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Westward Expansion by *Juniperus virginiana* of the Eastern United States and Intersection with Western *Juniperus* Species in a Novel Assemblage

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Abstract: Eastern redcedar (*Juniperus virginiana* L.) is increasing in density in the eastern United States and expanding in range to the west, while western *Juniperus* species also are increasing and expanding, creating the potential for a novel assemblage. I estimated range expansion and intersection by comparing recent USDA Forest Service Forest Inventory and Analysis surveys (mean year = 2009) to the oldest available surveys (mean year = 1981), with adjustments for sampling changes, and predicted climate envelopes during the following year ranges: 1500–1599, 1800–1849, 1850–1899, 1900–1949, and 1960–1989. During approximately 28 years, eastern redcedar range expanded by about 54 million ha (based on $\geq$0.5% of total stems $\geq$12.7 cm in diameter in ecological subsections). Combined range of western species of juniper did not expand. Range intersection of eastern redcedar and western *Juniperus* species totaled 200,000 km^2 and increased by 31,600 km^2 over time, representing a novel assemblage of eastern and western species. Predicted ranges during the other time intervals were 94% to 98% of predicted area during 1960–1989, suggesting major climate conditions have been suitable for centuries. The southern western *Juniperus* species and Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) have the greatest potential for intersection with eastern redcedar, whereas eastern redcedar may have concluded westward expansion.

Keywords: densification; eastern redcedar; encroachment; range shift; Rocky Mountain juniper

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1. Introduction

During the past century, native tree and shrub species have changed in density within existing ranges and also changed in distribution within both forested ecosystems and non-forested ecosystems [1–3]. Spread of native woody vegetation is described as encroachment, densification, thicketization, and woodification, evoking alteration in the characteristics and condition of ecosystems that threaten native biodiversity [4]. Changes in density within existing or novel ranges occur because of changes in land use, natural disturbances, and climate change among other factors.

Eastern redcedar (*Juniperus virginiana* L.) is a native tree species of the eastern United States that is spreading, in part through deliberate introduction. Eastern redcedar has increased in density within eastern forests, doubling in percentage of all trees in the central eastern and northern southeastern regions [5]. More notably, eastern redcedar is expanding westward into the Great Plains grasslands of the central U.S. Eastern redcedar received an assist in migration into the central grasslands, as this species was, and continues to be, planted for windbreaks and fence rows, and additionally is dispersed widely by birds and small mammals [6,7].

Most area of the central grasslands is likely outside of the native distribution of eastern redcedar, but eastern redcedar has overcome historical boundaries to survive and reproduce in grasslands. Expansion of numerous tree species into the westernmost eastern grasslands was noted in historical accounts during the first half of the 1800s [8,9])and tree expansion into central grasslands was noted by 1860 [10,11]. However, eastern redcedar generally was delayed in expanding into central grasslands compared to other tree species or else largely remained unobserved, due to initial relative rarity at ecotones (e.g., almost no observations in historical tree surveys of Missouri and Illinois circa 1800 to 1860) [12,13]. Beilmann and Brenner [14] dated early eastern redcedar expansion by 1874 in Missouri, but Gleason [11] did not include eastern redcedar with numerous tree species that were expanding into grasslands. Bruner [15] mentioned eastern redcedar as being restricted to steep slopes in Oklahoma, but expansion occurred by 1950 [16].

The most common western *Juniperus* species are Utah (*J. osteosperma* (Torr.) Little), oneseed (*J. monosperma* (Engelm.) Sarg.), Ashe (*J. ashei* J. Buchholz), and Rocky Mountain (*J. scopulorum* Sarg.) junipers. Western *Juniperus* species can be associated with pinyon pines (e.g., *P. edulis* Engelm., *P. monophyla* Torr. and Frém.); however, this association appears to be enforced by historical disturbance regimes and new genus- and species-specific dynamics are emerging. Indeed, juniper species probably are benefiting from drought declines of pinyon pines [17–19]. Range expansion and increased density of pinyon and juniper have occurred across the Great Basin and Colorado Plateau during the past 200 years with a rapid increase in the late 1800s and peaking during the early 1900s [20]. Ashe juniper expansion was noted in Texas by 1917 [21]. Similarly to eastern redcedar, western juniper species have expanded from dry, rocky, and shallow soils, sometimes on steep slopes along stream channels, to productive sites with deep soils [22–27]. Eastward expansion specifically has not been evident for the western species; rather, expansion generally has been multidirectional, into riparian and aspen ecosystems [20], upslope in elevation into ponderosa pine forests (*Pinus ponderosa* Douglas ex P. Lawson and C. Lawson) [28], and downslope into shrub- or grass-dominated ecosystems [24]. Increases have been attributed to climate change, overgrazing due to livestock, and reduced frequency of surface fire in locations with enough continuous vegetation to support surface fires [20]. Regarding past climate change, woodlands typically increased when climate was wetter and declined when climate became warmer and drier [20].

Because eastern redcedar has been expanding westward while western *Juniperus* species also have been expanding, novel assemblages of eastern and western *Juniperus* species may be developing. Paleoecological evidence has demonstrated that novel tree species assemblages emerged during range shifts in response to climate change after the glacial maximum 20 thousand years ago, but recent novel tree assemblages of have not been documented in the United States, to my knowledge [29]. My objectives were to quantify (1) recent ranges of *Juniperus* by species, (2) expansion, or increases in range, of eastern redcedar and all combined western *Juniperus* species, (3) intersection of eastern redcedar and all combined western *Juniperus* species ranges in the central United States for documentation of a modern novel assemblage, and (4) potential range expansion for intersection. To establish potential ranges and range expansion, I predicted climate envelopes during the years 1500s (1500 to 1599), 1800–1849, 1850–1899, 1900–1949, and near present climate (1960–1989).

