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Eastern Redcedar Reduces Regeneration and Diversity in the Forests of the Niobrara River Valley

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Disclaimer: The following thesis was produced in the Environmental Studies Program as a student senior capstone project.

Eastern Redcedar Reduces Regeneration and Diversity in the Forests of the Niobrara River Valley

An Undergraduate Thesis

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Thesis Reader: Dr. Christian Elowsky

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Abstract:

Boundary forests are found growing interdigitated with grasslands across the Great Plains. The Niobrara River valley boundary forest has a unique composition of species not seen anywhere else in North America. Encroachment of eastern redcedar (*Juniperus virginiana* L.) into grasslands and forests is significantly increasing eastern redcedar's presence in the Niobrara River Valley as well as in the rest of the Great Plains region. This tree species is capable of significantly decreasing recruitment and diversity in grasslands, which can change the composition of the entire ecosystem. However, the effect of eastern redcedar on recruitment and diversity of naturally forested ecosystems is not as well understood. We conducted a forest inventory and seedling census in the Niobrara River valley to investigate how eastern redcedar is impacting the density and diversity of both the understory and overstory woody community in this unique forest. Using quantile regression, we found that eastern redcedar basal area had a significant negative effect on woody understory and overstory density, diversity, and richness in all cases. These results indicate that the Niobrara valley boundary forest is heading toward a future with decreased diversity and density of woody species, and corresponding reductions in the provisioning of ecosystem services, if eastern redcedar increases its presence in this ecosystem.

Acknowledgements:

The Niobrara Valley Preserve currently occupies the traditional lands of the Pawnee, Lakota, and Comanche peoples. This ecosystem's rapid change over the past 300 years is largely due to the suppression of Indigenous culture and the expansion of European culture.

Thank you to Dr. Sabrina Russo for her continuous guidance, mentorship, and knowledge provided throughout this process and to Dr. Christian Elowsky for being my reader and for helping me understand the research process. Additionally, I am grateful to Bailey McNichol for assisting with data management and field training, and to Lillie Hoffart and Emma Decker for assistance in the field. Dr. Russo and Bailey helped me write the proposal and apply for funding and assisted with the data analysis and coding in R. I also want to thank Dr. David Gosselin for providing me with an opportunity to write a thesis. I would like to thank the staff of the Nature Conservancy's Niobrara Valley Preserve for their support throughout the field season. This project was made possible by The Nebraska Nature Conservancy who provided us with housing and Smithsonian Forest Global Earth Observatory (ForestGEO). Funding was provided by the Cabela's Apprenticeship Program and the Undergraduate Creative Activities and Research Experience (UCARE) Program through the University of Nebraska-Lincoln.

Introduction:

Humans have been significantly altering terrestrial communities for over 6,000 years. The fossil record shows that global biodiversity began to decline early in the evolution of *Homo sapiens* (Lyons et al., 2016). This trend of declining biodiversity has continued into present day, with modern extinction rates of many taxonomic groups being among the highest ever recorded (Ellis et al. 2020). One hypothesis proposed to explain the decline in biodiversity associated with increasing human population sizes is that humans dominate global resource use (Foley et al., 2005).

Resource use by humans and human-associated plants and animals not only limits resource availability for wild species, but also causes other anthropogenic stressors (Foley et al., 2005). One such anthropogenic stressor is climate change (Weiskopf et al., 2020). Anthropogenic greenhouse gas emissions have caused global temperatures to increase by approximately 1° C since the industrial age (IPCC, 2021). Climate change has significantly impacted global biodiversity, and scientists expect it to further decrease biodiversity in the future. Climate change affects the way that species interact within an ecosystem. For example, changing climate patterns impact growth, survival, and reproduction of individuals in a population, which then alters ecosystem structure and diversity. On a global scale, changing precipitation patterns, extreme weather events, and sea-level rise further threaten natural populations of animals and plants that may already be diminished by changing land-use patterns (Weiskopf et al., 2020).

Colonization and global trade have caused both destruction of natural lands, as well as the spread of invasive species (Weiskopf et al., 2020). Many non-native species are introduced to areas outside of their native range, for use in agricultural or horticultural contexts. Additionally, humans introduce species through seeds, pests, and animals that are unintentionally brought from other regions of the world (Tedeschi et al., 2021). Eventually, propagules like plant seeds spread and establish natural populations, potentially becoming invasive. One of the things that makes some invasive species so successful in non-native climates is their lack of natural enemies, *i.e.*, predators and pathogens (Wolf, 2002). Consequently, invasive species often outcompete native species because they are not limited by natural enemies. This may lead to the competitive exclusion and potential extinction of the native species from specific landscapes (Mooney & Cleland, 2001).

There is also an increasing prevalence of generalist, opportunistic native species that are “acting like” invasive species (Garrott et al., 1993). These are species that are native to a landscape, but due to changing species composition, climate, land use, management, and overplanting, they have become over-dominant in their native habitats, similar to an invasive species. These native species are often opportunistic and stress-resilient and appear to be benefiting from the particular combination of human-modified changes that have been made to landscapes and the environment. What makes these species invasive in their native habitat is that their numbers grow so substantially that they dramatically alter habitat composition and structure and may even be responsible for converting a region from one ecosystem type to another. Thus, these species change the dynamics and characteristics of entire ecosystems, which can have detrimental effects on the biodiversity and ecosystem services provided by the landscape (Valéry et al., 2013). One example of this is woody encroachment, which is the process of woody species recruiting into grasslands and savannas and suppressing the growth of grasses and herbaceous plants. A form of woody encroachment also occurs when a particular woody species increases its canopy cover in an ecosystem that already has some woody canopy cover and becomes over-dominant. By limiting understory light and affecting other aspects of the understory environment, such as soil moisture and pH, these species may limit the establishment of woody seedlings or have particularly detrimental effects on certain other species, which ultimately could change the structure and composition of the ecosystem. A meta-analysis of grassland and savanna communities in North America found that species richness declines by an average of 45% in response to woody encroachment (Ratajcak et al., 2012). While much work has been done on woody encroachment in grasslands and savannas, how overdominance by native invasive woody species affects forested ecosystems is not as well understood.

