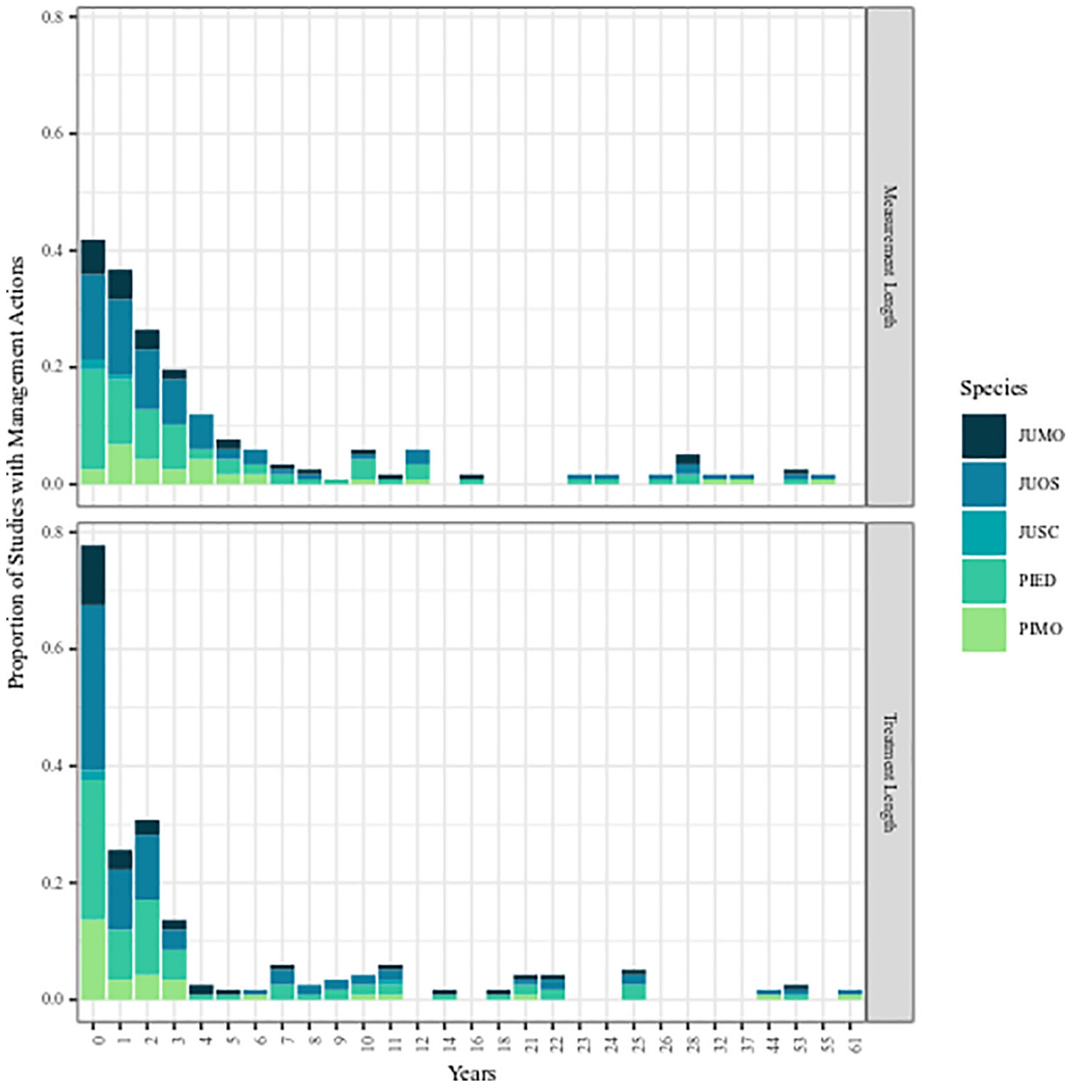
Bivariate climate contour plots (warmest quarter precipitation and coldest quarter precipitation) for each species show a mismatch in monsoonal precipitation climate space between the study and range climate space for J. monosperma. Yellow contour lines indicate increasing density of climate space for study locations. Blue contour lines denote increasing climate space across the distribution for each species as described by Little 1971. Blue shading shows the overall climate space across the distribution of each species.