2. Materials and Methods

I used USDA Forest Service Forest Inventory and Analysis surveys (FIA) [30], which contain thousands of long-term plots located about every 2000–2500 ha across the country. From all states of the continental United States, I selected the most recently completed cycles in FIA surveys, ranging from years 2000 to 2013 (mean year = 2009) and the oldest FIA surveys, ranging from years 1966 to 2001 (mean year = 1981). Survey years uniquely vary by U.S. state, but surveys were initiated earlier in the eastern states. I grouped all plots within ecological subsections, which are the smallest ecological unit provided in FIA surveys (mean area = 642,000 ha, SD = 777,000) [31] and represent spatial area that share common ecological characteristics. I determined recent ranges where presence was $\geq$0.5 percent composition (i.e., percent of all stems) in ecological subsections and also quantified ranges at $\geq$10% composition and $\geq$30% composition.

Caveats include that a standardized national survey design was phased in beginning in 1999 to improve precision of inventory parameter estimates and variance; however, the national sampling design preserved consistency with regional surveys to allow continuity of trend estimation because the pre-standardized survey design provides valuable and robust information [32–34]. Surveys switched from periodic inventories in which all plots were visited during an undefined time interval to inventory cycles of typically 5 years (eastern states) or 10 years (western states) in which each annual survey is a representative sample and about half of plots were re-located, generally close to the original plot location [33]. To account for sampling changes over time, I used adjustment factors [35]; additionally, I summarized changes by ecological subsections [31], a larger scale than plots, and limited the study to established trees ≥12.7 cm in diameter at 1.37 m height that are surveyed completely in each plot.

To make comparisons among old and recent survey data, adjustments to the old survey data were required to account for differing sampling intensity and also populate non-sampled areas [35]. Old surveys generally sampled timberland only (i.e., a specified productivity level and available for timber harvesting) across all ownerships. To adjust the old survey data sets for non-sampled areas, new survey plot data were added to the old survey data sets for non-sampled areas; this produced a data set that sampled changes between the old and new surveys for only those lands sampled in both surveys, with no change in the non-sampled areas. A plot weighting factor of survey intensity accounted for differences caused by various sampling intensities between states and over time; the survey intensity was proportional to area from which the sample plots were randomly selected divided by the number of plots in the sample survey. Density by species was computed following procedures described in Bechtold and Patterson [32] that account for differences in plot design (variable compared to fixed area) and size used in each survey. The adjustments are meant to provide better comparisons for change detection; nonetheless, adjustments do alter values, resulting in divergence from recent inventories.

For live trees with diameters ≥12.7 cm at 1.37 m height, I determined change in range area at ≥0.5%, ≥10%, and ≥30% of all stems by ecological subsection and composition of *Juniperus* species and range intersection of eastern redcedar and western *Juniperus* species. I provided information about combined western *Juniperus* species to help reduce variation due to survey standardization. For subsections where either eastern redcedar or all combined western *Juniperus* species increased by ≥5% composition, I determined species that decreased by ≥5% composition. I retained species that that decreased in at least four subsections. I also excluded hickory and ash species, due to unidentified species of these genera in older surveys.

I extracted 11 climate variables [36,37] by ecological subsection to model potential presence ranges (≥0.5 percent composition in ecological subsections) during years 1960 to 1989, 1900–1949, 1850–1899, 1800–1849, and 1500–1599. Six temperature variables included growing degree days above 0 °C and 5 °C and mean minimum and maximum temperature annually and for the coldest and warmest months. Total annual precipitation, the coefficient of variation for precipitation, percent winter (December and January) precipitation, July vapor pressure, and the aridity index of total annual precipitation to potential evapotranspiration indicated changing dryness. In addition, I used soil moisture [38] and topographic roughness [39] variables, which represent only current conditions, but provide additional information.

For modeling presence ranges (≥0.5 percent composition in ecological subsections) under current climate, I applied random forests and extreme gradient boosting classifiers in the caret package [40,41] and trained the model with 10-fold cross-validation. Validation occurred on withheld testing data, 25% presence range samples, to determine how well the classifier assigned classes using explanatory variables. For this modeling, prevalence, or the number of present samples (≥0.5 percent composition in ecological subsections) to pseudoabsent samples (<0.5 percent composition in ecological subsections) was equal. Then, I predicted potential presence (≥0.5 percent composition) ranges for the different year intervals. I combined some species to increase sample size of ecological subsections with species presence to ≥74. I grouped the more southern species of oneseed, Ashe, alligator (*Juniperus deppeana* Steud.), Pinchot (*Juniperus pinchotii* Sudw.), and redberry (*Juniperus coahuilensis* (Martiñez) Gaussen ex R.P. Adams) junipers and the more western species of western juniper (*Juniperus occidentalis* Hook.) and the relatively widespread but uncommon California juniper (*Juniperus californica* Carrière). I also modeled two pinyon pine species (*P. edulis*, *P. monophylla*), which are somewhat associated with juniper.

3. Results

To summarize recent status in forest inventories, the most abundant western *Juniperus* species generally maintained spatially differentiated ranges, where western *Juniperus* species occurred at ≥10% of composition, or percent of all stems in ecological subsections (Figure 1). Utah juniper was the most common western *Juniperus* species according to FIA surveys, representing 42% of western *Juniperus* species percent composition and 2% of all combined trees, even though Rocky Mountain juniper covered a presence range (≥0.5% of all trees by ecological subsection) of 110 million ha compared to 95 million ha for Utah juniper (Table 1). Utah juniper was ≥10% of composition in about twice the area as Rocky Mountain juniper and Utah juniper was ≥30% of composition in almost four times the area as Rocky Mountain juniper. Eastern redcedar was the second most common *Juniperus* species, at 1% of all trees, and the most widespread *Juniperus* with a range of almost 200 million ha, but because most of eastern redcedar's range was within forested ecosystems of the eastern United States, eastern redcedar did not occur at ≥10% of composition throughout about 85% of its range.