There are a few hypotheses for why woody species are becoming more dominant in many grasslands and semi-arid ecosystems around the globe. Decreasing biodiversity of prairie and savanna ecosystems is due in part to disruptions to disturbance regimes. Specifically, fire suppression alters the dynamics of grasslands and savannas; without this disturbance that kills off many woody seedlings, woody species continue to grow and recruit more successfully in grasslands and savannas (Mariano et al., 2018). Additionally, woody encroachment into prairies can be partially attributed to the economic benefits of planting certain species for agroforestry or horticultural purposes, such as in windbreaks. When one species is planted in high numbers across a region, the number of seeds dispersed into the surrounding natural ecosystems increases, thereby subsidizing seedling recruitment (Donovan et al., 2018). Combined with fire suppression, these alterations to recruitment processes increase the birth rate and decrease the mortality rate of woody species (Figure 1), helping to encourage woody encroachment into herbaceous vegetation. In the North American Great Plains, where forests are interdigitated with the dominant grassland biome, these processes also cause overdominance of invasive species in forested ecosystems (Donovan et al., 2018).

Juniperus virginiana, or eastern redcedar, is a canopy tree species that is native to Nebraska. The species grows well in areas that do not have canopy closure such as prairies and savannas (Lamb et al., 2010), but can also recruit and persist in moderately shaded environments. When young, eastern redcedar seedlings are intolerant of fire, and presettlement prairie fires would dramatically increase the mortality of smaller trees, effectively suppressing eastern redcedar populations in areas that were routinely burned (DeSantis et al., 2010). Fire suppression over the last two hundred years has reduced or eliminated this source of mortality, which may be operating to increase eastern redcedar population growth rates across the landscape by reducing individual mortality rates of young trees (Torquato et al., 2020; Figure 1). Additionally, eastern redcedar is often utilized by farmers in shelterbelts, as its dense foliage and persistent branches are ideal for windbreaks. The species is drought resistant and thus provides a cost-

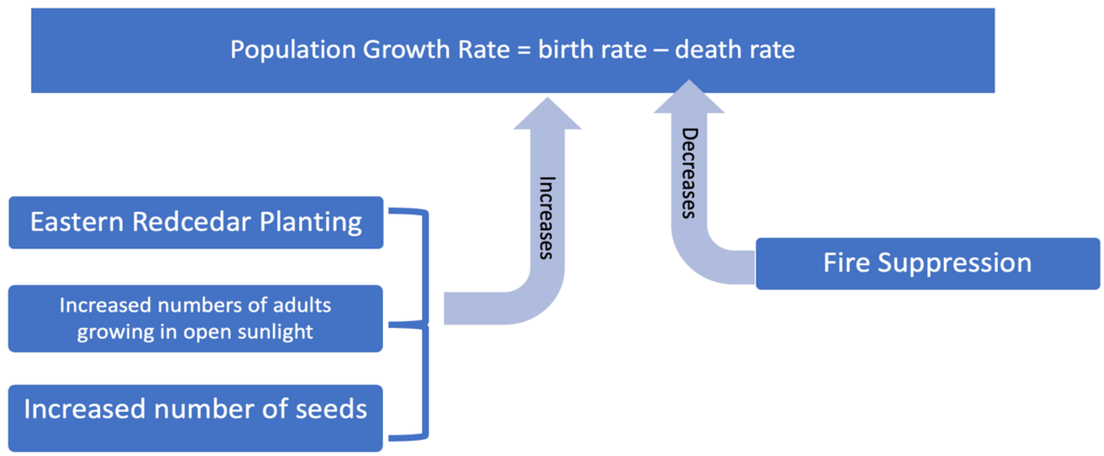

Figure 1: Eastern redcedar encroachment increases the number of seeds coming from outside the system as well as the number of seeds produced in the system. Fire suppression leads to decreased deaths of eastern redcedar within a system. Thus, increased eastern redcedar seeds and decreased deaths leads to an increase in eastern redcedar population growth rate.

effective tool for farmers for use in shelterbelts. However, widespread planting of eastern redcedar for such agroforestry uses across the North American Great Plains has dramatically increased the number of sources of seed, causing massively higher rates of seedling recruitment, which can increase population growth rates (Figure 1). Moreover, the stress tolerant life history strategy of eastern redcedar has contributed to its growing overpopulation problem by reducing the mortality rate in Great Plains landscapes. Forests with abundant eastern redcedar increased by 287,000 acres across eight states in the Great Plains between 2005 and 2012, diminishing the dominance of other species, such as Ponderosa pine and white oak (Meneguzzo & Liknes, 2015). In Oklahoma, Wang et al. (2016) found that eastern redcedar increased its canopy cover by around 8% every year between 1984 and 2010.

When eastern redcedar invades and subsequently dominates both forest and prairie ecosystems, it has dramatic, transformative effects. Eastern redcedar forms dense monocultures that decrease recruitment of other native woody species such as oaks and pines (DeSantis et al., 2010, 2011). The dominance of eastern redcedar has been found to dramatically alter the services provided by an ecosystem. One study found that encroachment of the species resulted in decreased carbon and nitrogen litter on the forest floor. It also found that there was an increased arbuscular mycorrhizae content in soils of eastern redcedar-dominated systems, which could promote further encroachment (Williams et al., 2013). Eastern redcedar trees are associated with high rates of transpiration and decreased soil water content (Torquato et al., 2020). In Oklahoma, canopies of eastern redcedar were found to decrease throughfall of precipitation, reducing rainfall reaching the ground by 33 – 39%. This reduces the water available for runoff and groundwater recharge (Starks et al., 2014). Since seedlings and many herbaceous forest understory plants have shallow root systems, they may be more susceptible to reductions in soil moisture or changes in soil chemistry caused by eastern redcedar. These alterations to the environment have consequences for the forest community. A study of trees with at least 1 cm in trunk diameter in midwestern forests found that plots with eastern redcedar present had reduced richness of woody species (Meneguzzo & Liknes, 2015). This trend creates serious problems, as forests made up of fewer species have been shown to provide fewer ecosystem services (Gamfeldt et al., 2013). Limb et al. (2010) found that herbaceous biomass and diversity declined over a canopy gradient of increasing eastern redcedar tree cover. They suggested further study of canopy diversity and structure across a gradient to better understand the effects of eastern redcedar management, particularly on seedlings and other forest understory plants, on which much less work has been done.