Appendix F. Geographic distribution of studies with stand dynamics of structure



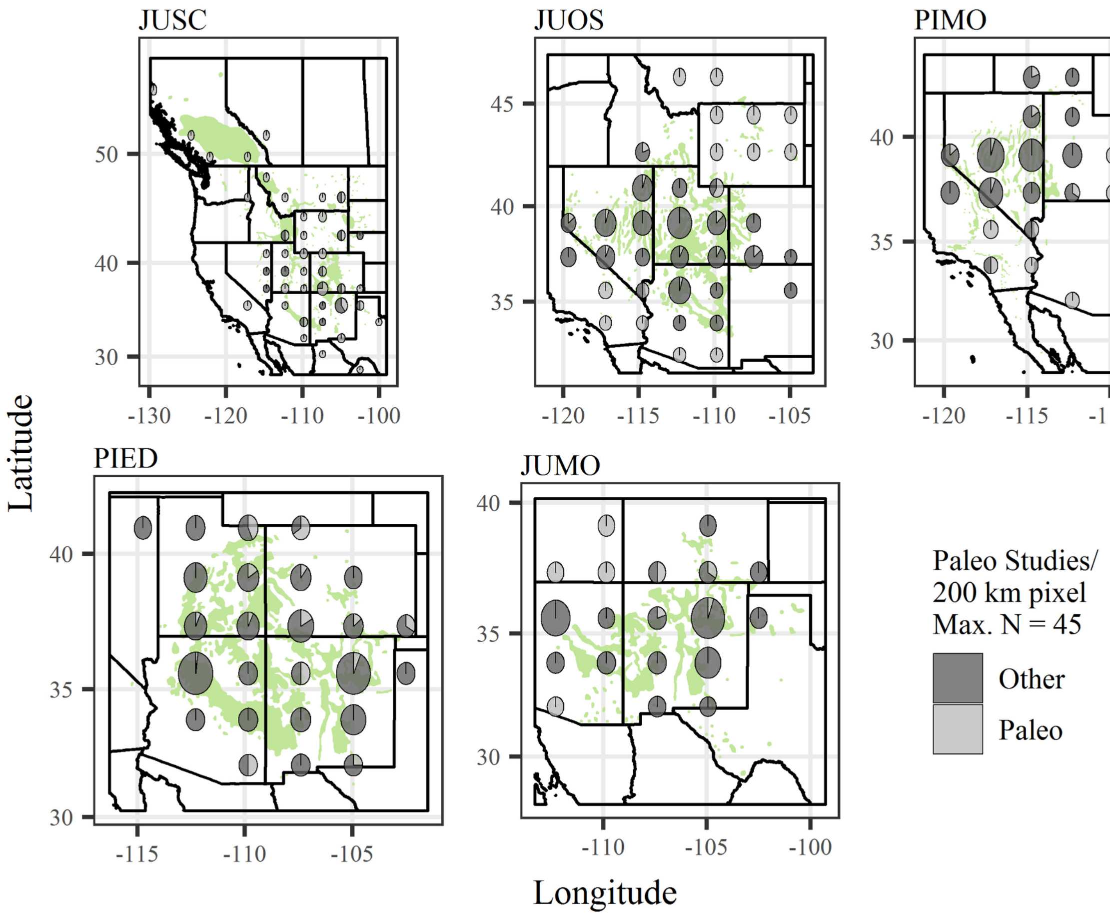
The proportion of studies having aspects of stand structure (tree age, tree density or tree size) or stand dynamics (tree establishment, mortality or succession) show a limited amount of research across the range of J. scopulorum and a gap in northwestern New Mexico for P. edulis and J. monosperma. Green shading denotes the range for each species as described by Little 1971. Larger pie charts denote areas of greater research effort.

Appendix G. Treatment and measurement lengths



Most studies had a treatment and measurement length of one year or less. Studies with > 20 years of measurement were often long-term comparisons of relict sites.

Appendix H. Geographic distribution of paleological studies versus all other studies



The proportion of studies with a paleoecological focus versus all other included studies show a greater proportion of paleoecological studies on the range edges for each species. Larger pies indicate a greater research effort. The resolution is 200 km/pixel. Green shading denotes the range for each species as described by Little 1971.

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