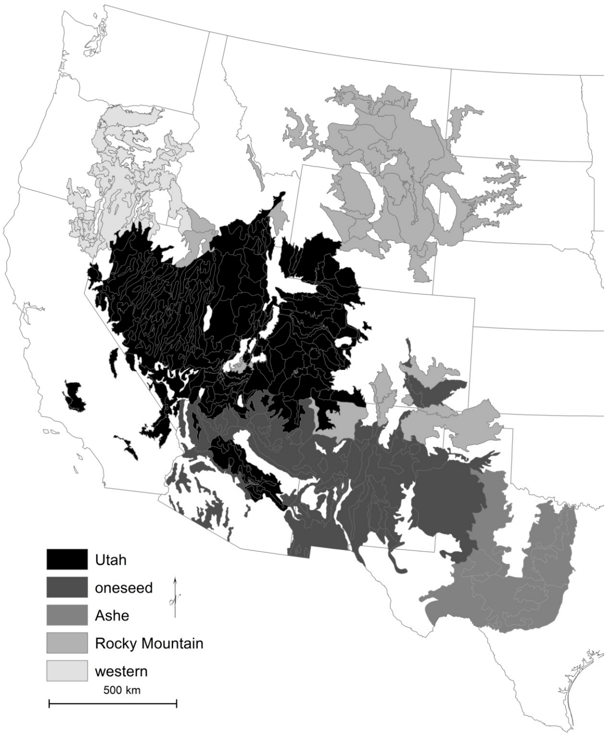

Figure 1. Range of most abundant western *Juniperus* species where recent composition was ≥10% in ecological sections (outlined and shaded). There was little overlap among species ranges at ≥10% composition, although less common Pinchot juniper and redberry juniper (not shown) overlapped Ashe juniper and alligator juniper (not shown) overlapped oneseed juniper.

Comparing compositional change between oldest and most recent surveys, eastern redcedar doubled in number of trees. Survey adjustments equalized survey intensity and thereby improve trend detection but concurrently resulted in some divergence from recent inventory information. Utah juniper, the most abundant western juniper slightly decreased, from 1.8% to 1.7% of all recorded trees. Indeed, all western juniper species decreased, except for Rocky Mountain juniper, which increased slightly (from 0.61% to 0.66% of all recorded trees). For calculation of expansion, which also required survey adjustments, where eastern redcedar was present (≥0.5% of composition), eastern redcedar increased 125% in area, from 207.6 to 261.5 million ha. Where eastern redcedar occurred at 10% composition, eastern redcedar more than doubled in area (215%), from 48.5 million ha to 104.1 million ha. Where eastern redcedar occurred at 30% composition, eastern redcedar almost tripled in area (280%), from about 6.9 to 19.5 million ha. The areas where all combined western *Juniperus* species occurred at the three different percent composition remained stable (recent values were 0.98 to 1.05 of older areas). However, this represented only 19 years of change due to later surveys and areas without older surveys were filled in with current values. By species, results were similar. Where each of the western *Juniperus* species was present (≥0.5% of composition), maximum expansion was 103% of the older range; where each of the western *Juniperus* species occurred at 10% composition, the maximum expansion was 100%; where each of the western *Juniperus* species occurred at ≥30% composition, the maximum expansion was 101%, except for Rocky Mountain juniper that expanded 127%.

Table 1. Summary statistics of *Juniperus* species for recent surveys, not limited by areas with older surveys. Percent values are percent of total stems.

Species	Scientific Name	% of Western Junipers	Range at ≥0.5% of All Trees (km^2)	Range at ≥10% All Trees (km^2)	Range at ≥30% All Trees (km^2)
Utah juniper	*J. osteosperma*	42.2	946,571	764,094	499,995
Oneseed juniper	*J. monosperma*	17.5	757,882	472,246	194,949
Ashe juniper	*J. ashei*	11.8	293,600	192,553	81,157
Rocky Mountain juniper	*J. scopulorum*	10.9	1,103,090	399,009	131,736
Western juniper	*J. occidentalis*	6.1	289,313	136,213	97,493
Alligator juniper	*J. deppeana*	5.7	277,667	77,883	0
Pinchot juniper	*J. pinchotii*	2.9	385,019	95,775	37,071
Redberry juniper	*J. coahuilensis*	2.3	477,101	112,413	0
Eastern redcedar	*J. virginiana*	N/A	1,978,270	339,504	86,258

Intersection between eastern redcedar and all combined western *Juniperus* species (≥0.5% composition) increased in a net total of two ecological subsections between oldest and most recent surveys (Figure 2). Intersection increased in four ecological subsections covering 48,365 km^2 but decreased in two subsections covering 16,765 km^2 and remained stable in eleven subsections covering 176,845 km^2. In three subsections, only eastern redcedar was recorded previously; that is, Rocky Mountain juniper and Ashe juniper increased in the two or one subsections, respectively.

In areas where eastern redcedar increased over time, decreasing species primarily were pine and oak species (Table 2). In addition, decreasing species included boxelder (*Acer negundo* L.) and eastern cottonwood (*Populus deltoides* Bartram ex Marsh.) that are located along riparian channels. In areas where western *Juniperus* increased, primarily pine species decreased, particularly ponderosa pine and two-needle pinyon pine.

For potential ranges, modeled ranges were accurate, with a mean AUC (area under the curve; area under the receiver operating characteristic curve, which plots the true positive rate compared to false positive rate at all classification thresholds) value of 0.98, ranging from 0.96 to 1.0. The climate envelopes during 1500–1599 were relatively similar in area to near present climate envelopes, with a mean value of 94% of the near present area, ranging from 82% to 102%. Similarly, area during 1800–1849, 1850–1899, and 1900–1950 overall were slightly less than near present climate envelopes, with mean areas of 94% to 98% by time interval of near present climate envelopes, ranging from 87% to 107%. When compared to current realized ranges, the combined western juniper and California juniper had the greatest potential for expansion, with a 4.4-fold increase when comparing the near present climate envelope (years 1960–1989) to realized range (Figure 3A). The Rocky Mountain juniper climate envelope was 2.3-fold greater than the realized range (Figure 3B), whereas the climate envelopes of other species were almost double (1.8- to 1.9-fold) the realized ranges (Figure 3). However, potential for intersection was greater between eastern redcedar and the southern western junipers, albeit consisting of multiple species, at 656,845 km^2 than between eastern redcedar and Rocky Mountain juniper at 254,860 km^2 (Figure 4).