Because of the adverse effects of eastern redcedar on natural landscapes, natural resource managers and ranchers have spent considerable effort removing them through a combination of manual clearing, herbicides, and prescribed fire. There are many drawbacks to these management techniques. For example, while seedlings and saplings of eastern redcedar are vulnerable to fire, large established adults are relatively tolerant of prescribed fires. Thus, fire alone will do little to effectively clear a stand of adult eastern redcedar trees. Currently, a combination of cutting and burning eastern redcedar stands is considered the most effective strategy to thin an eastern redcedar canopy (Ortmann et al., 1998). However, in some areas cleared of eastern redcedar, this species has been found to re-establish, which is likely related to the abundant sources of its seed on the landscape, promoting widespread recruitment of new individuals.

The Niobrara River valley forests are biogeographically unique in North America because eastern deciduous, northern boreal, and coniferous rocky mountain species coexist in the moist, spring-fed canyons where most forest cover is located (Kaul et al., 1988). Since many of the woody species in the Niobrara forests exist at the extremes of their geographic ranges, they may be particularly vulnerable to stress and disturbance. Additionally, these boundary forests, which are interdigitated with prairie, rangeland, and croplands, may be at increased risk of eastern redcedar encroachment due to their proximity to human activities. In particular, eastern redcedar has increased encroachment along streams adjoining uplands and on arid and rocky slopes (Limb et al., 2010). The decreased soil moisture associated with eastern redcedar could create drought-like conditions for seedlings and herbaceous plants.

The overarching goal of this project is to understand the effects of eastern redcedar management on Nebraska’s forests, and the first step towards this goal is to quantify how forest structure and diversity depend on variation in eastern redcedar tree cover. To address this goal, we used a gradient in eastern redcedar tree cover present within a permanent forest monitoring plot (hereafter, Niobrara plot) at the Nature Conservancy’s Niobrara Valley Preserve. The Niobrara plot was managed for eastern redcedar in 2017 and 2020 through a combination of manual clearing and prescribed burns. Many eastern redcedars on the site were cleared at this time, except for individuals found on steep slopes. This management, and natural variation in tree cover, have produced a gradient in eastern redcedar tree cover in the Niobrara plot. In the Niobrara plot, every woody stem at least 1 cm in trunk diameter at breast height (DBH) was individually tagged, mapped, identified to species, and measured for DBH in 2019. As a result, we can quantify the spatial gradient in eastern redcedar and relate it to the structure and diversity of the forest community in the canopy and the understory. We quantified the density and diversity of woody species in the understory in both 2021 and 2022 in 1-m^2 subplots throughout the Niobrara plot. We addressed the following specific research questions: (1) How do the density and diversity of the understory woody community vary with variation in tree cover of eastern redcedar? (2) How do the density and diversity of sapling and adult stems vary with differences in tree cover of eastern redcedar? Owing to the effects of eastern redcedar on throughfall, we expected soil moisture to be lower in areas with higher tree cover compared to areas with lower eastern redcedar tree cover. In addition, eastern redcedar's dense crowns dramatically reduce infiltration of light into the understory. Thus, we predicted that areas with a higher density of eastern redcedar would have lower seedling establishment and performance, resulting in lower density and diversity of the understory woody community. If eastern redcedar limits recruitment, then we predict that there will also be lower density and diversity of saplings and adults in areas with greater eastern redcedar cover.

Methods:

Study site and census data. This research was conducted in the Niobrara plot, which was established in 2019 as part of the ForestGEO network (https://forestgeo.si.edu/sites/north-america/niobrara) and is located in the Nature Conservancy's Niobrara Valley Preserve. The 360 x 560 m (20.2 hectare) Niobrara plot is separated into 504 20 x 20 m quadrats. In 2019, all woody stems with a trunk diameter at breast height (DBH) of at least 1 cm were tagged, measured for DBH, identified to species, and mapped using georeferenced surveyed posts. In 2021, seedlings (young and mature stems with a DBH smaller than 1 cm) were censused in 504 1 m^2 subplots (one in each quadrat). A total of 2,988 seedlings from 36 woody species were identified, measured for height and diameter, and tagged, providing detailed spatial information about seedling recruitment. In the summer of 2022, we re-censused all seedling subplots. Each individual seedling present in 2021 was assessed for survival. New seedlings were tagged, and these seedlings in addition to surviving seedlings from the 2021 census were measured for height.

Seedling density and diversity. We calculated seedling density as the number of total seedlings in a subplot. Subsequently, seedling diversity was estimated as the species richness (total number of species in a subplot) and as the Shannon Diversity Index (*H*) using the following formula:

$$H = -\sum_{i=1}^{s} p_i * \ln(p_i)$$

where s is the total number of species in the subplot, *i* indexes species, and p_i represents the proportion of seedlings in the subplot that are species *i* (Magurran, 2021). Adult stem density and diversity was calculated in the same way.

Eastern redcedar tree cover. To quantify variation in eastern redcedar tree cover, we used the Niobrara plot tree inventory data to calculate the stem density and total basal area of eastern redcedar in each quadrat. Since the quadrats are all the same size, stem density is equivalent to the total number of eastern redcedar stems in the quadrat. Stem density was expressed on a per hectare basis. The basal area of eastern redcedar in each quadrat (*BA*) was calculated as,

$$BA = \sum_{i=1}^{n} \pi(DBH/2)^2$$

where *i* indexed stems, and *n* was the total number of eastern redcedar stems in the quadrat (Magurran, 2021). This gave us a value for eastern redcedar tree cover (stem density and basal area) in each quadrat, defining a gradient from quadrats with zero eastern redcedar tree cover to quadrats where tree cover was solely made up of eastern redcedar.