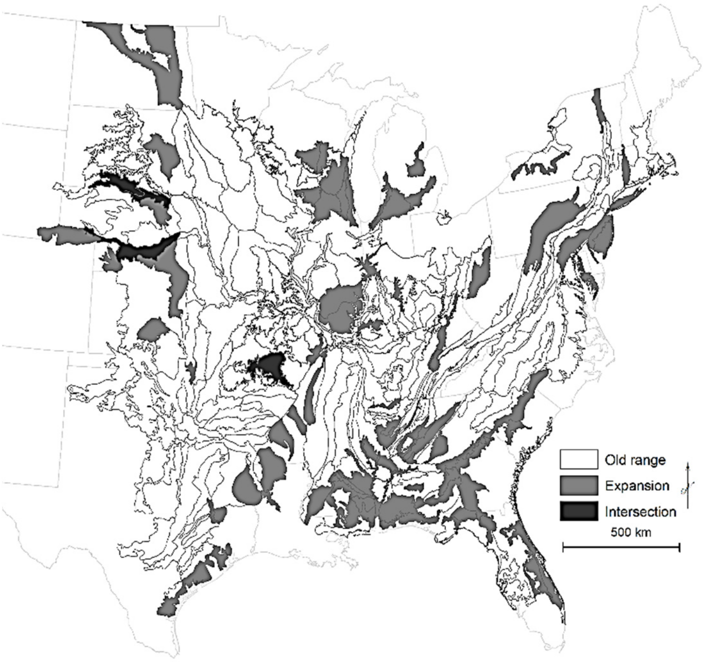

Figure 2. Recent expansion of presence range (composition ≥0.5%; outlined and shaded gray) of eastern redcedar. Subsections shaded black indicate areas of recent intersection with presence range of western *Juniperus* species (the most northern subsections are connected).

Table 2. Species that decreased by ≥5% composition where *Juniperus* species have increased by ≥5% composition.

Species	Scientific Name	# Subsections	Change % Composition	Change % *Juniperus* Composition
Eastern redcedar				
Shortleaf pine	*Pinus echinata*	13	−11.6	9.1
Boxelder	*Acer negundo*	12	−17.4	20.3
Eastern cottonwood	*Populus deltoides*	9	−24.0	24.2
Blackjack oak	*Quercus marilandica*	7	−6.9	10.4
Post oak	*Quercus stellata*	5	−7.8	10.3
Virginia pine	*Pinus virginiana*	5	−11.1	6.7
White oak	*Quercus alba*	5	−9.1	9.3
Ponderosa pine	*Pinus ponderosa*	4	−22.5	15.9
Sugar maple	*Acer saccharum*	4	−8.9	8.8
Western *Juniperus*				
Ponderosa pine	*Pinus ponderosa*	12	−9.6	11.9
Quaking aspen	*Populus tremuloides*	9	−19.3	26.7
Two-needle pinyon	*Pinus edulis*	8	−9.0	9.50
Lodgepole pine	*Pinus contorta*	6	−23.3	25.4
Subalpine fir	*Abies lasiocarpa*	6	−15.9	27.4
Limber pine	*Pinus flexilis*	5	−13.1	15.6
Singleleaf pinyon	*Pinus monophylla*	4	−7.4	8.0

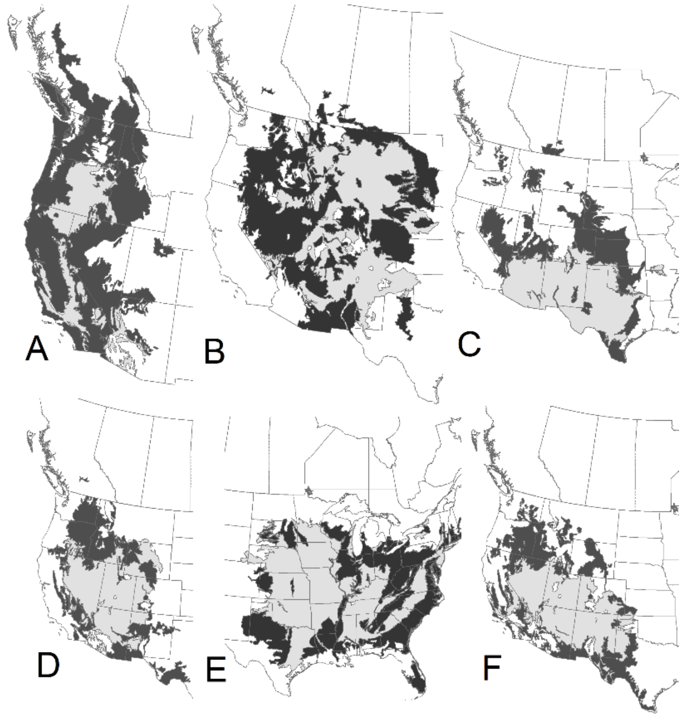

Figure 3. Potential for continued expansion (potential under near present climate in black) compared to current ranges (shaded gray) for combined western juniper and California juniper (**A**), Rocky Mountain juniper (**B**), southern western *Juniperus* (**C**), Utah juniper (**D**), eastern redcedar (**E**), and combined two-needle and singleleaf pinyon pines (**F**).

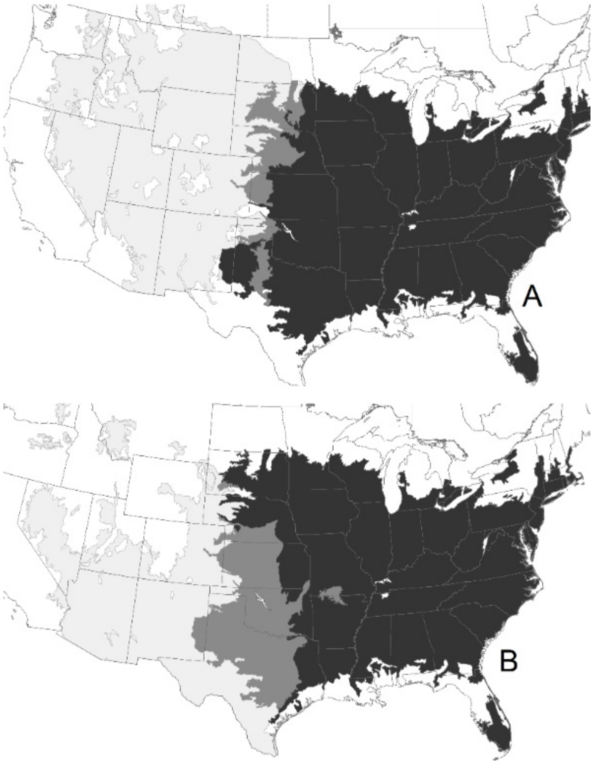

Figure 4. Potential for intersection (shaded dark gray) according to climate envelopes for Rocky Mountain juniper (light gray) and eastern redcedar (shaded black; (**A**)) and the southern western *Juniperus* species (light gray) and eastern redcedar (shaded black; (**B**)).

4. Discussion

Eastern redcedar has increased in relative density and expanded in range, one of the great range expansions in the United States during the past few decades, according to adjusted FIA surveys. Additionally, eastern redcedar has increased in relative density within its range, by two- to three-fold where it occurred at $\geq$10% composition (or percent of all stems) and $\geq$30% composition. Potential bias in comparing FIA surveys over time arises from survey standardization to a national standard, and while adjustments to equalize survey intensity may correct change detection, exact values are altered. Nonetheless, these results concur with studies reporting eastern redcedar expansion and in-filling that were documented as early as 1875 [14,42,43].

Although older surveys in the western United States are limited in time and space, recent recorded trends in western *Juniperus* species suggest stability, or even minor decreases, with Rocky Mountain juniper as the one species that slightly has increased and expanded overall. The FIA surveys offer a long-term record to detect species trends in composition and ranges for the entire United States, based on thousands of plots covering millions of ha, but some trends may vary in time and space or may be distorted by survey changes to a national standard. For western *Juniperus*, the time interval of measurement was only about 19 years, and coverage in older surveys was incomplete in some portions of the western United States, which resulted in conservative estimates. It may be that some western *Juniperus* species expanded but incomplete surveys, particularly in Washington, Oregon, southern California, and western Texas, prevented detection. Alternatively, it may be that reduced rates of expansion and spatiotemporal variability [20,44] resulted in the relative stability indicated by surveys. In addition, spatial scales of expansion may be small relative to expansion by more abundant species during the past few decades throughout the country. For example, western juniper (*Juniperus occidentalis*) has expanded by a few million ha over 100 years, which is important to invaded shrub steppe communities in Oregon and California [45]. Indeed, western juniper has the greatest potential to expand into appropriate climate conditions that match current conditions, as demonstrated by the area of the climate envelope that was greater by a factor of 4.4 than the area of the realized range.

In terms of intersection, eastern redcedar and western *Juniperus* species overlapped in ecological subsections representing about 200,000 km^2 during the older surveys and increased slightly by 31,600 km^2 over time. Despite greater expansion by eastern redcedar than western *Juniperus* species, it appears that western *Juniperus* species have expanded into the central United States in areas that intersect the range of eastern redcedar. Eastern redcedar expansion, particularly as planted windbreaks, may be greater in areas unoccupied by another juniper species than in occupied areas. Based on climate suitability, the southern western *Juniperus* species followed by Rocky Mountain juniper have the greatest potential for intersection with eastern redcedar.

Intersection of eastern and western junipers may represent the first new, viable assemblage during recent millennia in the United States. Although native tree species have changed in relative composition and become less spatially differentiated within regions during the past century or two due to land use change, including fire exclusion, native tree species shared at least limited spatial overlap within regions [46]. However, association of an eastern tree species with western species is novel, given that fires in the Great Plains grasslands historically prevented tree expansion and intermixing during the past 10,000 or more years [47,48]. Additionally, junipers are widespread and abundant, resulting in multiple subsections with overlap, and junipers have similar traits that may allow coexistence into an established long-term association, as indicated by increasing spatial intersection over time. In contrast, ponderosa pine, another western species, decreased where eastern juniper expanded (Table 2), and likely this trend indicates a non-viable, transient association during the replacement of ponderosa pine by eastern juniper. Novel assemblages documented by paleoecological evidence captured common associations that were stable during hundreds or thousands of years, rather than brief transitions [29]. Novel assemblages are expected to form under current climate change. Nonetheless, novel assemblages also can develop due to land use change rather than climate change.

If the climate envelopes are approximate depictions of climate limitations, eastern redcedar mostly has finalized westward expansion, with some scope for southwestern expansion across Texas (Figure 4). Without a fire regime, and particularly with aided migration by windbreak plantings and birds, climate may not limit western expansion of eastern redcedar. Potential eastern redcedar expansion throughout the eastern United States is possible, but competition from other expanding native tree species may prevent long-term establishment.

Junipers have become more abundant compared to other tree species, despite having traits of early-successional colonizers. Juniper densification and expansion reduced already fragmented or deteriorated ecosystems of open grassland and shrubland ecosystems and open pine and oak forests of savannas and woodlands that coexist with herbaceous vegetation, as demonstrated by reduction of fire-dependent pines and oaks (Table 1) [43,49,50]. Junipers replace herbaceous vegetation, which is important for a variety of animals associated with open ecosystems [23,25,45,51,52]. Species such as eastern cottonwood and boxelder that are present in riparian networks decreased where junipers increased. Broadleaf species are relatively important to wildlife in gymnosperm-dominated forests of the western United States [53].