Statistical analysis. To test our hypotheses, we quantified the relationships between the seedling and adult/sapling density, richness, and diversity with eastern redcedar stem density and BA in each quadrat. Preliminary plots of the metrics of forest structure and diversity versus eastern redcedar density and BA indicated triangular relationships in the data. For example, when the total percent of eastern redcedar basal area was low, seedling density ranged from low to high, but when the percent of eastern redcedar basal area was high, seedling density was consistently lower. The resulting triangular shape of the point cloud indicated that there was an upper limit to the seedling density that depended on the total percent of eastern redcedar basal area (Figure 1). We therefore used quantile regression (Cade & Noon, 2003) to analyze these relationships, using the second and third quartiles (or, equivalently, the 50^{th} and 75^{th} quantiles) to estimate the slopes of the central tendency and upper bound of these relationships, respectively. If our prediction that eastern redcedar reduces seedling diversity and recruitment was supported, then we expected statistically significant negative slopes of the relationship of eastern redcedar stem density and basal area with the density, richness, and diversity of understory and overstory woody stems. We controlled the Type I error rate using Holm's Sequential test (Holm, 1979). Due to the large numbers of zeros in the data, we excluded subplots that had no stems in the understory or overstory size classes. We also excluded quadrats that had no eastern redcedar trees for the overstory analyses, and so these analyses are conditioned on the presence of at least one eastern redcedar sapling or tree >1 cm in DBH in a quadrat.

Results:

Negative effects of eastern redcedar on density and diversity in the woody understory community

The density of understory woody stems (i.e., woody stems < 1 cm in DBH) declined with increasing eastern redcedar cover in 2021 and 2022 (Figure 1; Table 1). However, the triangular shape of the point cloud indicated that there was an upper limit to the understory stem density that depended on the total percent of eastern redcedar basal area. Specifically, using quantile regression, we found that the second and third quartile slopes were both significantly negative, indicating the understory stem density declined significantly as the total percent of eastern redcedar basal area increased in both 2021 and 2022 (Figure 1; Table 1). However, for 2022, the decline at higher density values was steeper than at moderate densities, in that the 3rd quartile slope was significantly more negative than for the 2nd quartile slope (Table 1). The results were similar when analyzed with respect to total eastern redcedar basal area, rather than proportion of total basal area (results not shown).

Understory woody diversity declined as the proportion of eastern redcedar basal area increased (Figure 2; Table 1). This relationship was consistent and statistically significant in both 2021 and 2022 for species richness and Shannon's diversity index (Figure 2; Table 1). Species richness in both years had strongly triangular shapes of the point clouds, indicating that there was an upper limit to understory species richness that depended on the total percent of eastern redcedar basal area (Figure 2B, 2C). The decline in species richness was significantly steeper for higher (3rd quartile) than moderate richness values (2nd quartile) (Table 1). The results were similar when analyzed with respect to total eastern redcedar basal area (results not shown).

Negative effects of eastern redcedar on density and diversity of adults and saplings

The density of adult and sapling woody stems decreased as the proportion of eastern redcedar basal area increased (Figure 3; Table 2). A similar negative relationship was exhibited when stem density was plotted against total eastern redcedar basal area (results not shown). The diversity of adult and sapling woody stems significantly decreased as the proportion of eastern redcedar basal area increased (Table 2; Figure 4). Both species richness and density of adults and saplings produced a triangular point cloud when plotted against proportion eastern redcedar basal area, indicating an upper limit to species richness that depended on eastern redcedar basal area (Figure 3, 4B). However, Shannon diversity did not produce a triangular point cloud when plotted against the proportion eastern redcedar basal area, with the 2nd quartile exhibiting a steeper slope than the 3rd quartile (Table 2). A similar negative relationship was exhibited when density, Shannon's diversity index, and species richness were plotted against total eastern redcedar basal area (results not shown).

Table 1. Summary statistics for quantile regression analyses of understory density and diversity (species richness and Shannon diversity index) with respect to percent basal area in eastern redcedar in the Niobrara plot in Nebraska, USA. The slope estimate and the lower and upper 95% confidence bounds in parentheses for the second and third quartiles using the 2021 and 2022 seedling census data are shown.

	2nd Quartile	**3rd Quartile**
Density		
2021	-7.71 (-9.45, -3.02)	-7.85 (-14.01, -3.97)
2022	-5.04 (-8.33, -1.79)	-13.99 (-16.87, -9.77)
Species richness		
2021	-2.26 (-2.92, -2.02)	-4.13 (-4.20, -2.89)
2022	-2.36 (-2.81, -2.03)	-4.08 (-4.37, -2.81)
Shannon diversity index		
2021	-1.15 (-1.34, -0.97)	-1.14 (-1.49, -0.66)
2022	-1.16 (-1.34, -0.96)	-1.37 (-1.51, -0.78)

Table 2. Summary statistics for quantile regression analyses of adult and sapling density and diversity (species richness and Shannon diversity index) with respect to percent basal area in eastern redcedar in the Niobrara plot in Nebraska, USA. The slope estimate and the lower and upper 95% confidence bounds in parentheses for the second and third quartiles using the 2019 forest census are shown.

	2nd Quartile	**3rd Quartile**
Density	-23.24 (-27.58, -21.10)	-31.58 (-33.61, -20.99)
Species richness	-4.87 (-5.69, -4.3)	-6.23 (-7.05, -4.84)
Shannon diversity index	-1.29 (-1.52, -0.96)	-1.09 (-1.33, -0.77)