Recent expansion of fire-sensitive species, such as eastern redcedar, has been attributed to multiple mechanisms. The very similar areas of climate envelope during the time intervals indicate that major climate indices, such as precipitation and aridity, may not have been limiting factors for expansion. Otherwise, eastern redcedar already would have expanded, rather than starting during the late 1800s [12]. In the eastern and central U.S., fire exclusion may be the main factor driving tree expansion and densification [2,6,7,42,43,46,48,49,54–56]. Fire exclusion, as opposed to fire suppression, incorporates a land use change component through reduction in herbaceous fine fuels by agriculture and intensive herbivory or high tree densities and reduction in fire spread by landscape fragmentation, particularly linear barriers of roads and trails. Similarly, fire reduction and intensive grazing have been implicated in Ashe juniper increases in Texas [23,25]. Moreover, species that decreased where eastern redcedar and western *Juniperus* increased generally were fire-dependent pines and oaks (e.g., shortleaf pine [*Pinus echinata* Mill.] and oaks in the eastern U.S., ponderosa pine in the western U.S.) or else post-fire-disturbance species, with traits such as prolific seeding or sprouting (e.g., quaking aspen, *Populus tremuloides* Michx.; lodgepole pine, *Pinus contorta* Douglas ex Loudon; Virginia pine, *Pinus virginiana* Mill.) that are competitive after overstory disturbance (Table 2).

Western *Juniperus*, particularly the southern species, may be expanding primarily into locations where fire exclusion has occurred, but fire exclusion with land use change may not be sufficient to explain expansion of western *Juniperus* into arid locations where surface fuels were not continuous enough to support frequent fire regimes [20]. Although tree expansion is a long process, weather oscillations may be influential, including severe droughts and pluvials [18,19,56]. However, the pluvial of the years 1905 to 1917 occurred after rapid juniper expansion was noted during the late 1800s and the pluvial was not unprecedented as an analogous pluvial occurred during the years 1825 to 1850 [57]. Major droughts also have occurred regularly, such as during years 1855 to 1865, but also with long gaps during which juniper expansion did not occur prior to the late 1800s, while more minor droughts occurred during 1870–1883 and 1897–1904 with juniper expansion [57]. Hydraulic characteristics of junipers may help confer greater drought tolerance relative to pinyon pines, which were decreasing species where western Juniperus increased. Junipers have been documented to continue leaf gas exchange and carbon assimilation with decreasing soil water potential during drought compared to other co-occurring tree species that experience declines in leaf gas exchange with declining soil moisture [18,19].

5. Conclusions

Trends revealed by large-scale, long-term FIA surveys, despite limitations, can provide the current status of tree species and inform future studies. Eastern redcedar had one of the greatest recent range expansions in the United States by increasing presence ($\geq$0.5% composition) in about 54 million ha, along with increased density within the range. In contrast, western *Juniperus* species appeared relatively stable, which may be due to survey gaps or may represent stability during the past two decades. Range intersection between eastern redcedar and Rocky Mountain juniper or southern western *Juniperus* species totaled almost 200,000 km^2 and increased by 31,600 km^2 over time, representing one of the first new assemblages of native tree species for millennia in the United States. Based on climate suitability, the southern western *Juniperus* species and Rocky Mountain juniper have the greatest potentials for intersection with eastern redcedar; western juniper has the greatest potential for expansion, whereas eastern redcedar may have finalized westward expansion, excepting expansion across Texas. Predicted areas of climate envelopes during a range of time intervals were 94% to 98% of predicted area during the recent past, indicating that the major climate conditions have been suitable for juniper species and realized ranges may be due to other constraints. Juniper increases were at the expense of other ecosystems, such as shrublands, grasslands, riparian forests, and open pine and oak forests, with consequent impacts on plant and wildlife species that flourish in open or unique ecosystems.

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References

1. Archer, S.; Schimel, D.S.; Holland, E.A. Mechanisms of shrubland expansion: Land use, climate, or CO$_2$? *Clim. Chang.* **1995**, *29*, 91–99. [CrossRef]
2. Van Auken, O.W. Causes and consequences of woody plant encroachment into western North American grasslands. *J. Environ. Manag.* **2009**, *90*, 2931–2942. [CrossRef] [PubMed]
3. Eldridge, D.J.; Bowker, M.A.; Maestre, F.T.; Roger, E.; Reynolds, J.F.; Whitford, W.G. Impacts of shrub encroachment on ecosystem structure and functioning: Towards a global synthesis. *Ecol. Lett.* **2013**, *14*, 709–722. [CrossRef]
4. Hanberry, B.B.; Bragg, D.C.; Alexander, H.D. Open forest ecosystems: An excluded state. *For. Ecol. Manag.* **2020**, *472*, 118256. [CrossRef]
5. Hanberry, B.B. Recent shifts in shade tolerance and disturbance traits in forests of the eastern United States. *Ecol. Process.* **2019**, *8*, 32. [CrossRef]
6. Briggs, J.M.; Hoch, G.A.; Johnson, L.C. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. *Ecosystems* **2002**, *5*, 578–586. [CrossRef]
7. Horncastle, V.J.; Hellgren, E.C.; Mayer, P.M.; Ganguli, A.C.; Engle, D.M.; Leslie, D.M., Jr. Implications of invasion by *Juniperus virginiana* on small mammals in the southern Great Plains. *J. Mammal.* **2005**, *86*, 1144–1155. [CrossRef]
8. Shaler, N.S. *Kentucky: A Pioneer Commonwealth*; Houghton, Mifflin and Company: Boston, MA, USA, 1885. Available online: https://www.google.com/books/edition/Kentucky_a_Pioneer_Commonwealth/eIAxAQAAMAAJ?hl=en&gbpv=1&printsec=frontcover (accessed on 2 June 2021).
9. Stewart, O.C. Burning and natural vegetation in the United States. *Geogr. Rev.* **1951**, *41*, 317–320. [CrossRef]
10. Hind, H.Y. *Narrative of the Canadian Red River Exploring Expedition of 1857 and of the Assinniboine and Saskatchewan Exploring Expedition of 1858*; Longman, Green, Longman, and Roberts: London, UK, 1860; Volume 2. Available online: https://www.google.com/books/edition/Narrative_of_the_Canadian_Red_River_Expl/L6kNAAAAQAAJ?hl=en&gbpv=1&printsec=frontcover (accessed on 11 August 2021).