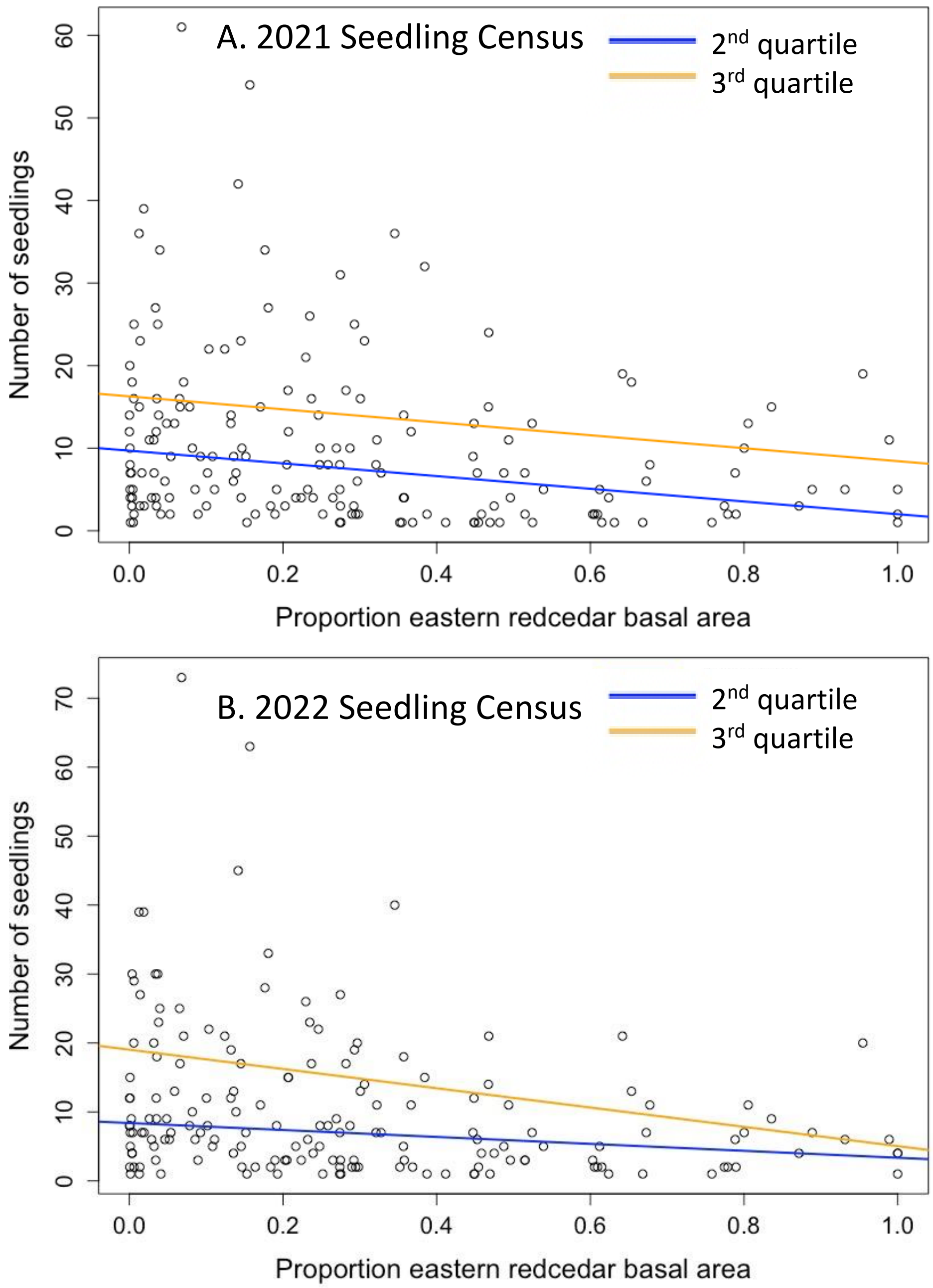

Figure 1. Variation in seedling density with respect to the proportion of basal area that is eastern redcedar in the Niobrara plot in Nebraska, USA. The density of understory stems (i.e., woody stems < 1 cm in DBH) declined with increasing eastern redcedar basal area in both 2021 and 2022. Relationships are shown based on the 2021 (A) and 2022 (B) seedling censuses. Seedling density is the number of seedlings per 1-m^2 subplot. Proportion eastern redcedar basal area is the proportion of the total tree basal area in the quadrat that is eastern redcedar.

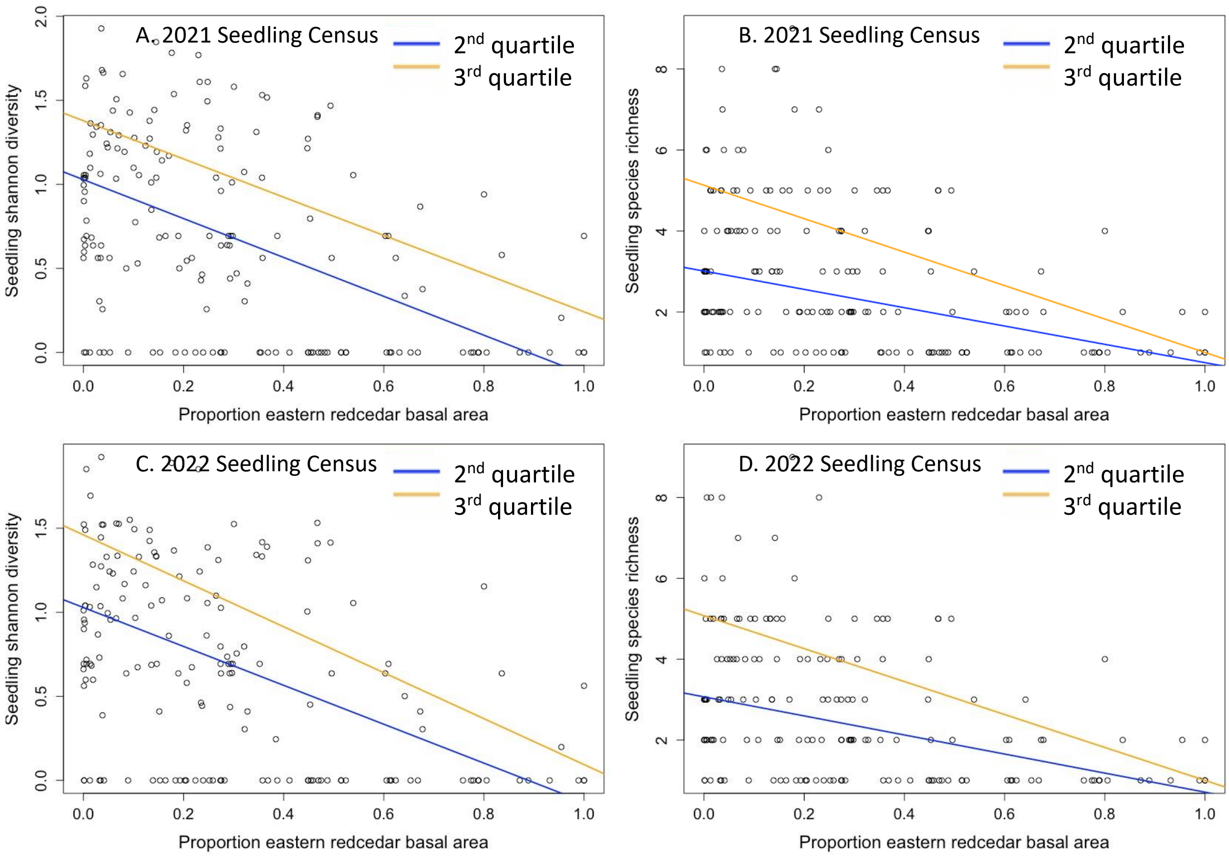

Figure 2. Variation in seedling diversity with respect to the proportion of basal area that is eastern redcedar in the Niobrara plot in Nebraska, USA. The diversity and density of understory stems (i.e., woody stems < 1 cm in DBH) declined with increasing eastern redcedar basal area in both 2021 and 2022. Relationships are shown based on the 2021 (A and B) and 2022 (C and D) seedling censuses. Seedling diversity is the Shannon diversity of each 1-m^2 subplot and the species richness of each 1-m^2 subplot. Proportion eastern redcedar basal area is the proportion of the total tree basal area in the quadrat that is eastern redcedar.

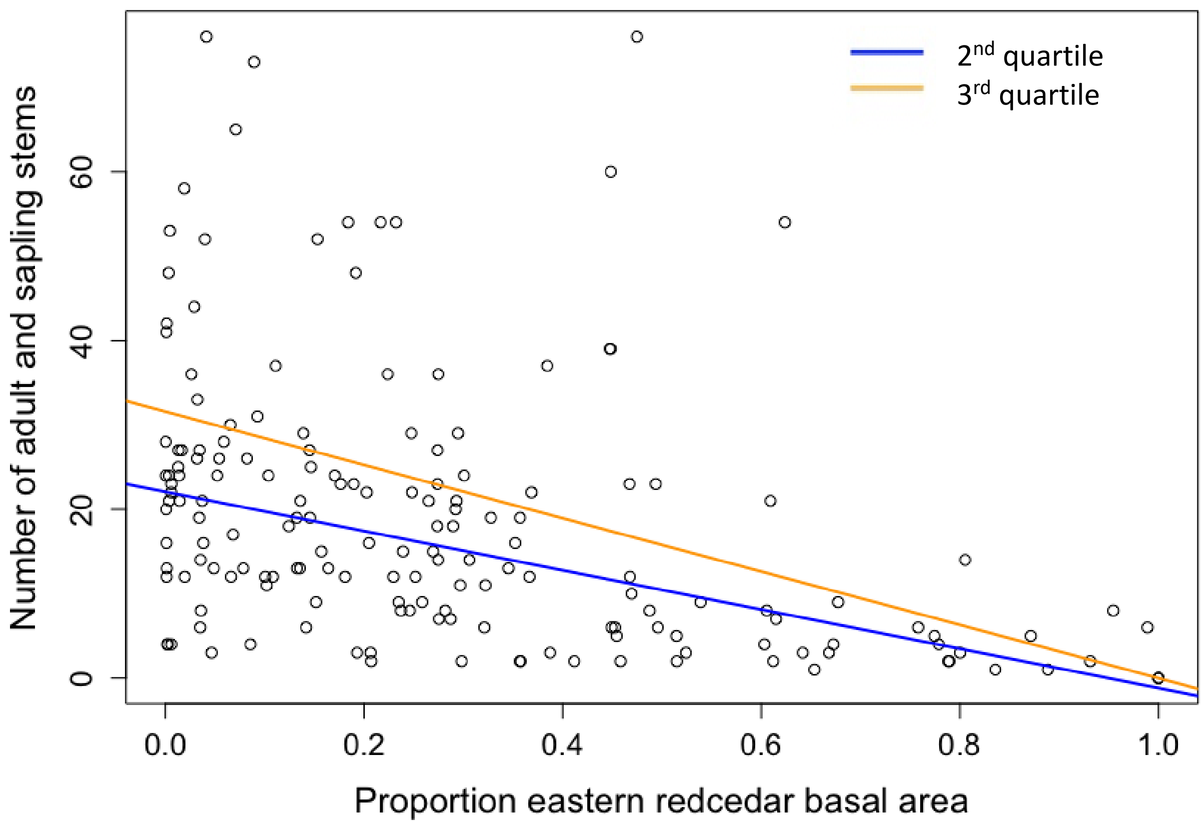

Figure 3. Variation in adult/sapling density with respect to the proportion of basal area that is eastern redcedar in the Niobrara plot in Nebraska, USA. The density of overstory stems (i.e., woody stems > 1 cm in DBH) declined with increasing eastern redcedar basal area. Relationships are shown based on the 2019 forest census. Adult and sapling density is the number of adult and sapling stems that are not eastern redcedar in each 20x20m quadrat. Proportion eastern redcedar basal area is the proportion of the total tree basal area in the quadrat that is eastern redcedar.