11. Gleason, H.A. The vegetational history of the Middle West. *Ann. Am. Assoc. Geogr.* **1922**, *12*, 39–85. [CrossRef]
12. Hanberry, B.B.; Kabrick, J.M.; He, H.S. Changing tree composition by life history strategy in a grassland-forest landscape. *Ecosphere* **2014**, *5*, 34. [CrossRef]
13. McLachlan, J. Settlement Trees, Illinois Level 0 ver 0. Environmental Data Initiative. 2020. Available online: https://portal.edirepository.org/nis/mapbrowse?packageid=msb-paleon.28.0 (accessed on 30 December 2020).
14. Beilmann, A.P.; Brenner, L.G. The recent intrusion of forests in the Ozarks. *Ann. Mo. Bot. Gard.* **1951**, *38*, 261–282. [CrossRef]
15. Bruner, W.E. The vegetation of Oklahoma. *Ecol. Monogr.* **1931**, *1*, 100–188. [CrossRef]
16. Bidwell, T.G.; Engle, D.M.; Moseley, M.E.; Masters, R.E. *Invasion of Oklahoma Rangelands and Forests by Eastern Redcedar and Ashe Juniper*; Circular E-947; Oklahoma Cooperative Extension Service, Division of Agricultural Sciences and Natural Resources, Oklahoma State University: Stillwater, OK, USA, 1995. Available online: https://extension.okstate.edu/fact-sheets/invasion-of-oklahoma-rangelands-and-forests-by-eastern-redcedar-and-ashe-juniper.html (accessed on 7 April 2021).
17. Allen, C.D. Interactions across spatial scales among forest dieback, fire, and erosion in northern New Mexico landscapes. *Ecosystems* **2007**, *10*, 797–808. [CrossRef]
18. Koepke, D.F.; Kolb, T.E.; Adams, H.D. Variation in woody plant mortality and dieback from severe drought among soils, plant groups, and species within a northern Arizona ecotone. *Oecologia* **2010**, *163*, 1079–1090. [CrossRef]
19. Plaut, J.A.; Yepez, E.A.; Hill, J.; Pangle, R.; Sperry, J.S.; Pockman, W.T.; McDowell, N.G. Hydraulic limits preceding mortality in a piñon-juniper woodland under experimental drought. *Plant Cell Environ.* **2012**, *35*, 1601–1617. [CrossRef]
20. Miller, R.F.; Chambers, J.C.; Evers, L.; Williams, C.J.; Snyder, K.A.; Roundy, B.A.; Pierson, F.B. *The Ecology, History, Ecohydrology, and Management of Pinyon and Juniper Woodlands in the Great Basin and Northern Colorado Plateau of the Western United States*; U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: Fort Collins, CO, USA, 2019.
21. Foster, J.H. The spread of timbered areas in central Texas. *J. For.* **1917**, *15*, 442–445.
22. Tausch, R.J.; West, N.E. Differential establishment of pinyon and juniper following fire. *Am. Midl. Nat.* **1988**, *119*, 174–184. [CrossRef]
23. Rasmussen, G.A.; Wright, H.A. Succession of secondary shrubs on Ashe juniper communities after dozing and prescribed burning. *J. Range Manag.* **1989**, *42*, 295–298. [CrossRef]
24. Miller, R.F.; Wigand, P.E. Holocene changes in semiarid pinyon-juniper woodlands. *BioScience* **1994**, *44*, 465–474. [CrossRef]
25. Yager, L.Y.; Smeins, F.E. Ashe Juniper (*Juniperus ashei*: Cupressaceae) canopy and litter effects on understory vegetation in a juniper-oak Savanna. *Southwest Nat.* **1999**, *44*, 6–16.
26. Miller, R.F.; Svejcar, T.J.; Rose, J.A. Impacts of western juniper on plant community composition and structure. *J. Range Manag.* **2000**, *53*, 574–585. [CrossRef]
27. Hanberry, B.B. Compositional changes in selected forests of the western United States. *Appl. Geogr.* **2014**, *52*, 90–98. [CrossRef]
28. Allen, C.D.; Breshears, D.D. Drought-induced shift of a forest- woodland ecotone: Rapid landscape response to climate variation. *Proc. Natl. Acad. Sci. USA* **1998**, *95*, 14839–14842. [CrossRef] [PubMed]
29. Delcourt, P.A.; Delcourt, H.R. Late-Quaternary dynamics of temperate forests: Applications of paleoecology to issues of global environmental change. *Quat. Sci. Rev.* **1987**, *6*, 129–146. [CrossRef]
30. FIA DataMart. Forest Inventory and Analysis [FIA]. 2021. Available online: https://apps.fs.usda.gov/fia/datamart/datamart.html (accessed on 30 January 2021).
31. Keys, J.E.; Cleland, D.T.; McNab, W.H. *Delineation, Peer Review, and Refinement of Subregions of the Conterminous United States*; Gen. Tech. Report WO-76A; Department of Agriculture, Forest Service: Washington, DC, USA, 2007.
32. Bechtold, W.A.; Patterson, P.L. *The enhanced Forest Inventory and Analysis Program—National Sampling Design and Estimation Procedures*; USDA Southern Research Station: Asheville, NC, USA, 2005.
33. Lichstein, J.W.; Wirth, C.; Horn, H.S.; Pacala, S.W. Biomass chronosequences of United States forests: Implications for carbon storage and forest management. In *Old-Growth Forests*; With, C., Gleixner, G., Heimann, M., Eds.; Springer: Heidelberg, Germany, 2009.
34. Lichstein, J.W.; Dushoff, J.; Ogle, K.; Chen, A.; Purves, D.W.; Caspersen, J.P.; Pacala, S.W. Unlocking the forest inventory data: Relating individual tree performance to unmeasured environmental factors. *Ecol. Appl.* **2010**, *20*, 684–699. [CrossRef]
35. Hanberry, B.B.; Hansen, M.H. Advancement of tree species across ecotonal borders into non-forested ecosystems. *Acta Oecol.* **2015**, *68*, 24–36. [CrossRef]
36. Lorenz, D.J.; Nieto-Lugilde, D.; Blois, J.L.; Fitzpatrick, M.C.; Williams, J.W. Downscaled and debiased climate simulations for North America from 21,000 years ago to 2100AD. *Sci. Data* **2016**, *3*, 1–19. [CrossRef] [PubMed]
37. Lorenz, D.J.; Nieto-Lugilde, D.; Blois, J.L.; Fitzpatrick, M.C.; Williams, J.W. Data from: Downscaled and Debiased Climate Simulations for North America from 21,000 Years Ago to 2100AD. 2016. Available online: https://doi.org/10.5061/dryad.1597g (accessed on 1 December 2020).
38. Hengl, T.; Gupta, S. Soil Water Content (Volumetric %) for 33 kPa and 1500 kPa Suctions Predicted at 6 Standard Depths (0, 10, 30, 60, 100 and 200 cm) at 250 m Resolution. (Version v0.1). 2019. Available online: http://doi.org/10.5281/zenodo.2784001 (accessed on 28 January 2021).
39. Amatulli, G.; McInerney, D.; Sethi, T.; Strobl, P.; Domisch, S. Geomorpho90m, empirical evaluation and accuracy assessment of global high-resolution geomorphometric layers. *Sci. Data* **2020**, *7*, 1–18. [CrossRef] [PubMed]
40. Kuhn, M. Building predictive models in R using the caret package. *J. Stat. Softw.* **2008**, *28*, 1–26. [CrossRef]
41. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation for Statistical Computing: Vienna, Austria, 2021.