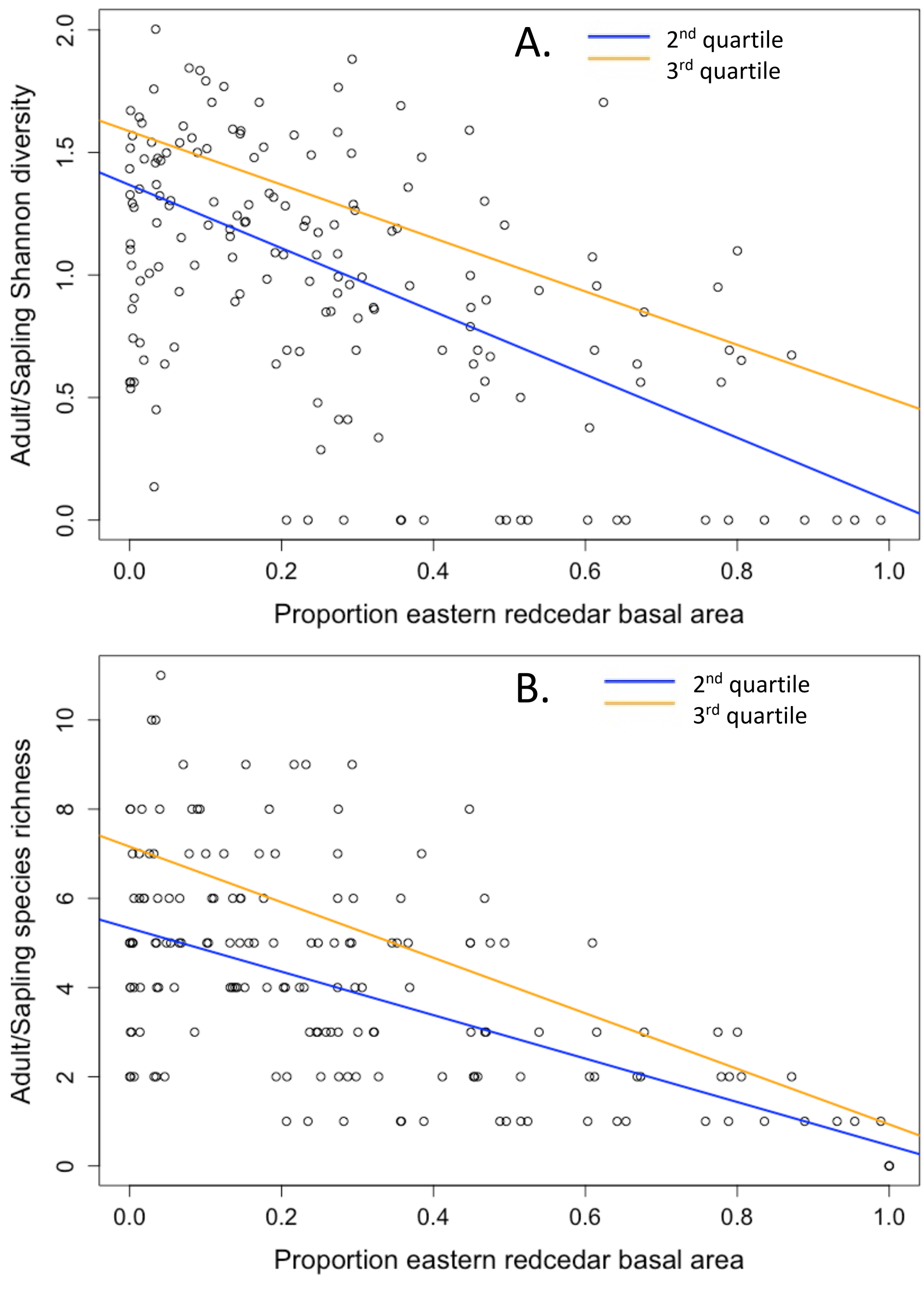

Figure 4. Variation in adult/sapling diversity with respect to the proportion basal area that is eastern redcedar in the Niobrara plot in Nebraska, USA. The diversity and richness of overstory stems (i.e., woody stems > 1 cm in DBH) declined with increasing eastern redcedar basal area. Relationships are shown based on the 2019 forest census. Adult and sapling diversity is the Shannon diversity of each 20x20m quadrat (A) and the species richness of 20x20m quadrat (B). Proportion eastern redcedar basal area is the proportion of the total tree basal area in the quadrat that is eastern redcedar.

Discussion:

Eastern redcedar is an example of a native species that, due to several interacting anthropogenic factors, is experiencing rapid population growth and expansion across the North American Great Plains. There is much focus on its effects on grasslands. However, eastern redcedar populations are also increasing dramatically in the forests of the Great Plains, but its effects on tree recruitment and forest structure and diversity are much less well understood. We found these effects to be dramatic and consistent across size classes in a boundary forest in Nebraska. Eastern redcedar contributed to decreased understory and overstory stem density. Additionally, diversity and species richness of both the overstory and understory woody community was significantly decreased by the presence of eastern redcedar. Our findings show that eastern redcedar is pushing this forested ecosystem towards a future with reduced density of non-eastern redcedar stems and reduced diversity and richness. Moreover, if eastern redcedar population growth is not effectively checked, our results paint a grim picture of a future landscape with forests dominated by large eastern redcedar individuals and a reduced number of woody species. The Niobrara forests have a unique coexistence of species that is not seen anywhere else in North America. Due to its suppressive effects, eastern redcedar threatens to displace native woody species that are adapted to the Niobrara's environment. This is especially problematic because many of these species are at the edges of their respective ranges, and displacement from the Niobrara River valley could shrink a species' range and dramatically alter the structure and reduce the diversity of these biogeographically significant forests.

Effects of eastern redcedar on forest diversity and ecosystem services

Other studies have focused solely on how eastern redcedar affects adult trees (Donovan et al., 2018). Additionally, most eastern redcedar research has focused on woody encroachment into grasslands, with its effect on existing forested ecosystems being less studied (Limb et al., 2010; Stipe & Bragg, 1989). This study is unique in that it focuses specifically on eastern redcedar's effect on woody seedlings in addition to woody adults/saplings. Additionally, unlike other studies (Meneguzzo & Liknes, 2015; Stipe & Bragg, 1989), this study evaluated eastern redcedar's effect across a gradient of canopy cover, rather than in two distinct classes. Eastern redcedar negatively affects both grasslands and forests, and an understanding of how it affects these two types of ecosystems differently is crucial to more effective management. Moreover, this study's results contribute to a better overall understanding on how eastern redcedar affects individual stems as they grow from seedling to adulthood, as the results indicate that woody species are negatively impacted by high eastern redcedar tree cover at all life stages.

Meneguzzo and Liknes (2015) conducted a similar study to ours, evaluating eastern redcedar encroachment in forests and its effects on diversity. However, they did not directly analyze seedling and adult density and diversity in comparison to eastern redcedar tree cover, but rather quantified how the eastern redcedar forest type was increasing across a region of eight US states. Their study reached a similar conclusion, finding significantly decreased species richness in size classes ranging from seedling to adult when eastern redcedar basal area was high. These results add credibility to the data we collected in the Niobrara River valley and provide context to how our data can be interpretated in other at-risk ecosystems. Since eastern redcedar is shown to decrease diversity throughout the region, we can infer that boundary forests and other ecosystems in the Great Plains are at risk of losing diversity.

A 1989 study conducted by Stipe and Bragg was similar to this study in that it evaluated how seedling establishment is affected by eastern redcedar tree cover. However, while our study focused solely on woody species, Stipe and Bragg focused their research on grass and forb species found in prairies. The results found by Stipe and Bragg were less significant than ours, with *Coreopsis palmata* being the only one of the five species tested having a statistically significant reduction in seedling establishment. However, four of the five species had decreased seedling establishment in areas with high eastern redcedar tree cover. One reason that this study found less significant effects could be because both the eastern redcedar and prairie plots in this study were manually watered. Since eastern redcedar is associated with decreased soil water content (Torquato et al., 2020), watering the seeds may have produced results that inflated the seedling establishment rate of species other than eastern redcedar. Meanwhile our study measured seedling recruitment across a gradient of eastern redcedar tree cover, rather than in two cover classes, and measured seedlings that established naturally.

Reduced species diversity in the Niobrara caused by eastern redcedar may cause declines in the forest's ability to sequester carbon dioxide largely due to reduction in tree growth and increased tree mortality. Gamfeldt et al. (2013) found that lower species richness is linked to reduced forest productivity and soil carbon storage. Additionally, forests with high levels of eastern redcedar encroachment have reduced litter quality, since eastern redcedar leaf litter has a high concentration of secondary compounds; thus, soil fertility of eastern redcedar encroached forests is likely reduced due to decreased decomposition of nutrients back into the soil (Williams et al. 2013). This means that forest productivity may be reduced, leading to less carbon being captured in the Niobrara forests than what could be captured if eastern redcedar tree cover was reduced. With landscapes across the Great Plains becoming increasingly dominated by eastern redcedar (DeSantis et al., 2011) and potentially capturing less carbon dioxide as a result, eastern redcedar invasion may be causing decreased forest carbon sequestration at a regional scale. Additionally, eastern redcedar recruits well even under drought conditions (DeSantis et al., 2011). With drought frequency and severity increasing as a result of climate change (IPCC, 2021), eastern redcedars are likely to see increased recruitment potential (DeSantis et al., 2011). Given that forest carbon capture is one of the leading climate change mitigation methods (IPCC, 2021), eastern redcedar management should be prioritized when making decisions regarding how to best manage natural landscapes for climate change mitigation.

The significant relationship of decreasing diversity with increasing eastern redcedar cover is problematic for the uncertain future of boundary forests. If eastern redcedar tree cover continues to increase, the one-of-a-kind species composition found in the Niobrara River valley may be at heightened risk. For example, *Betula papyrifera*, or paper birch, is already rapidly declining in numbers throughout the valley (Stroh & Miller, 2009). Therefore, increased eastern redcedar cover may accelerate the transition of paper birch out of the Niobrara River valley forests. Frost & Powell (2011) found decreased species richness of bird species in areas with increased eastern redcedar on the Niobrara Valley Preserve. Thus, if eastern redcedar tree cover increases in the Niobrara River valley, many components of the living ecosystem could show declining trends in biodiversity. Declining woody species richness in particular would negatively impact the wildlife that rely on those species for food resources, further decreasing the species richness of each component of the ecosystem.

The increased negative slope found in the quantile regressions for overstory density versus understory in our study may be explained by increased seedling mortality leading to decreased number of stems growing to become part of the overstory. This indicates that eastern redcedar may have a negative effect on the survival of stems. Since we conducted seedling censuses in both 2021 and 2022, our data can be further analyzed to evaluate eastern redcedar's effect on the survival and growth of understory stems. Analysis using growth and mortality data can help us to better understand how *Betula papyrifera* and other key Niobrara species are being affected by eastern redcedar. Stipe and Bragg (1989) evaluated how eastern redcedar affects different prairie species. Similarly, we could do this with the data from our study by evaluating the mortality and density of different species as compared to eastern redcedar basal area proportion.

Given that eastern redcedar basal area had an increasingly negative affect on both density and diversity, management of eastern redcedar should be prioritized in areas with the highest levels of encroachment. Additionally, since areas with the highest eastern redcedar encroachment had low density and diversity of both adult and seedling stems, seed stores in the encroached ecosystem are likely significantly deplenished. In boundary forests, depleted seed stores are a serious issue, as they are interdigitated with ecosystems that may offer a different type of seed than what grows in the boundary forest. Thus, reseeding this forested landscape with preferred native species after eastern redcedar removal may be beneficial to ensure the ecosystem recovers to a preferred state. This management technique could be implemented by planting germinated seedlings to ensure that there are established non-eastern redcedar stems in the plot.

Conclusion:

We conducted a seedling census and forest inventory in a permanent forest monitoring plot in the Niobrara River Valley in order to understand how eastern redcedar tree cover affects the diversity of this unique forested ecosystem. We were specifically looking at how increasing eastern redcedar tree cover affects the diversity and density of both understory and overstory woody species. The results showed a significant and consistent negative correlation between increasing proportion of eastern redcedar basal area and stem density and diversity; this was true for both the over and understory size classes. Thus, we concluded that eastern redcedar is negatively impacting recruitment, density, and diversity of woody species in this forest. If eastern redcedar's population grows in the Niobrara River Valley, the boundary forest will likely reduce the number of ecosystem services that it provides.

The results of this research gave us insights into the future of the Niobrara Forest ecosystem as well as other boundary forests in the region, as seedlings provide the blueprint for the next generation of the forest. It also gave insights on the magnitude and effects that eastern redcedar has on forests, which provides a foundation for better management of this native invasive species. Future management of eastern redcedar should focus on removing trees that have a large basal area, since these are the trees that are producing the most seeds and are most negatively impacting stem diversity and density. Since adult eastern redcedars are more fire tolerant than seedlings and saplings, it is recommended that the largest eastern redcedars be killed before prescribed burning takes place. To better understand how woody ecosystems recover from eastern redcedar management, future research evaluating woody species recruitment both before and after management is needed. Additionally, more research focused on how boundary forests are changing across the great plains is needed to fully understand what the ecosystem will look like in the future as well as what the best management might be for these threatened ecosystems.

Through this process I learned about the importance of effective planning and communication. I had the opportunity to work alongside highly educated mentors and peers who taught me how to break up the research into workable sections. One of the most important things I learned was the importance of asking for help when needed, as that is the only way people can know how to assist you. Conducting research on how the Niobrara Valley is impacted by one species of tree, has shown me just how fragile many of our ecosystems have become. Creating a sustainable natural ecosystem requires effective science-based management that supports the ecosystem's natural dynamics. At present, eastern redcedar populations are likely decreasing the present and future diversity of Midwestern forests. To sustainably manage natural forests in the Great Plains we need to create a landscape where all native species are given a chance to thrive.

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