42. Abrams, M.D. Historical development of gallery forests in northeast Kansas. *Vegetatio* **1986**, *65*, 29–37. [CrossRef]
43. Gehring, J.L.; Bragg, T.B. Changes in prairie vegetation under eastern red cedar (*Juniperus virginiana* L.) in an eastern Nebraska bluestem prairie. *Am. Midl. Nat.* **1992**, *128*, 209–217. [CrossRef]
44. Murray, D.B.; White, J.D.; Swint, P. Woody vegetation persistence and disturbance in central Texas grasslands inferred from multidecadal historical aerial photographs. *Rangel. Ecol. Manag.* **2013**, *66*, 297–304. [CrossRef]
45. Miller, R.F.; Bates, J.D.; Svejcar, T.J.; Pierson, F.B.; Eddleman, L.E. *Biology, Ecology, and Management of Western Juniper (Juniperus occidentalis)*; Oregon State University Agricultural Experiment Station Technical Bulletin 152; Oregon State University: Corvallis, OR, USA, 2005.
46. Hanberry, B.B. Transition from fire-dependent open forests: Alternative ecosystem states in the southeastern United States. *Diversity* **2021**, *13*, 411. [CrossRef]
47. Delcourt, P.A.; Delcourt, H.R. Paleoclimates, paleovegetation, and paleofloras during the Late Quaternary. In *Flora of North America*; Oxford University Press: New York, NY, USA, 1993. Available online: http://beta.floranorthamerica.org/Chapter_4 (accessed on 24 January 2021).
48. Hanberry, B.B. Timing of tree density increases, influence of climate change, and a land use proxy for tree density increases in the eastern United States. *Land* **2021**, *10*, 1121. [CrossRef]
49. Noson, A.C.; Schmitz, R.A.; Miller, R.F. Influence of fire and juniper encroachment on birds in high-elevation sagebrush steppe. *West. N. Am. Nat.* **2006**, *66*, 343–353. [CrossRef]
50. Limb, R.F.; Engle, D.M.; Alford, A.L.; Hellgren, E.C. Tallgrass prairie plant community dynamics along a canopy cover gradient of eastern redcedar (*Juniperus virginiana* L.). *Rangel. Ecol. Manag.* **2010**, *63*, 638–644. [CrossRef]
51. Brockway, D.G.; Gatewood, R.G.; Paris, R.B. Restoring grassland savannas from degraded pinyon-juniper woodlands: Effects of mechanical overstory reduction and slash treatment alternatives. *J. Environ. Manag.* **2002**, *64*, 179–197. [CrossRef]
52. Coultrap, D.E.; Fulgham, K.O.; Lancaster, D.L.; Gustafson, J.; Lile, D.F.; George, M.R. Relationships between western juniper (*Juniperus occidentalis*) and understory vegetation. *Invasive Plant Sci. Manag.* **2008**, *1*, 3–11. [CrossRef]
53. Briggs, J.M.; Knapp, A.K.; Blair, J.M.; Heisler, J.L.; Greg, A.; Lett, M.S.; Mccarron, J.K. An ecosystem in transition: Causes and consequences of the conversion of mesic grassland to shrubland. *BioScience* **2005**, *55*, 243–254. [CrossRef]
54. Frost, J.S.; Powell, L.A. Cedar infestation impacts avian communities along the Niobrara River Valley, Nebraska. *Restor. Ecol.* **2011**, *19*, 29–536. [CrossRef]
55. Hanberry, B.B.; Bragg, D.C.; Hutchinson, T.F. A reconceptualization of open oak and pine ecosystems of eastern North America using a forest structure spectrum. *Ecosphere* **2018**, *9*, e02431. [CrossRef]
56. Gray, S.T.; Betancourt, J.L.; Jackson, S.T.; Eddy, R.G. Role of multidecadal climate variability in a range extension of pinyon pine. *Ecology* **2006**, *87*, 1124–1130. [CrossRef]
57. Fye, F.K.; Stahle, D.W.; Cook, E.R. Paleoclimatic analogs to twentieth-century moisture regimes across the United States. *Bull. Am. Meteorol. Soc.* **2003**, *84*, 901–910. [CrossRef]